THE AZORES MARINE ECOSYSTEM: AN OPEN WINDOW INTO NORTH ATLANTIC OPEN OCEAN AND DEEP-SEA ENVIRONMENTS

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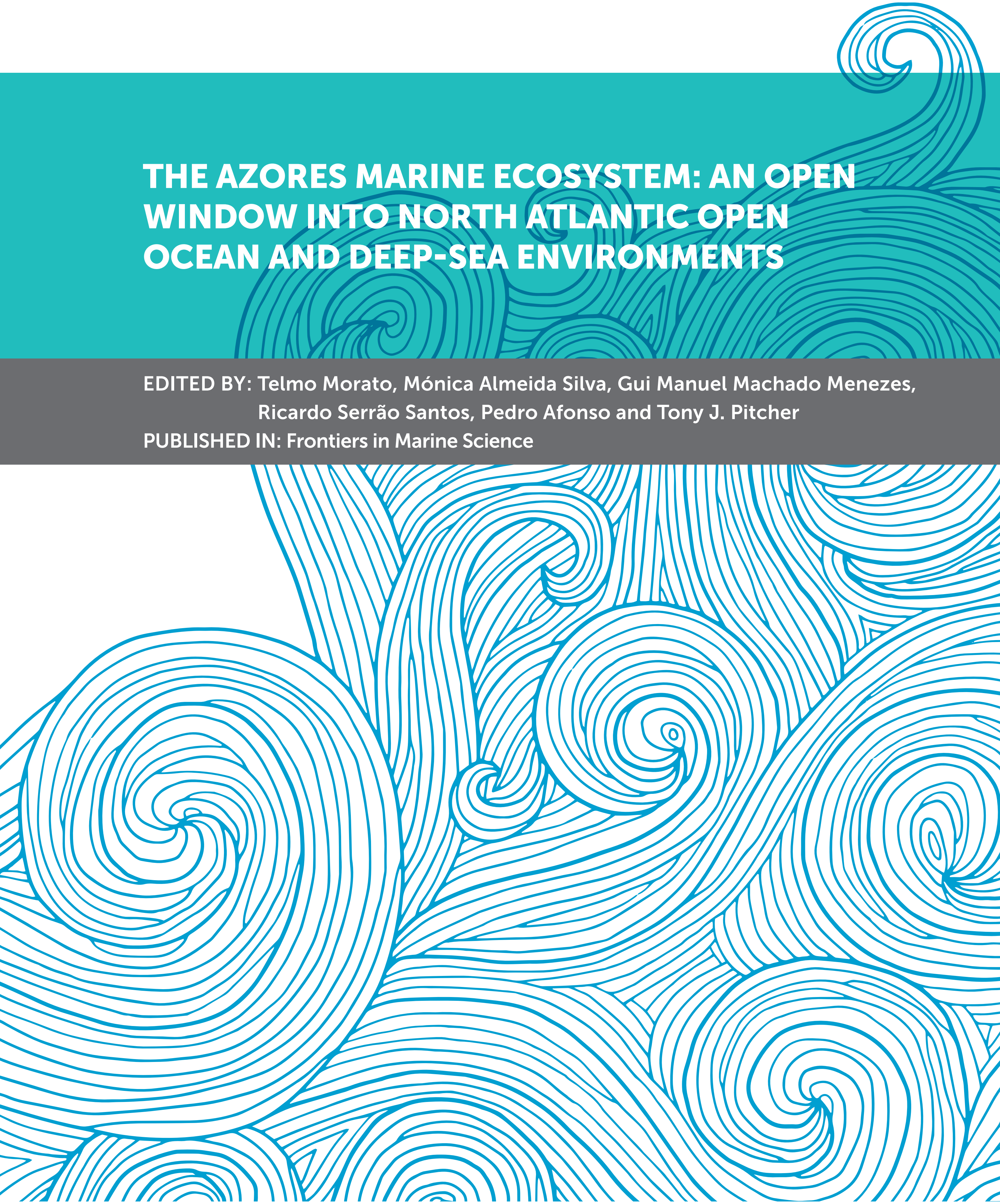
PUBLISHED IN: Frontiers in Marine Science



frontiers Research Topics

ISSN 1664-8714
ISBN 978-2-88966-428-3
DOI 10.3389/978-2-88966-428-3

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THE AZORES MARINE ECOSYSTEM: AN OPEN WINDOW INTO NORTH ATLANTIC OPEN OCEAN AND DEEP-SEA ENVIRONMENTS

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Citation: Morato, T., Silva, M. A., Menezes, G. M. M., Santos, R. S., Afonso, P., Pitcher, T. J., eds. (2021). The Azores Marine Ecosystem: An Open Window Into North Atlantic Open Ocean and Deep-Sea Environments.
Lausanne: Frontiers Media SA. doi: 10.3389/978-2-88966-428-3

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frontiers in Marine Science

EDITORIAL
published: 30 October 2020
doi: 10.3389/fmars.2020.601798

Editorial: The Azores Marine Ecosystem: An Open Window Into North Atlantic Open Ocean and Deep-Sea Environments

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Keywords: azores, deep-sea, open-ocean, scientific research, governance

Editorial on the Research Topic

The Azores Marine Ecosystem: An Open Window Into North Atlantic Open Ocean and Deep-Sea Environments

OPEN ACCESS

Edited and reviewed by:
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Specialty section:
This article was submitted to
Deep-Sea Environments and Ecology,
a section of the journal
Frontiers in Marine Science

Received: 01 September 2020
Accepted: 12 October 2020
Published: 30 October 2020

Citation:
Morato T, Afonso P, Menezes GM,
Santos RS and Silva MA (2020)
Editorial: The Azores Marine
Ecosystem: An Open Window Into
North Atlantic Open Ocean and
Deep-Sea Environments.
Front. Mar. Sci. 7:601798.
doi: 10.3389/fmars.2020.601798

Lying between continental Europe and North America, the Azores is the most isolated archipelago in the North Atlantic Ocean. Its one million square km Exclusive Economic Zone (EEZ) comprises mostly deep seafloor interspersed with shallower portions offered by the Mid-Atlantic Ridge, over 100 seamounts, and the slopes of the nine islands. After the seminal expeditions in the late nineteenth century (Porteiro, 2009), extensive scientific research based in the Azores in the last three decades opened a window on the functioning of oceanic, deep-sea and seamount ecosystems, as well as the impacts from human activities. These discoveries helped to raise awareness on the need for protecting a rather fragile marine environment, and resulted in a pioneering role on the implementation of multiple conservations actions within and beyond the EEZ (Santos et al., 1995, 2009). This Research Topic expands our current knowledge on the marine ecosystem of the Azores, and highlights the need for improved, science-based management and conservation. It brings together 12 research papers (nine research articles, one review, one data report, and one perspective article) within four main themes: (1) geological and environmental settings, (2) biodiversity and food web structure of open ocean and deep-sea environments, (3) anthropogenic impacts, and (4) the future of marine science, management, and conservation in the Azores.

GEOLOGICAL AND ENVIRONMENTAL SETTINGS OF THE AZORES REGION

A good understanding of the geological and environmental settings is the basis for an improved knowledge of the Azores region, but also helps addressing broader scientific questions and inform management. Peran et al. compiled and made publicly available 18 layers of seabed characteristics, providing new evidence of the high geomorphologic diversity and uniqueness of the Azores region in the North Atlantic context. Amorim et al. confirmed a high spatial, seasonal, and inter-annual variability of the marine climatology in the Azores. They further noticed the limited and unevenly distribution of environmental observations of the deep ocean, highlighting the need for expanded *in situ* observatories. Caldeira and Reis analyzed the meteorological and oceanographic conditions in the region to show that the western and eastern islands are dominated by different oceanographic processes and water mass properties, proposing the Azores as an oceanic confluence zone where such spatial environmental patterns produce significant effects on biological productivity.

BIODIVERSITY AND FOOD WEB STRUCTURE OF AZORES OPEN-OCEAN AND DEEP-SEA ENVIRONMENTS

Several studies included in this Research Topic increased the current knowledge on the biodiversity of the Azores region. Carreiro-Silva et al. analyzed the deep-sea zoantharians associated with cold-water corals and identified four new species and several new associations with stylasterids, antipatharians, and octocorals. They also found evidences of parasitic relationships and call for a better understanding of the effects of fishing and climate change on the severity of parasitic associations. Das and Afonso reviewed and updated the biodiversity of known elasmobranchs for the Azores, and provided an annotated checklist accounting for 61 species and 19 additions to previous checklists. They found local species diversity to be lower than in north-Atlantic continental margins at comparable latitudes, but also that the Azores represents a transition zone, and pinpointed the threat of systematic species misreporting and misidentification to the effectiveness of management and conservation policies.

Cascão et al. provided the first comprehensive analyses of the distribution and temporal dynamics of micronekton communities at two shallow seamounts. They found a persistent strong acoustic backscatter over the summits reflecting both the retention of vertically migrating micronekton and a resident seamount-associated micronekton community. Tobeña et al. developed species distribution models for 16 cetaceans and found great heterogeneity in distribution, reflecting the contrasting influence and strong dynamics of local oceanographic conditions. Yet, this study also identifies persistent areas of increased species richness, emphasizing the importance of both static and dynamic management approaches to protect cetaceans and their oceanic habitats.

Carreira et al. combined genetic and morphological analyses of Macaronesian limpets to find different patterns of phylogeographic structure among species, consistent with independent processes of colonization and demographic processes. The authors also suggested that the genetic divergence among the Azores, Madeira, and the Canaries archipelagos must be considered a conservative reflection of contemporary isolation, and recommend that each archipelago should be managed separately since isolation increases the vulnerability of local populations.

Morato et al. synthetized a wide range of scientific information and developed an ecosystem model for the Azores EEZ. The authors suggested that cephalopods, pelagic sharks, and toothed whales play a key ecological role for the ecosystem stability, but also that current knowledge gaps on the biomass and abundance of key functional groups still hamper the use of these models to evaluate management scenarios.

ANTHROPOGENIC IMPACTS

Marine noise pollution is an overlooked anthropogenic pressure that became an issue of special concern over recent decades. Romagosa et al. assessed the natural background and the shipping noise in the low-frequencies of most concern for baleen whales. They found lower levels of shipping noise in three seamounts in the Azores when compared to other regions of the globe, suggesting reduced noise-related impacts on the behavior of baleen whales. They also noted that noise might be higher in shipping routes or areas routinely used by whale watching boats and, therefore, requested additional measures to produce a detailed soundscape for the Azores region.

THE FUTURE OF MARINE SCIENCE, MANAGEMENT, AND CONSERVATION IN THE AZORES

A systematic review by Abecasis et al. critically examined the current network of marine protected areas (MPAs) and progress achieved during the three phases of MPA establishment. They concluded that Azores MPAs are limited in number, reduced in size, and lack management plans, apparently jeopardizing their potential net benefits. Yet, they also noted several opportunities for future improved management and conservation in the Azores. On this regard, Afonso et al. argued that the open-ocean in the Azores region is a hotspot of Essential Marine Habitats for key vulnerable or endangered marine megafauna, playing an important role in the migratory pathways of seabirds, cetaceans, reptiles, sharks, and fishes across the wider Atlantic Ocean. They argued that the Azores region offers exceptional conditions to be a priority area for research and conservation of megafauna in the Atlantic, and proposed an action plan to acquire new knowledge, develop synergies between marine science and technology, and promote/test effective management and conservation measures.

SUMMARY

A key finding from the collection of novel papers integrating this topic is that, despite the significant scientific advances, our current knowledge of the Azorean open-ocean and deep-sea biodiversity and biogeography results from the scientific exploration of only a small fraction of these habitats. Although the region has contributed internationally with a pioneering vision and action on many conservation measures, improved management needs to consider well-defined and clear objectives, be grounded on sound monitored and effectively enforced management plans, and sourced with the adequate resources. Thus, developing adequate long-term strategies and marine spatial planning to advance scientific knowledge and inform policies emerges as a strategic objective in the quest to ensure the sustainable use of natural resources while promoting conservation of its biodiversity in the wider north-Atlantic context. Such strategy should provide the appropriated infrastructures and technological means but also long-term, stable, and predictable scientific careers for current and future scientists.

AUTHOR CONTRIBUTIONS

All authors helped writing this summary and contributed to summarize the published papers.

FUNDING

This Research Topic received funding from Fundo Regional da Ciência, Tecnologia (FRCT), through the 2020 (M2.1.2/I/026/2011) and the PO2020 MapGES (Acores-01-0145-FEDER-000056) research projects. TM was supported by Program Investigador FCT (IF/01194/2013), and the IFCT Exploratory Project (IF/01194/2013/CP1199/CT0002) from the Fundação para a Ciência e Tecnologia (POPH and QREN), and by the European Union's Horizon 2020 research and innovation programme under grant agreements No. 678760 (ATLAS) and No. 689518. (MERCES). MS was supported by Program Investigador FCT (IF/00943/2013), and by the European Union's Horizon 2020 research and innovation programme under grant agreements No. 817806 (SUMMER). We acknowledge funds provided by the Fundação para a Ciência e a Tecnologia (FCT) through the plurennial strategic project (UIDB/05634/2020) granted to Okeanos.

ACKNOWLEDGMENTS

We thank all the contributing authors, reviewers, and the editorial staff at Frontiers in Marine Science for their support in producing this issue.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

REVIEW
published: 08 December 2015
doi: 10.3389/fmars.2015.00104

Marine Conservation in the Azores: Evaluating Marine Protected Area Development in a Remote Island Context

Rita C. Abecasis[1]*, **Pedro Afonso**[2], **Ana Colaço**[2], **Nancy Longnecker**[3], **Julian Clifton**[1], **Luisa Schmidt**[4] **and Ricardo S. Santos**[2]

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In the Archipelago of the Azores, over 110,000 km^2 of marine areas presently benefit from some form of protection, including a suite of coastal habitats, offshore areas, seamounts, hydrothermal vents, and large parcels of mid-ocean ridge. These areas are integrated in the recently established network of marine protected areas (MPAs), which stands as the cornerstone of Azorean marine conservation policies. This article describes and analyses the process of MPA establishment in the Azores and the current network of protected areas. Three phases of MPA development are identified, progressing from individual MPA establishment with little scientific support in the 1980s, the increasing scope of scientific research during the 1990s under European Union initiatives and the gradual implementation of an MPA network in the 2000s. Expert critical evaluation of the contemporary situation demonstrates that this network must be integrated within a wider regional marine management strategy, with MPA success being contingent upon the implementation of management plans, appropriate enforcement and monitoring, and bridging gaps in scientific knowledge.

Keywords: marine protected area establishment, island settings, networks of marine protected areas, marine policy development, marine spatial planning

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Specialty section:
This article was submitted to
Deep-Sea Environments and Ecology,
a section of the journal
Frontiers in Marine Science

Received: *12 July 2015*
Accepted: *13 November 2015*
Published: *08 December 2015*

Citation:
Abecasis RC, Afonso P, Colaço A, Longnecker N, Clifton J, Schmidt L and Santos RS (2015) Marine Conservation in the Azores: Evaluating Marine Protected Area Development in a Remote Island Context.
Front. Mar. Sci. 2:104.
doi: 10.3389/fmars.2015.00104

INTRODUCTION

Marine protected areas (MPAs) have been established worldwide in an effort to halt marine ecosystem degradation. Initial steps for the establishment of MPA were mainly initiated in the 1980s, with a few pioneer nations such as Australia, the USA and the islands of the Azores in Portugal. The 1980s were a time of increasing environmental concern and awareness about marine ecosystems and the severe threats they were facing, coupled with widespread belief that traditional fisheries management methods allowed the overexploitation and collapse of several fish stock (Kenchington and Agardy, 1990; Guenette et al., 1998). Around the world, many coastal nations slowly developed their own efforts to establish MPAs (Tisdell and Broadus, 1989; Jones, 2001), which were typically small individual MPAs designated with little supporting scientific advice, as the rationale behind MPA establishment was yet to be properly tested (Roberts and Polunin, 1993).

The increasing number of designated MPAs, however, came to provide a wider variety of suitable study sites to test the efficacy of MPAs in achieving ecological goals (Ballantine, 1991). Moreover, with politicians and decision-makers demanding hard evidence to support MPA establishment, and more funding allocated for applied conservation research, MPA science received a significant boost in the 1990s (Lubchenco et al., 2003). As MPA science developed, so did the concept of using networks of MPAs to match criteria of representativeness and connectivity (Halpern and Warner, 2003). In the 2000s, upscaling into comprehensive, representative and effectively managed networks of MPAs became the plan of action recommended by the scientific community (Laffoley, 2008) and agreed by coastal nations around the world under international instruments such as the World Summit on Sustainable Development (UN, 2002), the Convention on Biological Diversity (CBD, 2006, 2010) and IUCN's World Parks Congress (IUCN, 2003).

To date, the large volume of MPA research has improved our understanding of different factors that influence MPA design, establishment and management; yet it has also revealed serious shortfalls that undermine the action of current MPAs worldwide as effective marine conservation tools. While MPAs have been described as "simple yet elegant solutions to managing complex (…) fisheries" (Anonymous, 2006), most studies reveal that their establishment and management are anything but simple, and often result in failure to achieve the goals of either biodiversity conservation or fisheries management (Edgar, 2011; Mora and Sale, 2011). Besides the underlying complexity of marine ecosystems, MPAs entail intricate socio-economic and socio-political dimensions that affect governance, public support and compliance with regulations, undermining the proper implementation of these tools. Understanding the interplay between these dimensions and how they affect MPA establishment under different settings is key to ensure future MPA success.

There is widespread recognition of the need to assist the design and implementation of MPAs in island states through improving legal, institutional and political frameworks, data availability and decision-making capacity within organizations (Fanning et al., 2009). The urgency of these actions is grounded in the high significance of marine ecosystem services in supporting island states' economic and cultural wellbeing (Niesten et al., 2012). However, progress in implementing networked MPAs has been slow in island states and most literature focuses on single MPA "success stories" (Weeks et al., 2009), rather than tracing the phases of MPA network development and thereby identifying the drivers of policy-making. Through undertaking such a task in a case study—the Azorean Archipelago—it is hoped that the specific needs and problems faced by island states tasked with the creation of MPA networks can be identified.

In the Azorean archipelago, the most isolated group of islands in the North Atlantic, the current MPA network covers 110,000 km^2 of coastal habitats, offshore seamounts, hydrothermal vents and mid ocean ridges, both within and beyond its extensive Exclusive Economic Zone (EEZ; **Figure 1**). This article traces the establishment of Azorean MPAs, taking into account the socio-economic and socio-political context, particularly in terms of marine resource use, conservation research, and administrative backdrop. The latter is particularly complex because the archipelago is an autonomous region of Portugal, which imposes shared sovereignty and is itself a member of the European Union

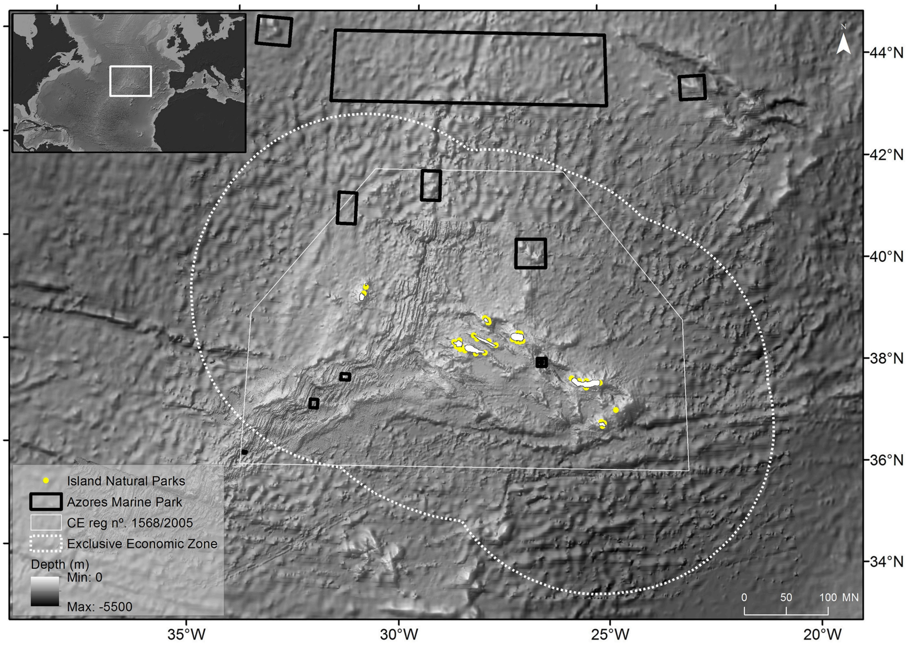

FIGURE 1 | The Archipelago of the Azores, located in the mid-North Atlantic, including the distribution of bathymetries and the current marine protected areas included in the Island Natural Parks and the Azorean Marine Park. The map also shows the limits of the Azorean Exclusive Economic Zone (EEZ) and the no-trawl area imposed by EU regulations (CE reg. 1568/2005). *Graphics: R. Medeiros ©ImagDOP.*

(EU). Consequently, the Regional Government is empowered to make decisions and produce environmental legislation, but these must be aligned with national, European and international policies and agreements.

We argue that Azorean MPAs have gone through three distinct phases which roughly coincide with the development of MPAs worldwide: the early establishment of isolated MPA with little scientific support, an intermediate phase dominated by international (EU) initiatives that promoted scientific research and conservation policies, and finally an integrative approach to conservation that led to the establishment of a regional MPA network. Tracing back the history of MPA establishment in the Azores allowed us to undertake a comprehensive critical analysis that reflects how the strengths and weaknesses of the current MPA network have arisen and how external factors that affect this MPA network have developed. This critical analysis reveals that this MPA network is of key importance to the Azores, as it provides several opportunities to enhance marine conservation, reduce user conflicts, and promote sustainable development and research. Yet, it also shows that to achieve conservation goals, this network must be effectively implemented and integrated into a wider marine management strategy for the region. From the analysis, we make recommendations regarding future directions for Azorean MPAs, and draw conclusions about the significance of the lessons learned for the science and policy of marine reserves globally.

METHODS

Review of Azorean MPA Establishment

We conducted an extensive literature review to trace the development of MPAs in the Azores and the context in which this occurred. This encompassed legislation at the European, national and regional levels, government reports and gray literature along with scientific publications. Eleven key government officers and 10 researchers who have been mostly involved in MPA establishment in the Azores assisted in the identification of relevant information sources. To illustrate the overall trend in the production of scientific knowledge to support marine conservation, we conducted a simple bibliometric analysis in which every article listed on the Web of Knowledge that included the words "marine" and "Azores" as topics was examined. Of the initial 437 articles returned by the Web of Knowledge on a search conducted on September 24 2015, we identified 256 articles that focused on the Azorean marine environment.

Critical Evaluation of the Current Azorean MPA Network

Two strategic tools commonly used in business studies were used to critically evaluate the current Azorean MPA network. A SWOT (strengths, weaknesses, opportunities, threats) analysis was used to link internal and external factors that influence the MPA network, enabling the identification of strategic options and considerations for its successful implementation. It included an internal analysis, which identified characteristics of the MPA network that work particularly well (strengths) and specific features that compromise its goals (weaknesses), and an external analysis highlighting external factors that positively (opportunities) or negatively (threats) affect the MPA network. SWOT analysis is limited as a stand-alone tool because it may ignore important external factors, especially in broader contexts (Henry, 2008). Therefore, we combined it with a PESTLE analysis, which facilitated the wider scan of real and potential factors inherent to the overall context surrounding the MPA network. PESTLE identified the external factors included in the SWOT, using the prompts: Political-administrative, Economic, Social, Technology-research, Legal and Environmental. Both analyses were conducted over two consecutive focus groups composed of four experts in Azorean marine conservation research, which took place in October and November of 2012. All factors from both analyses were discussed between the experts until consensus was reached and consubstantiated by current available research.

AZOREAN MPAs

The 1980s – First Azorean MPAs

The Azores were a poor and isolated region when they were granted autonomy in 1976. To overcome this, socio-economic development was promoted and communications improved through both aerial and maritime transport linkages. Exploitation of marine resources was encouraged through financial incentives designed to increase the number of larger and better equipped fishing boats. New markets developed, fish value increased and extractive activities such as fishing and harvesting evolved from subsistence activities to business operations. Throughout the 1980s, catches significantly increased, new species and fishing grounds were exploited and the fishing season was extended (Gordon et al., 2003). Marine extractive activities were regulated to promote the rational management of stocks and the effective control of fishing activities, and several exploited species were provided with legal protection, which either banned their capture or set minimum size limits. Nevertheless, drastic declines of limpet populations in the late 1980s were early signs of overexploitation (Santos et al., 1990).

Environmental protection services were underdeveloped, understaffed and limited to a small office within the regional administration. Nevertheless, during the 1980s eight MPAs were established under the 1976 Portuguese national legal framework that defined different types of protected areas. The first one included a small coastal no-take MPA (0.01 km^2) that would correspond to the International Union for Conservation of Nature (IUCN) category I, and it was the only Azorean MPA for which a specific management plan was developed. The remaining MPAs were designated marine reserves (IUCN category VI), as they imposed certain limitations to specific activities to promote the sustainable use of marine resources. These MPAs consisted of one relatively large offshore reef (ca. 378 km^2), and six small coastal sites ranging in size from 0.05 to 4.5 km^2 (**Table 1**).

These early MPAs were mostly "paper parks," reflecting (a) limited data availability relating to the marine environment; (b) absence of an overall plan for MPA implementation; (c) emphasis

TABLE 1 | Marine protected areas (MPAs) established in the Archipelago of the Azores between 1980 and 2015, both within and beyond the Exclusive Economic Zone (EEZ), and including those MPAs legally established and driven by the Regional Government, included in NATURA 2000, and recognized by the OSPAR Commission and UNESCO.

Marine Protected Areas (MPAs) in the Azores		Period		
		1980–1989	1990–1999	2000–2015
Total number of designations		8	24	79
Total protected area (km^2)	Inside EEZ	384.08	435.59	11,175.04
	Outside EEZ	–	–	100,206.54
REGIONAL GOVERNMENT MPAs				
Total number	Inside EEZ	8	8	40
	Outside EEZ	–	–	4
Total protected area (km^2)	Inside EEZ	384.08	384.08	11,175.04
	Outside EEZ	–	–	100,206.54
Minimum MPA area (km^2)	Inside EEZ	0.05	0.05	0.10
	Outside EEZ	–	–	22.15
Maximum MPA area (km^2)	Inside EEZ	377.14	377.14	4013.00
	Outside EEZ	–	–	93,568.00
NATURA 2000				
Total number		–	16	18
Total protected area (km^2)		–	87.59	372.72
Minimum MPA area (km^2)		–	0.50	0.50
Maximum MPA area (km^2)		–	35.94	190.23
OSPAR NETWORK OF MPAs				
Total number	Inside EEZ	–	–	7
	Outside EEZ	–	–	4
Total protected area (km^2)	Inside EEZ	–	–	5674.15
	Outside EEZ	–	–	100,206.54
Minimum MPA area (km^2)	Inside EEZ	–	–	95.00
	Outside EEZ	–	–	22.15
Maximum MPA area (km^2)	Inside EEZ	–	–	4012.53
	Outside EEZ	–	–	93,568.00
UNESCO BIOSPHERE RESERVE				
Total number		–	–	3
Total protected area (km^2)		–	–	750.13
Minimum MPA area (km^2)		–	–	55.10
Maximum MPA area (km^2)		–	–	445.03

on top-down implementation and absence of community participation; (d) lack of management plans for individual MPAs; and (e) scarcity of resources allocated for enforcement (Martins and Santos, 1988; Santos et al., 1995b). To overcome these shortcomings, Martins and Santos (1988) pointed out the need to reform the regional environmental strategy and legal framework, and suggested the creation of a regional organization that could be responsible for MPA management and the articulation with other regional, national and European conservation institutions.

The scarcity of scientific data reflects the fact that most fieldwork was conducted by institutions based outside of the Azores and occurred only occasionally (Santos et al., 1995a). Nevertheless, some fieldwork conducted at this time was instrumental in recommending MPA establishment in the Azores (Saldanha, 1988). The founding of the University of the Azores in 1976 promoted the deployment of permanent researchers in the Archipelago, enhancing the region's capacity for scientific research (Santos et al., 1995b). Furthermore, following Portugal's accession to the EU in 1986, European funds became available for the development of a regional environmental strategy, including the necessary baseline research. The first EU-funded conservation project in the Azores—project BIOTOPES—identified and characterized 55 sites of community interest that were later used to establish protected areas (Vasconcelos and Gomes, 1988). **Table 2** summarizes the main marine conservation research projects carried out in the Azores.

The 1990s – EU-Driven Initiatives

The 1990s were a period of rapid socioeconomic development due to capital transfers, subsidies and tax exemptions aimed at developing the EU's ultra-peripheral regions. Commercial fisheries in particular experienced a phase of full exploitation as a result of fisheries enhancement policies developed in the previous decade, along with improvements in fisheries knowledge, technology and market conditions. The number of fisheries regulations increased and the EU's Common Fisheries Policy was put into practice. Due to the collapse of Azorean limpet populations in the 1980s (Santos et al., 1990), the Fisheries Department established limpet reserves for every island in 1993. Nevertheless, a combination of poor enforcement and high commercial pressure brought this resource close to commercial extinction (Santos et al., 2010). Tourism was another economic activity that significantly increased during this decade as specific economic policies targeted this sector (De Menezes et al., 2008). The first marine tourism operators were established early in the decade, specializing in whale-watching, scuba-diving and big-game fishing.

Several advances in marine conservation took place in the 1990s. Firstly, its political relevance increased with the creation of a regional government department dedicated to environmental issues. Secondly, based on national laws, a regional legal framework for protected areas was defined in 1993, which promoted the establishment of a regional network of protected areas and defined regional administrative procedures, management entities, and a new classification system. The pivotal move was the implementation of EU environmental policies, particularly the NATURA 2000 network of protected areas. This was a major impetus for the systematic and integrated approach to environmental conservation and led to the preliminary designation of 23 Sites of Community Importance in 1998, 16 of which included or consisted of marine areas totalling around 90 km^2 (**Table 1**). However, NATURA 2000 was a long, bureaucratic and demanding process, so final designations and specific regulations would only be produced in the following decade.

As the ocean became a central theme in the Portuguese public arena in the 1990's, decision makers recognized its key role for future socio-economic development and implemented important marine-related governmental policies and programs,

TABLE 2 | Scientific projects carried out in the Archipelago of the Azores that focused on marine conservation and provided relevant outputs for the establishment of marine protected areas in the region, including their main funding sources and institutions involved.

Date	Project	Funding institutions	Research institutions	Main objectives and outputs for marine conservation in the azores
1986–1987	Biotopes	EU	GovAzores; Parks and Reserves National Services	Identification of 55 biotopes as Sites of Community Interest
1995–1998	Seabird Conservation *“Conservation of marine birds and their habitats in the Azores”*	EU RGAzores	UAc; GovAzores; RSPB, University of Glasgow	Seabird conservation actions (public outreach; data collection; standardization of monitoring methodology)
1996–1998	TURISUB “*Studies for the development of underwater tourism of the Azores”*	RGAzores	UAc/IMAR	Data collection
1996–1999	CLIPE “*Climatic effects on the ecology of littoral fishes*”	EU GovPortugal	UAc/IMAR	Data collection, standardization of coastal fish monitoring methodology
1998–2003	MARE *“Integrated management of coastal and marine zones in the Azores”*	EU RGAzores	UAc/IMAR RGAzores	Management plans for NATURA 2000 areas; public outreach; data collection; socioeconomic studies
1999–2002	Bird Atlas *“New Atlas of Birds Nesting in Portugal”*	EU	SPEA; RGAzores	Data collection; revision of regional network of SPAs
1999–2003	MAROV *“Coastal marine habitats, thematic mapping of the seabed using GIS, AUV and ASV”*	GovPortugal	UAc/IMAR, Instituto Superior Técnico	Acoustic and visual mapping of marine habitats and biodiversity, including within SCIs
2001–2004	MAREFISH *“Marine Protected Areas of the Azores: Effects on Fish Communities”*	EU GovPortugal	UAc/IMAR	Evaluation of MPAs benefits on fish communities; data collection on fish dispersal and MPA connectivity
2002–2005	CETAMARH “*Ecology and population structure of bottlenose dolphins and sperm whales in the Azores”*	EU GovPortugal	UAc/IMAR	Collection of baseline data to adapt the Azorean Marine Park management model to cetacean conservation
2002–2005	OASIS *“Oceanic Seamounts: an Integrated Study”*	EU	UAc; IMAR, (+8 international partners)	Site-specific management plan for Sedlo seamount
2003–2006	OGAMP *“Planning and Management of Marine protected Areas”*	EU RGAzores	UAc/IMAR; RGAzores	Integrated management plans for NATURA 2000 areas; public outreach; data collection; socioeconomic studies
2004–2006	PARQMAR *“Characterization, planning and management of marine protected areas in Macaronesia”*	EU	UAc	Management plan proposal for NATURA 2000 areas; data collection; socioeconomic studies; public outreach
2004–2008	MARMAC and MARMAC II *“Knowledge, promotion and valorization for a sustainable use of MPAs”*	EU	UAc/IMAR; Nauticorvo; RGAzores	Environmental education and awareness campaigns; preparation of educational tools; baseline data collection
2004–2008	MARINE IBAs *“Important Areas for the Seabirds in Portugal”*	EU ICNB	SPEA; UAc/IMAR; Birdlife International	Identification of 11 Azorean marine IBAs; data collection
2005–2008	EMPAFISH *“Marine Protected Areas as tools for fisheries management and conservation”*	EU	UAc (+13 international partners)	Integrating Azorean case-studies in European MPA research
2009-	CONDOR *“Observatory for Long-Term Study and Monitoring of Azorean Seamount Ecosystems”*	EEA	UAc; IPIMAR; Institute of Marine Research (Norway)	MPA establishment with stakeholder participation; data collection to improve management of seamounts; public outreach
2007-	CORALFISH *“Assessment of the interaction between corals, fish and fisheries, in order to develop monitoring and predictive modeling tools for ecosystem based management in the deep waters of Europe and beyond”*	EU	IMAR (+16 international partners)	Data collection to improve management of deep-sea habitats
2007-	MADE *“Mitigating Adverse Ecological Impacts of Open Ocean Fisheries”*	EU	UAc/IMAR (+12 international partners)	Data collection to propose measures to mitigate adverse impacts of open ocean fisheries
2009-	CORVO and VILA FRANCA *“Sanctuary Islands for Seabirds”*	EU RGAzores	SPEA; RSPB; Corvo Municipal Council	Recovery of seabird habitats; public outreach
2009-	DEEPFUN *“Biodiversity and functioning of the deep-sea hydrothermal field Menez Gwen–a contribution to management policies”*	EU GovPortugal	UAc/IMAR; RGAzores; University of the Algarve; EMEPC	Data collection to improve management of hydrothermal vent fields

EMEPC, Task Group for the Extension of the Portuguese Platform; EU, European Union; GovPortugal, Government of Portugal; IMAR, Institute of Marine Research; RGAzores, Regional Government of the Azores; RSPB, Royal Society for the Protection of Birds; SPEA, Portuguese Society for the Study of Birds; UAc, University of the Azores.

many of which contributed to a substantial investment in marine sciences using both national and EU funding sources (Costa and Gonçalves, 2010). As a result, the number of scientific projects gathering baseline information for MPA establishment in the Azores significantly increased from the mid-1990s onwards (**Table 2**). Most projects received funding from EU programs and were led by the University of the Azores, usually in close collaboration with the Regional Government. They set monitoring methodologies, initiated regional-scale awareness campaigns, and included the first consistent efforts to involve local communities in marine conservation through information outreach, education and stakeholder engagement.

The 2000s – Toward an Integrated Approach to Marine Conservation

Throughout this decade, social and economic indicators greatly improved and marine-related activities became more relevant to the regional economy. Azorean fisheries showed increasing catches and profits in the early 2000s (Pham et al., 2013) as a result of higher fishing effort and the expansion of fishing grounds. Despite earlier warnings that some fish stocks were depleted or entering overexploitation (Santos, 1999), the Regional Government implemented a program of incentives in the mid 2000's to renew the commercial fleet, which served to increase fishing effort as vessels were able to operate for longer periods and travel greater distances. By the end of the decade, important demersal fish species were considered to be approaching a critical level of exploitation. Recreational fishing developed to the point of exerting considerable pressure on marine resources (Pham et al., 2013), as the number of recreational boats increased almost fourfold during this decade (www.estatistica.azores.gov.pt). As for tourism, the incentives and policies previously adopted resulted in the industry's rapid growth. With greater number of tourists, the number of licensed marine tourism operators increased and diversified into activities like boat tours and rentals, fishing, scuba-diving, shark-diving and whale-watching (Ressurreição and Giacomello, 2013).

The strong investment in marine science initiated in the previous decade resulted in the proliferation of marine conservation research projects during the 2000s (**Table 2**). This trend is also illustrated by the significant increase in the number of peer-reviewed scientific articles published yearly on the Azorean marine environment as of 2000 (**Figure 2**). The EU remained the leading funding source for marine conservation research projects (**Table 2**). Likewise, the University of the Azores, in association with the Institute of Marine Research ("Instituto do Mar"–IMAR), remained the leading research institution, participating in 75% of projects, while the participation of environmental NGOs and international partnerships increased. The main outputs of these research projects were baseline data and recommendations that were used for establishing the boundaries and regulations of current Azorean MPAs. The increasing desire to promote public support for MPAs is reflected in the inclusion of public outreach and stakeholder participation activities in most projects' goals. In addition, several projects incorporated the monitoring of MPAs that had been initiated in the 1990s, filling the gap of a long-term monitoring plan in the region.

International Conservation Tools

In the latter half of the 2000s, the Regional Government worked toward including international programs and specific agreements in its environmental conservation strategy. Between 2007 and 2009, UNESCO approved the applications submitted by the Regional Government to the Man and Biosphere Program, recognizing the islands of Corvo, Flores and Graciosa and their surrounding marine environment as Biosphere Reserves (**Table 1**). As the Regional Government would assure enforcement, these different zones were defined so that they matched official plans for marine conservation in those islands.

In a joint effort between the Regional Government, the University of the Azores and, and at a later stage, the Task Group for the Extension of the Portuguese Continental Shelf, several applications were submitted to the OSPAR Commission. Between 2006 and 2011, OSPAR included 11 Azorean MPAs in its network of MPAs (**Table 1**): seven within national waters and four outside national jurisdiction but within the limits of the areas proposed for legal continental shelf extension that Portugal submitted to the United Nations Commission on the Limits of the Continental Shelf. Eight of these OSPAR MPAs incorporated the protection of the seafloor and sub-seafloor for two coastal areas, three seamounts and two hydrothermal vent fields within the EEZ, and for an additional hydrothermal vent field located outside the EEZ. The latter, named "Rainbow" was the first national MPA to have been proposed under the high seas and accepted by OSPAR. This made Portugal, and particularly the Azores, a pioneer in the protection of marine biodiversity at an international level (Ribeiro, 2010) and a progressive player that helped to progress the ground-breaking OSPAR high seas MPAs process. These eight MPAs encompassed a set of priority habitats like sponge aggregations, hydrothermal vent fields, deep-sea coral gardens and reefs, and species like the long lived and late maturing orange roughy, reflecting the growing importance and knowledge of deep-sea ecosystems. During the 2010 OSPAR ministerial meeting in Bergen (OSPAR, 2010), OSPAR adopted measures to establish and manage the high seas superjacent to the seabed of three areas (Altair, Antialtair, and the Mid-Atlantic Ridge North of the Azores) as OSPAR MPA. This complemented the measures for management of these MPAs reported by Portugal to the OSPAR Commission as components of the OSPAR network of MPAs, which were integrated into the Azores Marine Park. The collaboration between OSPAR and Portuguese entities toward the development of common management strategies for these three MPAs located outside the Azorean EEZ was also a ground-breaking step for the establishment of OSPAR's Network of High Seas MPAs (O'Leary et al., 2012) and was welcomed as significant progress at the inter-ministerial OSPAR meeting in Bergen.

EU initiatives

Following the development of a legal Sectorial Plan, based on studies undertaken by the University of the Azores and

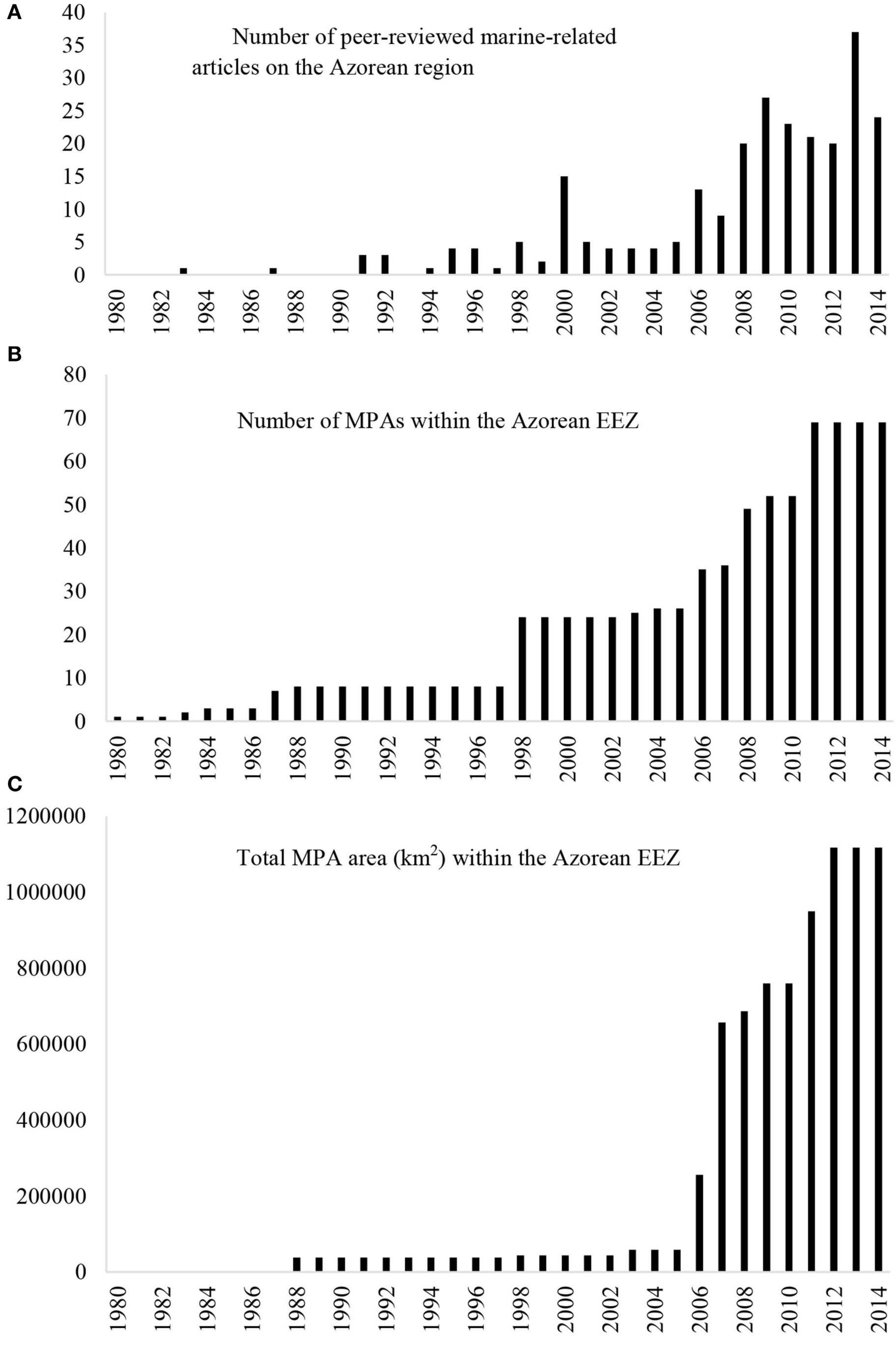

FIGURE 2 | Main marine conservation trends in the Archipelago of the Azores since 1980. (A) number of peer-reviewed scientific articles about the Azorean marine environment published each year; **(B)** total number of MPAs in force each year within the Azorean Exclusive Economic Zone (EEZ); **(C)** total MPA area (km^2) in force each year within the Azorean EEZ.

the Portuguese Society for Study of Birds, the NATURA 2000 protected areas were formally recognized and established by the Regional Government and the EU. In addition, two new Azorean MPAs consisting of hydrothermal vent fields were designated, increasing the number of NATURA 2000 MPAs to 18 (**Table 1**).

Regional Conservation Tools

Under the legal framework approved in 1993, the Regional Government embarked on the creation of a Regional Network of Protected Areas by reclassifying existing MPAs and establishing the first Regional Natural Park in Corvo Island, which included the island's entire marine surrounding. However, the 1993 legal framework proved to be ill adapted to the Azorean administrative backdrop. There was no coherence nor territorial integration in the way that protected areas within this network were organized (Calado et al., 2009), and this was worsened with the introduction of a wider range of legal tools including NATURA 2000 and OSPAR MPAs. As each protected area was created and regulated by regional decree, it involved a tremendous legislative effort. Furthermore, the institutional organization was complex, as the attribution of responsibilities presented both gaps and overlaps (Calado et al., 2009) and did not include spatial management tools created outside the Environmental Department.

To overcome these difficulties, the legal framework was reviewed in 2007 to standardize the diversity of designations into IUCN categories and to establish a management model adapted to the Archipelago's geographic and administrative conditions. This new model integrated all existing protected areas, including the early 1980's MPAs, NATURA 2000 and OSPAR MPAs, and other spatial tools such as the limpet reserves and coastal zone management plans. It also integrated new protected areas that resulted from significant advances in scientific knowledge or were necessary to assure the ecological continuity of ecosystem services and functions (Calado et al., 2009), such as Important Areas for Birds identified by project MARINE IBAs (**Table 2**). This way, two pivotal tools for spatial management were established in the Azores between 2008 and 2011: (1) a network of nine Island Natural Parks, autonomous in management and including all terrestrial and coastal MPAs within territorial waters, and (2) the Azorean Marine Park, including all MPAs located outside the territorial sea. As a result of this reorganizing process, the total marine area under protection increased substantially because the new MPAs units were enlarged and their limits simplified into polygon shapes. In total, they include 44 MPAs covering more than 10 thousand km^2 (1.12%) of Azorean waters and over 100 thousand km^2 of the continental shelf outside the Azorean EEZ (**Table 1**), which constitutes a major increase in MPA number and total area comparing with the previous decades (**Figure 2**).

CRITICAL ANALYSIS OF AZOREAN MPAs

The recently established MPA network described in the previous section is now the cornerstone of Azorean marine conservation policies. In this section, we conduct a critical analysis of the current Azorean MPA network and identify factors that might influence its future success. The results of this analysis are summarized in **Table 3** and are discussed below.

Strengths and Weaknesses

The relatively healthy Azorean marine environment, geographically distant from significant pollution sources and with limited coastal construction, is a significant strength of Azorean MPAs. Another major asset is the completion of the legislative process that established the Azorean Network of Protected Areas, as a clear legislative framework defining conservation goals has been found to be an important governance attribute to MPA establishment (Osmond et al., 2010). Moreover, this process introduced several conservation measures for Azorean MPAs, like strict regulation of activities that disrupt the seafloor (mineral extraction and depositing, equipment installment), exclusion of certain fishing activities and establishment of governmental authority over specific economic and research activities. For small island contexts, the Azorean MPA establishment process is pioneering in achieving a representative coverage of a full range of ecosystems habitats and vulnerable marine environments whilst enabling the establishment of large offshore MPAs both within and beyond the Azorean EEZ (Glowka, 2003; Ribeiro, 2010; Ribeiro and Santos, 2010; O'Leary et al., 2012). It leveraged itself on the involvement of recognized international organizations and programs such as OSPAR, UNESCO, and NATURA 2000, providing international recognition for the region's conservation efforts. The involvement of the scientific community was a major strength because it resulted in a large volume of MPA research and baseline data, providing the basis for much of the design of the Azorean Marine Park and some other MPAs (Calado et al., 2011). Finally, the design of some MPAs included the views and interests of local stakeholders (Abecasis et al., 2013a), a feature that is widely advocated as essential for MPA success (Reed, 2008). Moreover, the legal requirement to develop Consulting Councils for each Island Natural Park is an important step toward stakeholder participation in MPA management.

As for weaknesses, MPAs comprise only 1.12% of Azorean waters, which is considerably lower than the minimum 10% coverage considered necessary to ensure marine conservation established in the Aichi Biodiversity Targets (CBD, 2010). Effective marine conservation is impaired by shortcomings in the design of coastal MPAs, as they lack the appropriate ecological criteria and forecast necessary to maximize spill-over, connectivity, and the potential net benefits of MPAs. Moreover, current no-take areas are unlikely to achieve significant conservation goals because they are small and limited in number. This situation is worsened by the absence of management plans and the allocation of limited resources for enforcement and long-term monitoring plans, which derive from limited funding for MPA implementation. Consequently, Azorean MPAs so far have had little influence on the previously exploited populations within their limits (Schmiing et al., 2014). Weaknesses also include social factors, as most of the MPAs established in the Azores over the past three decades included low levels of community involvement and insufficient provision of public information throughout the process (Calado et al., 2011). Moreover, the profusion of MPA designations that resulted from the different phases of MPA establishment described in Section Methods undermined the public understanding of MPAs (Abecasis et al., 2013a).

Opportunities and Threats

Political and Administrative Factors

Recent regional policies and legislation aim at reconciling economic and social development with marine environment conservation. This vision of sustainable development has been a basic principle not just for MPA establishment, but also for the regulation of different economic activities (e.g., aquaculture, mineral extraction, tourism, fisheries). At an international level,

TABLE 3 | Summary of the critical analysis of the current Azorean MPA network, including identified internal factors (strengths and weaknesses) and external factors (opportunities and threats provided by the different PESTLE factors: political and administrative, legal, economic, social, environmental, and technology and research).

	Strengths	**Weaknesses**
	Healthy marine environment Legal basis for the Azorean Network of Protected Areas Azorean MPA establishment considered pioneer Representativeness Large offshore MPAs Involvement of international organizations and programs Involvement of scientific community Science-based process Incorporation of stakeholder's interests in MPA design in some cases Legal requirement for stakeholder consultation	Only 1.12% of EEZ is legally protected MPA design in most PNI is largely inadequate Small and very few no-take areas Current absence of management plans Low resources for enforcement and monitoring plans Weak community involvement and information Profusion of MPA designations
	Opportunities	**Threats**
Political and administrative	International political incentives for MPA establishment Regional policies follow vision of sustainability	Conflicting within different governmental sectors Inadequate governmental structure for marine issues Lack of political will
Legal	Current MPA legal framework Development of legislation on marine spatial planning	History of unregulated MPAs in the region Legal obstacles to cooperation between different agencies
Economic	Sustainable practices of Azorean commercial fisheries MPAs as fisheries management tools High potential to develop ecotourism in the region Promoting ecotourism activities and products Applying precautionary principle to economic activities Spatial mediation of conflicts between economic activities Introducing mitigating measures to economic activities	Over-exploitation by commercial fisheries Reducing available fishing grounds Increasing economic pressure to develop mineral extraction Sporadic impacts of shipping activities Potential threats from developing economic activities
Social	Maintaining recreational extractive activities at sustainable levels High public awareness about conservation issues Potential to increasing public awareness on marine conservation Mediating spatial conflicts between users and stakeholders Improving environmental standards and quality of life	Increasing pressure from extractive recreational activities Low levels of compliance
Environmental	Partial protection of migratory species Partial protection of seabirds Protection of Vulnerable Marine Ecosystems	Invasive species Migratory and highly mobile species Seabird species Vulnerable Marine Ecosystems
Technology and research	Independent research assists in MPA monitoring Research progress may improve MPA design VMS technology MPAs provide research opportunities	Knowledge gaps Reduced expression of social sciences Low levels of interdisciplinary research

approval of the Marine Strategy Framework Directive was a step toward the application of ecosystem-based management in EU waters (Markus et al., 2011), in which the establishment of an ecologically representative network of MPAs is instrumental. National commitments under the Biodiversity Convention and OSPAR also provide key political incentives for MPA establishment (Marinesque et al., 2012; O'Leary et al., 2012).

However, Azorean MPAs are also affected by political and administrative constraints. Governance is not just vertically fragmented (UE, national, regional, and local levels of government), but also horizontally fragmented, with different administrative departments providing competences and representing different interests in marine issues (e.g., Environment, Fisheries, Tourism, Science, and Technology). Conflicts often arise as different departments, pressured by different lobbying groups, have contradictory strategies and agendas. In particular, fisheries and environmental agencies are frequently in opposition. Furthermore, this government structure entails fragmented and overlapping jurisdictions. For instance, although several enforcement agencies operate in Azorean marine areas, as each agency has specific and different jurisdictions and inter-agency cooperation is low, the amount of resources required for enforcement is tremendous. This is a typical problem of overly-bureaucratic administrative systems (Rodríguez-Martínez, 2008; Gerhardinger et al., 2011) and a frequent excuse for sub-optimal MPA effectiveness. Finally, as

MPAs entail controversial measures there is little political will to implement them, a common threat to European MPAs (Fenberg et al., 2012) that results in limited funding and, consequently, the absence of management plans and insufficient resources.

Legal Factors

The initial legal framework for MPA establishment failed by protecting isolated natural values, without considering environmental conservation as a whole. The 1993 legal framework that replaced it introduced the concept of protected area network, yet it failed to consider the complexity and administrative constraints underlying multiple types of protected areas. The 2007 review of this legal framework improved the legal process and provided opportunities for MPA success. By integrating every spatial management tool into island units and a wider Marine Park, it defined a management model adapted to the region's geographic and administrative conditions. By standardizing the many designations developed under different legal contexts, it simplified MPA objectives and how they are perceived. Finally, by including international and EU-driven conservation into the regional legal system, it assured that they are perceived as legally binding regulations by the public (Calado et al., 2011).

Presently, the Regional Government is developing marine spatial management plans. These should strengthen the role of MPAs as effective conservation tools while addressing common MPA shortfalls and reducing the gap between MPAs and fisheries management (Agardy et al., 2011). On the negative side, the conservation impact of most Azorean MPAs was seriously undermined because legally required management plans were never developed. Consequently, many stakeholders perceived them as "paper parks" and doubted that they would be implemented (personal observation). In matters of enforcement, inter-agency cooperation is frequently limited by the legal assignment of specific jurisdiction to enforcement agencies.

Economic Factors

Commercial fishing, tourism and marine transports represent sectors of economic activity of significance with respect to marine conservation in the Azores. MPAs are compatible with the environmental practices of Azorean commercial fisheries. Of the regional commercial fishing fleet, 90% is comprised of the small-scale sector, which employs more people, achieves higher landed volume and value, is less fuel intensive than the large-scale sector and has greater capacity to adapt to the changing economic, ecological, and social circumstances that stem from establishing MPAs (Carvalho et al., 2011). Moreover, Azorean fisheries have received renowned ecological certifications for the use of non-destructive fishing techniques. These practices have led regional authorities to legally contest the 2003 EU's Decision of opening Azorean waters to EU fishing fleets on the basis that it would enable the entry of industrial fleets using destructive fishing practices not allowed in the region. Consequently, the EU banned deep-sea trawling and other netting gears in Azorean waters to assure the protection of vulnerable ecosystems (**Figure 1**; Morato et al., 2010). These environmental practices, however, have not prevented the high exploitation levels that now threaten the region's marine resources, including within MPAs. With appropriate planning, management and evaluation, MPAs have the potential to improve fisheries management (Agardy et al., 2011) and may help achieve the sustainability goals set for this economic activity, even though they are likely to affect fisheries by reducing available fishing grounds.

Tourism has developed to become the main tertiary activity in the Azores (Soukiazis and Proença, 2008). Its sustainable development is assured through regional policies and legislation that regulate and manage marine tourism activities, and promote environmental conservation and education. Brand-awareness campaigns promote the islands as premium nature destinations, in which marine activities are major attractions. The region's potential to develop eco-tourism is an opportunity for Azorean MPAs because it provides alternative and supplementary livelihoods to extractive activities (Pollnac et al., 2001; Peterson and Stead, 2011). MPAs can add value to eco-tourism activities; for example, the recognition of Azorean natural assets by UNESCO and OSPAR have reinforced the Archipelago's image in the international tourism market. In addition, MPAs benefit tourism by maintaining healthy marine environments (Hall, 2001), and managing and promoting nature-oriented activities and certified local produce.

Marine transports are key for the Azorean economy, which like other remote islands depends on them for most import and export activities (marine shipping) and for passenger traffic, (mainly inter-island). However, marine transports can result in sporadic incidents such as oil pollution, collisions with marine mammals, and in the Azores are believed to have introduced invasive species (Cardigos et al., 2006; Amat et al., 2008). Other key economic activities also pose actual or potential threats to the Azorean marine environment, although it is unquestionable that their development is essential for the regional economy. Mineral resource exploitation significantly impacts the seabed and associated ecosystems. In Azorean inshore waters, sand dredging has been conducted despite the region's limited resources and its impacts on coastal habitats. There is also increasing economic interest to exploit Azorean deep-sea minerals, an activity that threatens the ecosystems where they are found, including hydrothermal vents and seamounts (Van Dover, 2011; Santos et al., 2012; Collins et al., 2013). MPAs are opportunities to protect these vulnerable ecosystems and, together with recent regional legislation, have applied the precautionary principle to this developing economic activity (Davies et al., 2007). Activities such as aquaculture and renewable energy generation hold promise of economic growth for the Azores, but may also cause negative environmental impacts (Read and Fernandes, 2003; Grecian et al., 2010). For all economic activities, however, MPAs are tools for reducing spatial use conflicts and introducing mitigating measures.

Social Factors

The marine environment is deeply rooted in Azorean livelihoods and culture (Ressurreição et al., 2012c). Recent studies show that most Azorean people consider marine conservation a priority and are willing to pay to avoid loss of marine biodiversity (Ressurreição et al., 2011, 2012a), both essential attitudes for MPA success. Conversely, MPAs may be used to increase environmental awareness regarding marine issues and sustainable development. They also provide opportunities to reduce conflicts between different users and stakeholders, improve environmental conditions and enhance quality of life in general. With improved coastal access and a growing number of private boats, recreational activities are widely popular, but the intensification of extractive activities like fishing, spear-fishing and harvesting threatens coastal marine resources (Diogo and Pereira, 2013a,b). While regional regulations like closures, minimum sizes and protected species have decreased their negative impacts, MPAs may facilitate maintenance of these activities at sustainable levels (McPhee et al., 2002). Unfortunately, compliance with regulations amongst Azorean recreational fishers is low, which is a threat to MPA success.

Environmental Factors

Invasive species represent a distinct threat to the isolated Azorean marine ecosystems. For example, in <10 years the invasive algae *Caulerpa webbiana* has caused major benthic landscape disruptions in coastal areas of Faial Island, some inside MPAs (Amat et al., 2008). Other environmental factors represent serious challenges for successful MPA design. Azorean MPAs cannot fully protect the populations of a large number of migratory cetaceans, sea turtles, seabirds, and fish species that visit the archipelago, many of which are considered threatened under the IUCN Red List, the Bern Convention and NATURA 2000 Annexes, because only part of their life cycle is spent within Azorean waters. Seabird conservation is rendered even more difficult as seabirds face a suite of threats to their nesting colonies on land, especially invasive predators and light-induced mortality (Fontaine et al., 2011). In addition, many commercial fish species exhibit high mobility within Azorean waters, which may limit the use of MPAs as fisheries management tools and require multispecies criteria when designing MPA networks (Afonso et al., 2009a,b). The region also includes "Vulnerable Marine Ecosystems" (VMEs) such as seamounts and deep-sea fields of hydrothermal vents, cold-water corals and deep-sea sponge aggregations. Easily damaged and slow to recover, these ecosystems are highly vulnerable to human impacts and represent a greater challenge to achieving the conservation goals set by MPAs (Davies et al., 2007; Morato et al., 2008a), as the timeline for anticipating a reserve effect is much longer than the socio-political complex may be willing to accept. Although challenging, Azorean MPAs represent opportunities to provide at least partial protection to these species and ecosystems.

Technology and Research

In spite of recent important findings, there is a worldwide critical need for research that bridges the knowledge gap on the functioning of marine communities and reserves (Sale et al., 2005). The Azores is no exception. Four reasons converge to explain this challenge. Firstly, the complexities of marine systems almost preclude us from drawing general conclusions about the benefits of MPAs and the best processes to achieve their goals. Secondly, even though fairly substantiated rules of thumb can be adopted when designing MPA networks, differences between local systems inevitably prompt the need for local baseline reference points and ecological indices. Thirdly, another common shortfall in the Azores is the limited reference to social sciences in MPA establishment. Lastly, there has been a prior absence of interdisciplinary research. The combination of these four factors results in the need to undertake interdisciplinary research that is locally driven and specifically oriented toward improving the performance of the Azorean MPA Network.

On the positive side, the last 25 years have seen much research progress that can directly or indirectly aid in designing and fine-tuning the Azorean MPA network. In the absence of specific long-term MPA monitoring programs, several independent fisheries research programs run by the University of the Azores have managed to collect important baseline data. Arguably, these have so far focused on coastal and seamount fish communities, which sustain local fisheries, and on a few protected species (e.g., seabirds) and VMEs (e.g., hydrothermal vents), lacking a full ecosystem assessment. Still, they should be able to provide the critical backbone to which effects of current and future protection can be compared. More recently, relevant research has been conducted on the identification of essential habitats and habitat use patterns (Menezes et al., 2006; Morato et al., 2008b; Amorim et al., 2009), predictive habitat modeling (Schmiing et al., 2013), connectivity and spill-over potential (Afonso et al., 2009a,b; Fontes et al., 2009), and trophic chain functioning (Morato et al., 2009; Martins et al., 2011; Colaço et al., 2013). In addition, considerable technological advances and synergies between academia and the technological sector have put the region at the forefront of some research areas, including animal tracking technologies (Olsen et al., 2009; Afonso et al., 2012), underwater robots, the maintenance of deep-water organisms under laboratory conditions and the application of Vessel Monitoring Systems to ecosystems research and management. The latter also constitutes an opportunity to greatly enhance enforcement, especially in the Azorean offshore MPAs. These and other areas of research should benefit from the solid and effective establishment of MPAs in the region, especially with regards to the ability to observe and study communities and systems in relatively undisturbed conditions (Morato et al., 2010).

FUTURE PROSPECTS

Marine conservation in the Azores has reached a critical point. The environmental sector is now well established in the regional administrative structure, and its political weight is expected to further increase with recent policies and agreements that push toward higher protection and ecosystem-based management. The region is equipped with a legal framework that establishes a comprehensive network of MPAs. This network is already bringing benefits to the region, such as added value to nature tourism products, application of the precautionary principle to certain VMEs and restrictions on harmful activities, in spite of still being at an implementation phase. It follows that it is essential to ensure an appropriate implementation of Azorean MPAs, overcoming the political, financial and administrative constraints previously described.

Given the history of unregulated Azorean MPAs, the development and implementation of management plans should become a priority for MPA implementation. To ensure that MPAs achieve both ecological and socio-economic objectives, MPA managers should develop these plans in partnership with scientific researchers, local stakeholders and communities, which in the Azores are known to have different views and expectations of MPAs as conservation and management tools (Ressurreição et al., 2012b; Abecasis et al., 2013a,b). This may promote the wider understanding and acceptance of MPA goals, outputs and shared responsibilities, reduce conflicts between users, and lead to higher levels of compliance with MPA regulations (Reed, 2008). MPA success has often been associated with co-management practices (Smith, 2012). In the Azores, this will largely depend on the Island Natural Parks Consulting Councils, which could become effective tools for stakeholder participation, thus increasing both accountability and compliance to regulations by assuring that MPA governance is based on shared visions and goals of what MPAs are for. Because these practices imply working with stakeholders and communities, it is important to convey simplified information about the MPA process and how to participate.

Effective MPA implementation will require funding so that sufficient resources are allocated for enforcement and long-term monitoring. Enforcement is essential to ensure that regulations are complied with and perceived as playing a role. Without it, a culture of disregard for the rules can become established and undermine future efforts if resource users become accustomed to breaking rules. This is of particular concern as local stakeholders in the Azorean island of Corvo already perceive MPAs as "paper parks" (Abecasis et al., 2013a). Promoting inter-agency cooperation may reduce enforcement costs and overcome legal and administrative constraints. In addition, stakeholder participation and co-management practices may increase compliance and further reduce enforcement costs, especially for coastal MPAs. For offshore MPAs, given the extent of the areas, the distance to the islands and the presence of a higher number of stakeholders, including foreign fleets, the use of remote sensing technologies such as Vessel Monitoring Systems is likely to increase enforcement capacity.

Another key factor for MPA success is long-term monitoring, which improves MPA science and feeds back into the performance of MPAs. Monitoring is especially important because it allows managers to follow an adaptive management approach based on sound science, whereby the design, goals, measures and methods might change over time as new information is obtained and new challenges develop, in contrast to a one-off attempt to set MPA design and management (Ban et al., 2012). Azorean MPAs would benefit from adaptive management to improve the network design by integrating more technical knowledge. Directions for future MPA monitoring in the Azores could include continuing partnerships with regional research institutes, which have proved to be instrumental in the past, assuring funding for research directed at overcoming previously identified knowledge gaps and citizen science programs to involve the community and other stakeholders potentially increasing their buy-in of MPA management. In particular, it should include specific research on:

- The performance of the MPA network as a fisheries management tool, including models that predict benefits such as spill-over and larval export;
- Maximizing the extent of protection provided to migratory species, seabirds and VMEs—e.g., by applying knowledge of aggregation sites, migratory bottlenecks and essential habitat—while articulating MPAs with other management and conservation measures—e.g., fisheries regulations, international agreements and species-specific management plans;
- Identification of key areas for marine conservation that might become no-take areas;
- Socio-economic aspects of MPAs, such as understanding social impacts, changes in the social context, the environmental management process and institutional design principles;
- Mechanisms for engaging communities and stakeholders in marine conservation.

In order to reach the 10% conservation target (CBD, 2010), MPA coverage within the Azorean EEZ should be increased, provided that new designated areas contemplate socio-economic dimensions and aim at achieving a network effect by following ecological criteria such as ecologically and biologically significant areas, representativity, connectivity, replicated ecological features and adequate and viable sites (CBD, 2008). However, emphasis should be put into achieving effective implementation of the current MPA network. Otherwise, designating more MPAs will only be a means to achieve the region's international conservation commitments on paper. Moreover, while MPAs are an important tool for Azorean marine conservation, they are not the solution for all problems. Instead, they should be integrated into a regional marine management strategy, which in turn should present sustainability goals and follow an ecosystem-based approach.

THE AZORES AS A MODEL OF MARINE CONSERVATION FOR ISLAND STATES AND REGIONS

Despite the need to progress in terms of effective management and governance and upgrading into a coherent network of MPAs, the Azores did in fact pioneer the implementation of a set of marine conservation instruments that may be a particular inspiration to other remote islands states or regions. Silva and Pinho (2007) identified a large number of island states/regions with high or medium seamount densities where seamount fisheries are occurring. The understanding that seamount fishing resources are particularly vulnerable and that industrial fishing may exert irrecoverable impacts on those ecosystems (Morato et al., 2006) has led the Azores to influence a non-trawling policy implemented by the EU, to establish several seamount MPAs within its EEZ and to promote the establishment of high-seas MPAs protecting large seamount areas under international agreements.

Some islands states or regions also harbor sought-after massive polymetallic sulfides and cobalt crusts which could be exploited by future mineral extraction. The pioneering actions taken by the Azores to protect hydrothermal vents in deep-waters, potentially rich in these noble minerals, in a time of increasing interest in deep-sea mining, has resulted in the establishment of several untouchable sites. While we recognize that the Azores, as part of the EU, is bound by important governance and policy instruments, the fact is that some EU directives were applied to deep-water and offshore in the Azores before they were applied elsewhere in Europe. For example, seamounts were first protected under the Habitats Directive in the Azores (namely D. João de Castro, Formigas and Dollabarat). Also, in anticipation of the Natura 2000 revision to include habitats beyond 200 m deep, in 2005 the Azorean government proposed the inclusion of the deep-sea hydrothermal vents Lucky Strike and Menez Gwen in this network (Probert et al., 2007). The background instruments and initiatives implemented in the Azores may be of particular inspiration for recent efforts of implementation of a regulatory framework for deep-sea minerals exploration and exploitation in oceanic island states and regions across the oceans that are facing interest on their deep-sea resources (SCP, 2012).

LESSONS LEARNED

The review and analysis presented in this study show that the Azorean case represents a true and valuable contribution to the global conservation policy arena and, more specifically, to the governance, research and societal processes involved in marine spatial management. Indeed, the region arguably offers one of the oldest experiences of the MPA "modern era" in the world, having started in the 1980's when few countries were actively engaged in marine spatial management for conservation. The value of the Azores as a case study is even more important if we consider the specific case of small island states, which face specific challenges and have an umbilical dependence on marine resources (Teelucksingh et al., 2013).

The importance of adequate financing across the MPA process is one lesson from the Azores. General political support and engagement of the scientific community have been a characteristic of the Azorean case study across its three decades, ultimately enabling the region to engage in the MPA experience. Yet, the intensity of phases requiring more actions in the field, whether scientific (characterization, monitoring), management (planning, implementation) or outreach (public and stakeholder engagement), seem to have fallen short of matching that same commitment. Underfunding is the main cause of a gap that ultimately explains most of the weaknesses identified. Of particular concern is the dependence of longer actions (e.g., monitoring, implementation), typically at the 5-year or even decadal scale, on external funding sources (e.g., EU research projects and infrastructural measures) that are not coincidental with such a time frame. Most island cases will face similar challenges, as many represent small island developing states or smaller, underfunded states within the sovereignty of larger countries. A longer term commitment to adequate budgetary resources and the identification of appropriate funding mechanisms, including governmental and stakeholder contributions, are key in achieving a long term, sustainable process concomitant to the adaptable management perspective.

Another aspect of wide significance is the emerging risk that without enforcement, particularly from the outset, a culture of disregard for the rules can become established and then be difficult to reverse. This behavior undermines not only the objectives of the MPAs *per se*, but also the shared responsibility for any successful spatial management involving a variety of interests and stakeholders. Therefore, it is essential that MPAs are enforced as early after their development as possible to avoid adversarial scenarios. This need has been recognized and pointed out as a major concern by all stakeholders, in the Azores (Abecasis et al., 2013a) as well as other places studied (e.g., Österblom and Sumaila, 2011; Perez De Oliveira, 2013).

From the point of view of the MPA network definition, achieving representativeness is a major challenge in highly fragmented and diverse systems typified by islands states. In the Azores, reaching such a goal has arguably been the hardest caveat within a system that encompasses nine inhabited islands, a variety of habitats from coastal reefs to deep-water hydrothermal vents to dynamic multispecies pelagic hotspots, and different fisheries coexisting with other extractive and non-extractive activities. Yet, reaching current level of legal representativeness has been a very long process requiring multiple steps, sometimes even undoing what had been done (e.g., legislative actions). The adoption of a long term, transversal sectorial plan may allow these shortcomings to be avoided.

While the case of Azorean MPAs presents the characteristic marine conservation challenges of remote island regions, some of the lessons it provides can be loosely applied to marine conservation at large or even to the spatial management processes of terrestrial species and habitats in island settings. Common conservation challenges worldwide include developing a shared vision amongst multiple stakeholders and community groups, sourcing sufficient funding for conservation initiatives, ensuring adequate enforcement and achieving representativeness. It is therefore essential to learn from past experiences such as the Azorean case when dealing with conservation issues elsewhere.

ACKNOWLEDGMENTS

This work is part of the research project "2020: toward ecosystem-based management of the Azores marine resources, biodiversity and habitats M2.1.2/I/026/2011." FCT/MCTES provided individual funding support to RA (SFRH/BD/46621/2008), AC was supported by Program Investigador FCT (IF/00029/2014/CP1230/CT0002) from FCT and PA (Ciência 2007 and 2008). IMAR-DOP/UAz is Research and Development unit no. 531 and LARSyS-Associated Laboratory no. 9 funded by the Portuguese Foundation for Science and Technology (FCT) through FCT—Pest/OE/EEI/LA0009/2011–2014 (COMPETE, QERN, and OE) and by the Azores Fund Science and Technology (FRTC) Pro-Convergencia and RAA.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 18 October 2016
doi: 10.3389/fmars.2016.00202

Modeling the Potential Distribution and Richness of Cetaceans in the Azores from Fisheries Observer Program Data

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OPEN ACCESS

Edited by:
Mark Meekan,
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Specialty section:
This article was submitted to
Deep-Sea Environments and Ecology,
a section of the journal
Frontiers in Marine Science

Received: 31 March 2016
Accepted: 29 September 2016
Published: 18 October 2016

Citation:
Tobeña M, Prieto R, Machete M and Silva MA (2016) Modeling the Potential Distribution and Richness of Cetaceans in the Azores from Fisheries Observer Program Data. Front. Mar. Sci. 3:202. doi: 10.3389/fmars.2016.00202

Marine spatial planning and ecological research call for high-resolution species distribution data. However, those data are still not available for most marine large vertebrates. The dynamic nature of oceanographic processes and the wide-ranging behavior of many marine vertebrates create further difficulties, as distribution data must incorporate both the spatial and temporal dimensions. Cetaceans play an essential role in structuring and maintaining marine ecosystems and face increasing threats from human activities. The Azores holds a high diversity of cetaceans but the information about spatial and temporal patterns of distribution for this marine megafauna group in the region is still very limited. To tackle this issue, we created monthly predictive cetacean distribution maps for spring and summer months, using data collected by the Azores Fisheries Observer Programme between 2004 and 2009. We then combined the individual predictive maps to obtain species richness maps for the same period. Our results reflect a great heterogeneity in distribution among species and within species among different months. This heterogeneity reflects a contrasting influence of oceanographic processes on the distribution of cetacean species. However, some persistent areas of increased species richness could also be identified from our results. We argue that policies aimed at effectively protecting cetaceans and their habitats must include the principle of dynamic ocean management coupled with other area-based management such as marine spatial planning.

Keywords: cetacean, spatio-temporal distribution, Azores, species distribution models (SDMs), richness, MaxEnt

INTRODUCTION

The world's oceans face increasing pressure from anthropogenic influences (Halpern et al., 2008). As a result, the rate of change in distribution and population fragmentation of marine organisms has intensified over the last few decades, upsetting the equilibrium of marine ecosystems (Pitois and Fox, 2006; Worm et al., 2006; Beaugrand, 2009; Poloczanska et al., 2013).

Marine mammals (of which cetaceans comprise nearly 70% of the extant species) are especially affected by changes in marine ecosystems and by human threats, with an estimated 74% of species facing high levels of human impact (Davidson et al., 2012; Bester, 2014). Being large-sized top predators with a high metabolic rate, cetaceans play an important role in maintaining the structure and functioning of the marine ecosystems they integrate (Bowen, 1997; Roman et al., 2014; Kiszka et al., 2015).

Cetaceans are expected to experience important changes in distribution due to direct effects of climate change and in response to climactic- and anthropogenic-driven reorganization of their ecosystems (Learmonth et al., 2006; Simmonds and Isaac, 2007; Moore and Huntington, 2008; Bester, 2014). For example, drastic changes in seawater temperature are expected to affect the geographical distribution of species with narrow thermal tolerance, such as some species that occur only in the Arctic or tropical species (Learmonth et al., 2006; Simmonds and Eliott, 2009). In fact, Salvadeo et al. (2010) proposed that a decline in the presence of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in the southwest Gulf of California could be explained by a consistent increase in water temperature in that region over three decades. Similarly, MacLeod et al. (2005) reported a decline of the relative frequencies of strandings and sightings of white-beaked dolphins (*Lagenorhynchus albirostris*) and a simultaneous relative increase in the strandings and sightings of the common dolphin (*Delphinus delphis*) in the northwest Scotland shelf and suggested that these changes could be due to distributional shift of the two species, driven by a steady increase in water temperature.

Distribution and abundance shifts of potential cetacean prey have also been recorded in some areas (e.g., Hátún et al., 2009; Chust et al., 2014; Cormon et al., 2014). Changes in the availability, distribution and abundance of prey will probably have a great impact over cetacean populations, especially species that have specialized feeding habits (Simmonds and Eliott, 2009).

Thus, obtaining a detailed understanding about the spatio-temporal distribution and habitat preferences of these highly mobile species is essential to manage potential hazards and forecast population effects from climate change (Guisan et al., 2013; Parsons et al., 2014, 2015).

Cetaceans are an important marine megafauna group in the Azores, with 28 species recorded so far (Silva et al., 2014), and are probably a key component of the Azores marine ecosystems.

Marine ecosystems in the Azores are utilized by several economic sectors, namely commercial and recreational fishing, tourism, cargo, and passenger transportation (Abecasis et al., 2015). Cetaceans are vulnerable to impacts from all these activities (Bester, 2014; Cressey, 2014) through direct injuries and mortality (e.g., ship collisions, by-catch), competition with fisheries, habitat degradation (e.g., chemical pollution, noise, seafloor alteration), and disturbance (e.g., whale watching).

Silva et al. (2014) pooled data from several sources to provide the first coherent characterization of temporal and spatial occurrence of cetaceans in the waters around the Azores archipelago. A combination of stranding records, nautical and land based surveys were used to characterize the seasonal patterns of cetacean occurrence (Silva et al., 2014). Those authors also utilized cetacean encounter rates calculated using data obtained by the fisheries observer program to characterize the spatial distribution of 12 species and 2 genera in relation to bathymetry. Notwithstanding, Silva et al. (2014) did not try to investigate how these patterns are influenced by other biophysical characteristics and productivity of the ecosystem. Additionally, the maps in Silva et al. (2014) have a crude resolution, both spatially and temporally: maps were created by pooling data from all seasons together and the spatial resolution used was 10 arc-min, which corresponds roughly to 18 km at the study area latitude.

Only few other works have tried to investigate the role of environmental factors in driving the occurrence and distribution of cetaceans in the region, for a restricted number of species (e.g., Visser et al., 2011; Prieto et al., 2016). However, that information is essential for identifying preferred and suitable habitats for each species or group of species, to identify cetacean hotspots, and to describe the interplay between cetacean populations and human activities for proper marine management.

Here we present species distribution models (SDMs) for 16 taxa of cetaceans in the Azores. SDMs have been increasingly used in marine spatial planning (MSP), especially in designing marine protected areas and for identifying areas of potential conflict between human activities and marine organisms (Robinson et al., 2011; Guisan et al., 2013).

We utilized a presence-only modeling approach based on the maximum entropy principle (Phillips et al., 2006) to create monthly predictive cetacean distribution maps for Spring and Summer. We then combined these maps to obtain species relative richness maps to help identifying areas and seasons of increased cetacean biodiversity (Calabrese et al., 2014).

METHODS

Study Region

Data were collected within the Azores Economic Exclusive Zone (EEZ; **Figure 1**), an isolated archipelago of nine volcanic islands disposed in three groups (Eastern, Central, and Western) aligned along a NW-SE orientation, and extending over 600 km. The archipelago is crossed by the Mid-Atlantic Ridge (MAR) between the Central and Western groups. The islands are positioned over the Azores plateau rising from the abyssal plain (∼4000 m), and defined roughly by the 2000 m depth isobath. As other oceanic islands, the Azores are characterized by steep slopes and narrow or absent island-shelves (Tempera et al., 2012). Additionally to the islands, more than 460 seamounts and seamount-like features are found within the archipelago (Morato et al., 2008a). These characteristics combine to create a wide range of habitat types and are responsible for complex circulation patterns that increase the ability of the archipelago to capture and retain particles and small organisms (Sala et al., 2015). The region is largely dominated by two eastward flows generated from the Gulf Stream: the cold southern branch of the North Atlantic Current that crosses the MAR to the north of the Azores at 45–48°N, and the warm Azores Front/Current system, a quasi-permanent feature located south of the islands at 34–36°N (**Figure 1**). Average sea surface temperature varies from 15 to 20°C in winter and 20 to 25°C in summer.

Cetacean Occurrence Data

Cetacean occurrences were obtained from the Azores Fisheries Observer Programme (POPA), from May to November, between

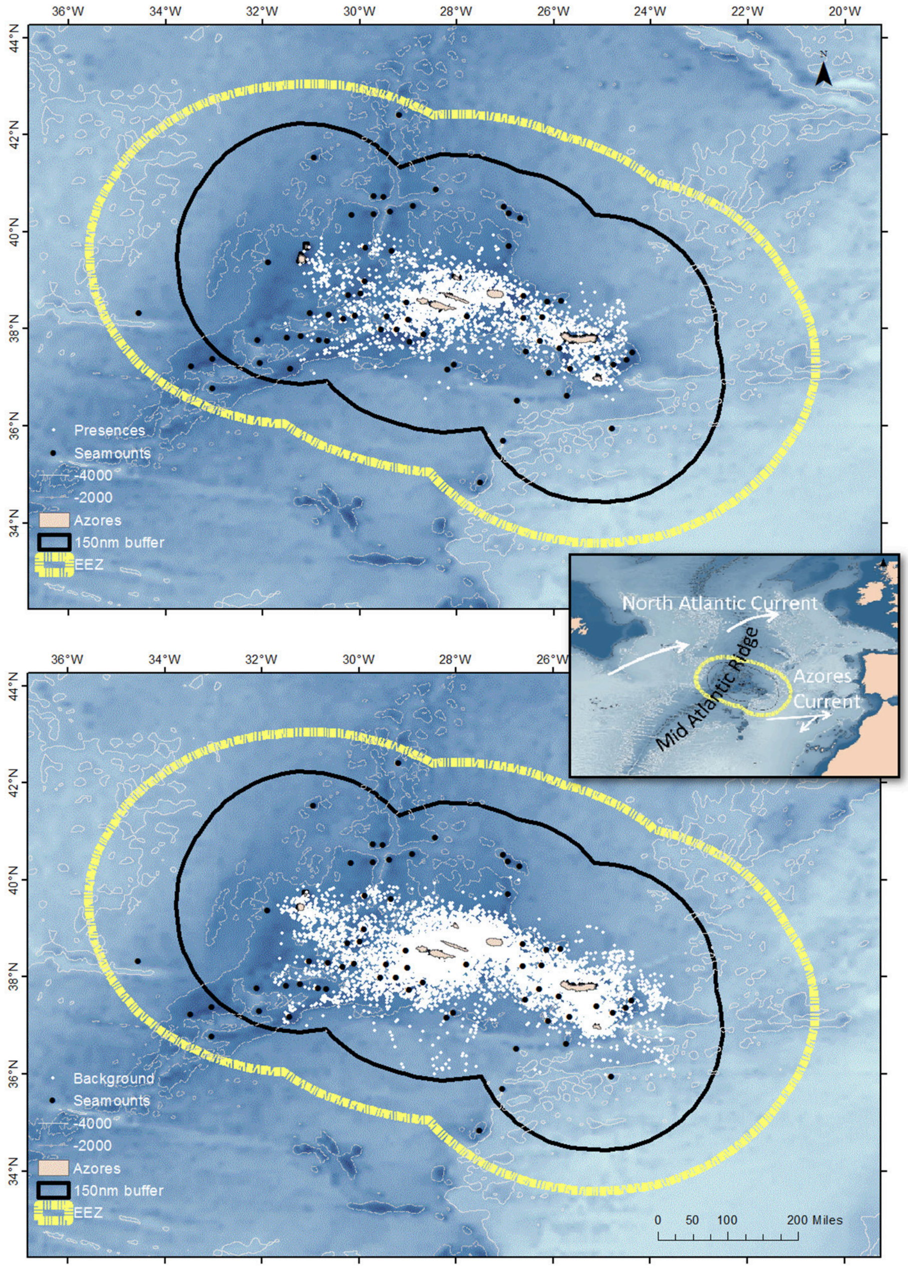

FIGURE 1 | Cetacean sighting positions (top panel) and environmental samples (lower panel) within the study region. The position of the Azores archipelago in the North Atlantic and the main oceanographic structures mentioned in the text are show in the inset. The yellow stippled line represents the limit of the 200 nautical miles economic exclusive zone (EEZ) and the thin black line represents the limit of the 150 nautical miles buffer applied to the predictions from the MaxEnt models. Bathymetry is shown as a scale of blue; the 2000 and 4000 m isolines are also shown. Large seamounts are shown as black dots; smaller seamount-like features are not shown.

2004 and 2009 (**Figure 1**). POPA places trained observers aboard tuna-fishing vessels to monitor and collect information on the fishery and on the presence and behavior of cetaceans, seabirds and turtles. Cetacean surveying effort is conducted when the vessel is cruising or searching for fish schools. During on-effort periods, vessel position and environmental conditions are recorded every 30 min or whenever vessel course changes >20°. All sightings and vessel positions are georeferenced using global positioning system with datum São Braz (EPSG 2190). Sightings are coded according to reliability of species identification, from 0 (low confidence) to 3 (definitive). In this study we analyzed only sightings recorded during on-effort survey periods conducted in sea states on the Beaufort scale ≤3 and with an identification score of 3. Each sighting was considered as a single occurrence, irrespective of the number of individuals within the group.

To avoid bias from clustered points (Hernandez et al., 2006) we used a Geographic Information System (ArcGIS 10.1; ESRI, Inc.; hereby referred as ArcGIS) to identify multiple occurrences within individual grid cells in the environmental space defined by the predictor variables (see Section Environmental data). When more than one occurrence was found within an individual grid cell, one occurrence was chosen randomly (to avoid temporal bias) and kept in the dataset and all remaining occurrences within that grid cell were removed from the dataset. Since this spatial filtering means that only one occurrence per grid cell was used to fit the models, in practice the number of occurrences used to fit the models and presences (grid cells where a species was detected) is the same, even if the number of sightings reported for the species was higher.

Occurrence data were available for 18 cetacean species or groups of species, but models were created only for 16 taxa (15 species and 1 genus: **Table 3**). Only four unequivocal sightings were recorded for the humpback whale (*Megaptera novaeangliae*) and one for either the pigmy or dwarf sperm whales (*Kogia* sp.), which were considered insufficient for creating credible models (Wisz et al., 2008; Herkt et al., 2016). Sightings of beaked whales of the Genus *Mesoplodon* were pooled together (*Mesoplodon* spp.) due to their ecological similarity and difficulty in identifying these animals to the species level at sea. Models for blue (*Balaenoptera musculus*), fin (*B. physalus*), and sei (*B. borealis*) whales were presented elsewhere (Prieto et al., 2016), but here they are combined with models of other species to produce cetacean relative richness maps for the Azores.

Environmental Data

A set of 18 candidate environmental variables (**Table 1**) were selected based on their perceived ecological relevance for cetaceans (Baumgartner et al., 2001; Cañadas et al., 2002; Davis et al., 2002; Yen et al., 2004; Johnston et al., 2008; Santora et al., 2010; Baines and Reichelt, 2014; Mannocci et al., 2014, 2015). **Depth** was obtained from the grid-centered bedrock version of the ETOPO-1 digital elevation model (Amante and Eakins, 2009). Remotely sensed **night-time sea surface temperature** (NSST) was derived from standard mapped images (level 3, monthly average composite) collected by the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument aboard NASA's Aqua satellite and obtained from the Ocean Color Discipline Processing System (Campbell et al., 1995). Remotely sensed near-surface primary productivity indicated by **Chlorophyll-a concentration** (Chl-a) data was used as a proxy for secondary production and was also derived from data collected by Aqua MODIS, with the same spatial and temporal resolutions as NSST. Location and physiography of **seamounts** and seamount-like features were obtained from Morato et al. (2008a) and digitized as a georeferenced database.

The remaining variables were derived from those four using ArcGIS. Variables based on distance/area calculation were first processed in UTM zone 26N with horizontal datum WGS84, and then all variables were projected to an Equidistant Cylindrical projection with horizontal datum WGS84 and resampled to the same extent, with 2.5 arc-min resolution, using bilinear interpolation. Derived variables were: terrain **slope**; **distance to shore**, **distance to bathymetric isoline** ($\text{Dist}_{(n)}$, with "n" representing isoline depth); **seamount density** (d-Seamounts); **minimum depth of seamount** (Seamount_dpt); **time-lagged Chlorophyll-a concentration** for one ($\text{Chl-a}_{(-1m)}$) and two ($\text{Chl-a}_{(-2m)}$) months prior to the sighting month; **local variation of Chlorophyll-a concentration** (V-Chl-a; calculated as standard deviation within a 8 × 8 pixel kernel); **time-lagged local variation of Chlorophyll-a concentration** for one ($\text{V-Chl-a}_{(-1m)}$) and two ($\text{V-Chl-a}_{(-2m)}$) months prior to the sighting month; and **local variation of night-time sea surface temperature** (V-NSST; calculated as standard deviation within a 3 × 3 pixel kernel).

Predictive Modeling

Our dataset comprised only presence records thus we chose to use the software MaxEnt 3.3.3k (Phillips et al., 2006; Dudík et al., 2007) to create monthly (April to September) SDMs for the 16 cetacean taxa in this study.

The MaxEnt algorithm was developed to infer species distributions from presence-only data as a function of a set of ecologically relevant environmental covariates (Phillips et al., 2006; Dudík et al., 2007). Models created in MaxEnt can be used to produce habitat suitability maps which translate the potential distribution of the modeled species under specific environmental conditions (Phillips et al., 2006). We have chosen to use MaxEnt partially because the algorithm has been shown to be among the best performing methods for presence-only data, yielding results comparable to presence-absence methods (Elith et al., 2006; Wisz et al., 2008; Elith and Graham, 2009; Aguirre-Gutiérrez et al., 2013; Duan et al., 2014). Additionally, we were concerned about the effect of small sample sizes from some of the species in this study. Different works quantifying the effect of sample size on the performance of multiple species distribution modeling algorithms sugest that MaxEnt is one of the most consistent accross sample sizes, even at sample sizes lower than 10 occurrences (Hernandez et al., 2006; Pearson et al., 2007; Wisz et al., 2008; Aguirre-Gutiérrez et al., 2013). However, it must be emphasized that even with MaxEnt, best performance is achieved when models are based on 30 or more occurrences and at lower sample sizes models can yield inconsistent results (Pearson et al., 2007; Wisz et al., 2008; Shcheglovitova and Anderson, 2013). Details about MaxEnt theoretical principles and utilization can be found in Phillips et al. (2006), Phillips and Dudík (2008), and Elith et al. (2011).

MaxEnt predictions are strongly affected by sample selection bias (Phillips et al., 2009); models suffering from that type of bias can be considerably improved by drawing the environmental samples from a distribution of locations with the same selection bias as the occurrence data to create an "informed" model (Phillips et al., 2009; Kramer-Schadt et al., 2013). POPA survey effort is dependent on fish distribution and fishing strategies of the boat captains and is neither random, nor homogeneously distributed (Silva et al., 2002, 2011). We dealt with sample selection

TABLE 1 | Candidate environmental variables used in the variable selection procedure prior to model fitting (see Supplementary Material S1 for details).

Environmental variable	Acronym	Transformation	Resolution Spatial/temporal	Units	Source
Depth	Depth	none	1 arc-min/static	M	NationalGeophysicalDataCenter(NGDC), National OceanicandAtmospheric Administration(NOAA) http://www.ngdc.noaa.gov/mgg/global/global.html. Amante and Eakins, 2009).
Night-time sea surface temperature	NSST	none	2.5 arc-min/month	°C	National Aeronautics and Space Administration (NASA) Goddard Space Flight Center's Ocean Data Processing System (ODPS) http://oceancolor.gsfc.nasa.gov. (Campbell et al., 1995).
Chlorophyll-a concentration	Chl-a	log10	2.5 arc-min/month	mg/m^3	National Aeronautics and Space Administration (NASA) Goddard Space Flight Center's Ocean Data Processing System (ODPS) http://oceancolor.gsfc.nasa.gov. (Campbell et al., 1995).
Seamounts	*None*	none	10 meters	unitless	http://www.int-res.com/articles/suppl/m357p017_app.pdf. (Morato et al., 2008a).
Derived environmental variables					**Original variable**
Slope within a 3 × 3 pixel kernel	Slope	log10	1 arc-min/static	Degrees from the horizontal	Depth
Euclidean distance to shoreline	Distance to shore	square root	1 arc-min/static	M	Depth
Euclidean distance to 200 m isobaths	Dist(200)	square root	1 arc-min/static	M	Depth
Euclidean distance to 500 m isobath	Dist(500)	square root	1 arc-min/static	M	Depth
Euclidean distance to 1000 m isobath	Dist(1000)	square root	1 arc-min/static	M	Depth
Euclidean distance to 2000 m isobath	Dist(2000)	square root	1 arc-min/static	M	Depth
Seamount density within 8 × 8 pixel kernel	d-Seamounts	none	1 arc-min/static	seamounts/km^2	Seamounts
Minimum depth seamounts	Seamount_dpt	none	1 arc-min/static	M	Seamounts
Time-lagged Chlorophyll-a concentration (-1 month)	Chl-a (-1 m)	log10	2.5 arc-min/month	mg/m^3	Chl-a
Time-lagged Chlorophyll-a concentration (-2 months)	Chl−a (-2 m)	log10	2.5 arc-min/month	mg/m^3	Chl-a
Chlorophyll-a local variation (calculated as standard deviation within a 8 × 8 pixel kernel of log-transformed Chlorophyll-a)	V-Chl-a	none	2.5 arc-min/month	SD log10(mg/m^3)	Chl-a
Time-lagged Chlorophyll-a local variation (-1 month)	V-Chl-a (-1 m)	none	2.5 arc-min/month	SD log10(mg/m^3)	Chl-a
Time-lagged Chlorophyll-a local variation (-2 months)	V-Chl-a (-2 m)	none	2.5 arc-min/month	SD log10(mg/m^3)	Chl-a
Nigh-time sea surface temperature local variation (calculated as standard deviation within a 3 × 3 pixel kernel of NSST)	V-NSST	none	2.5 arc-min/month	SD°C	NSST

bias in the POPA dataset by drawing environmental samples from a set of 10,000 randomly chosen vessel data points, thus creating informed models to correct for sampling bias (**Figure 1**).

MaxEnt accepts variables in two formats: (1) gridded, as raster datasets, or (2) in tabulated format, called "samples with data" (SWD) in the MaxEnt jargon (Elith et al., 2011). Raster datasets do not include a temporal dimension and thus models based on gridded datasets cannot account for seasonal changes in the variables. The only way to account for seasonality using gridded datasets is by partioning the data to produce a different model for each season, which in our case was not possible due to low sample sizes. Instead, we used SWD to enable including dynamic variables such as NSST, Chl-a, and variables derived from those. For any given sample, the values for dynamic variables were obtained for the respective month.

Cetacean occurrences and vessel data points were merged with candidate environmental variables in ArcGIS. Occurrences with missing corresponding environmental variables were discarded (**Table 2**).

Monthly (April-September) species distribution maps were produced for all species, from the individual models fitted in MaxEnt, after model tuning (see Supplementary Material S1 for details on model tuning). Dynamic environmental variables used to create those maps (NSST and Chl-a, and derived variables) were based on monthly climatologies covering the study period (2004–2009). Maps were produced by MaxEnt using logistic habitat suitability scores varying from 0 (unsuitable habitat) to 1 (highly suitable habitat), and exported in rasterized format. The multivariate environmental similarity surface (MESS) function in MaxEnt (Elith et al., 2010) was used to test the similarity between environmental conditions found during model fitting and the prediction area. Subsequently, based on the most restrictive results from the MESS analysis (Figure S1), prediction maps for all species were limited to an area within a buffer of 150 nautical miles around the Azores islands (Figure S1). Additionally, we enabled the "fade by clamping" option in MaxEnt to prevent extrapolations outside the environmental range of the training data (Owens et al., 2013). MaxEnt was run in command line mode using scripts, with maximum number of iterations set to 5000 for all models to guarantee model convergence.

The performance of models was assessed using two metrics: (1) the area under the receiver operating characteristic curve metric (AUC), which is threshold-independent (Fielding and Bell, 1997), and (2) the true skill statistic (TSS), which is threshold-dependent (Allouche et al., 2006). Calculations were performed using MaxEnt model outputs and in-built functionalities in biomod2 package for R (Thuiller et al., 2009).

We created test-SDMs for each species by splitting presences into training (90% of occurrences) and test (10% of occurrences) datasets using a 10-fold cross-validation procedure to estimate predictive performance on held-out folds (Elith et al., 2011; Peterson et al., 2011).

The AUC is widely used to assess predictive power of distribution models. In methods using presence-absence data, the AUC expresses the ability of the model to discriminate between suitable and unsuitable habitat (Fielding and Bell, 1997; Wiley et al., 2003). In presence-only methods, however, AUC is interpreted as being a measure of the ability of the model to discriminate between known presences and environmental samples (Phillips et al., 2006).

In presence-absence methods an AUC = 1.0 translates a perfect performance and AUC = 0.5 a performance no better than random (Fielding and Bell, 1997). However, Wiley et al.

TABLE 2 | Presences used to fit SDMs and performance statistics.

		Sightings [count]	Training presences [count]	Training AUC	Test AUC (mean)	Test AUC SD	AUC difference (training–mean test)	AUC difference (training–mean test) [in %]	TSS
Common minke whale	*Balaenoptera acutorostrata*	26	24	0.651	**0.631**	0.95	0.02	3.1	**0.34**
Sei whale	*Balaenoptera borealis*	35	33	0.725	**0.691**	0.128	0.034	4.7	**0.34**
Fin whale	*Balaenoptera physalus*	33	31	0.818	0.794	0.111	0.024	2.9	0.56
Blue whale	*Balaenoptera musculus*	18	17	0.850	0.821	0.135	0.029	3.4	0.61
Sperm whale	*Physeter macrocephalus*	381	338	0.772	0.760	0.44	0.012	1.6	0.42
Cuvier's beaked whale	*Ziphius cavirostris*	21	20	0.776	**0.687**	0.125	0.089	11.5	0.45
Northern bottlenose whale	*Hyperoodon ampullatus*	52	49	0.745	0.728	0.84	0.017	2.3	**0.37**
Mesoplodont beaked whales	*Mesoplodon spp.*	109	96	0.827	0.818	0.49	0.009	1.1	0.52
Bottlenose dolphin	*Tursiops truncatus*	296	240	0.755	0.748	0.46	0.007	0.9	0.42
Atlantic spotted dolphin	*Stenella frontalis*	828	728	0.801	0.798	0.29	0.003	0.4	0.48
Striped dolphin	*Stenella coeruleoalba*	74	69	0.774	0.725	0.123	0.049	6.3	0.43
Short-beaked common dolphin	*Delphinus delphis*	1280	1032	0.731	0.730	0.10	0.001	0.1	0.40
Killer whale	*Orcinus orca*	13	13	0.794	0.802	0.177	0.008	1.0	0.51
Risso's dolphin	*Grampus griseus*	144	97	0.743	0.726	0.98	0.017	2.3	0.40
False killer whale	*Pseudorca crassidens*	30	24	0.714	**0.683**	0.105	0.031	4.3	0.40
Short-finned pilot whale	*Globicephala macrorhynchus*	76	67	0.679	**0.673**	0.72	0.006	0.9	**0.32**

The number of initial sightings for each cetacean taxon is show for reference. The actual number of training presences can be lower than the number of sightings due to spatial filtering and quality control (please see text for explanation). Test AUC and true skill statistic (TSS) scores indicating below moderate predictive performance are shown in bold.

(2003) have shown that for presence-only methods the maximum achievable AUC is area dependent, being a quantity 1−a/2 (where "a" is the fraction of the geographical area covered by the species' unknown true distribution); consequently, in that case, AUC always assumes a value <1 (Wiley et al., 2003; Phillips et al., 2006). A wide range of values is used by different sources to categorize the predictive power of models based on AUC values (Merckx et al., 2011). Here we assumed that models with mean test-AUC values of AUC < 0.7 had poor predictive performance, 0.7 ≤ AUC < 0.8 moderate, and AUC ≥ 0.8 good to excellent performance (Merckx et al., 2011; Peterson et al., 2011; Duan et al., 2014).

Additionally, we investigated model robustness by computing the test-AUC standard deviation (SD) and the difference between the train-AUC values of each species' final SDM (SDM_f; using all presences) and the mean test-AUC values of the SDMs (**Table 2**). Low test-AUC SD and/or small difference between the train-AUC and mean test-AUC values indicate model robustness (Herkt et al., 2016).

Currently there is an open discussion about the reliability of AUC to measure the performance of models based on presence-only methods, and several authors advocate combining different model performance criteria to have a more robust evaluation of the results (Lobo et al., 2008; Merow et al., 2013; Radosavljevic and Anderson, 2014). To have a complementary measure of model performance we calculated the true skill statistic (TSS), which is similar to the well-known Kappa statistic (Fielding and Bell, 1997; Allouche et al., 2006). Similarly to the Kappa statistic, TSS reflects the rate of false positive and negative predictions, but has the advantage of not being sensitive to the frequency of presence points (Allouche et al., 2006). Allouche et al. (2006) defined TSS as:

$$TSS = \text{sensitivity} + \text{specifity} - 1$$

with *sensitivity* translating the proportion of observed presences that are correctly predicted as presences, and *specificity* as the proportion of observed absences that are correctly predicted as absences. Similarly to Kappa, the TSS can assume values between −1 and 1 and values of TSS < 0.2 can be considered as reflecting poor model predictive performance, 0.2 ≤ TSS < 0.4 as fair, 0.4 ≤ TSS < 0.6 moderate, and TSS ≥ 0.6 as good to excellent performance (Landis and Koch, 1977). As TSS is threshold-dependent, the suitability scores returned by MaxEnt must be converted in binary values using a threshold for predicting presence, which was done internally in biomod2 by testing a range of possible threshold values and selecting the value that maximized TSS.

Species Richness Maps

As we were also interested in identifying areas and seasons with conditions for increased cetacean biodiversity, we produced monthly (April–September) cetacean species richness maps. These maps were created by combining (stacking) the individual species prediction maps created in MaxEnt, to produce stacked species distribution models (S-SDMs) for each month evaluated in this study.

Usually, S-SDMs are built by creating binary (present or absent) distribution maps for each species and then calculating the number of predicted species present in a given site (Ferrier and Guisan, 2006). It is clear that the selection of the threshold to transform the continuous outputs from individual SDMs into binary values can heavily influence the predictive performance of the resulting S-SDMs. Thus, this approach must be only used when there is good ecological information to support the choice of the threshold value (Benito et al., 2013). Additionally, since S-SDMs do not account for negative biotic interactions (such as competition and inhibition), the practice of summing binary SDMs tends to lead to overprediction of species richness (Algar et al., 2009; Dubuis et al., 2011). Calabrese et al. (2014) and D'Amen et al. (2015) present convincing evidence that simply summing the per-site predictions of occurrence probabilities from individual SDMs is preferable to the widespread practice of setting arbitrary thresholds to obtain binary predictions and then combining those into a S-SDM.

Here we used the software ENM Tools (Warren et al., 2010) to standardize habitat suitability scores from each species prediction maps so that all scores within the geographic space summed to 1, making predictions comparable among SDMs. The resulting processed maps were then combined in ArcGIS by summing the standardized raw scores from equivalent cells to create the final monthly species relative richness maps. These maps do not intend to give an estimate of how many species are present in a given site, but only where cetacean richness is expected to be higher when compared to adjacent areas.

RESULTS

After quality control and spatial filtering, 84.5% of the sightings (2878) were retained (**Table 2**; **Figure 1**). Of these, nearly 73% belonged to three species: sperm whale (11.7%); Atlantic spotted dolphin (25.3%); and short-beaked common dolphin (35.9%). Of the 16 SDMs, 14 were based on 20 occurrences or more, and the remaining on more than 10 occurrences (**Table 2**).

The majority of the SDMs presented moderate to good discrimination power, with test-AUC scores ≥0.7 ($n = 11$), and TSS scores ≥0.4 ($n = 12$) (**Table 2**). Overall, there was good agreement among the two metrics: models with low test-AUC scores tended to also have low TSS values (although always well above 0.2), moderate test-AUC corresponded to moderate TSS values and the highest test-AUC scores tended to correspond to high TSS scores (**Table 2**). However, based on the TSS scores, only one model (for the blue whale) was considered as having above than moderate performance, compared to three models based on the test-AUC scores (**Table 2**).

The difference between mean AUC values from test-SDMs and the corresponding training AUC from the SDM_f was low (mean: 2.9%; median: 2.3%; **Table 2**) and most models had low test-AUC SD, comparable with similar multi-species studies (e.g., Herkt et al., 2016), indicating overall model robustness.

From the 18 variables initially considered, only half had a permutation importance score >5 and were considered as having a meaningful role in defining the environmental niche for the species (please refer to Supplementary Material S1 for definition of permutation importance and its use in variable selection). No single variable was retained in all models. The variable most commonly retained in the models was distance to shore (retained in 12 models), followed by the time-lagged Chlorophyll-a local variation 2 months prior to the sighting month (9 models), and Chlorophyll-a concentration from the previous month to the sighting date and nighttime sea surface temperature (8 models each). The remaining variables were retained in 2–6 models (**Table 3**).

DISCUSSION

Interpretation of Models

Giving full treatment of each species here is unpractical and beyond the scope of this work. Instead we summarize the main findings for four functional species groups according to phylogeny and ecology: (1) baleen whales (genus *Balaneoptera*); (2) sperm and beaked whales (genera *Physeter*, *Mesoplodon*, *Hyperoodon*, and *Ziphius*); (3) small Delphinids (genera *Delphinus*, *Stenella*, and *Tursiops*); and (4) large Delphinids (genera *Globicephala*, *Grampus*, *Orcinus*, and *Pseudorca*). Where relevant we highlight important results of individual taxa.

As an illustrative example, we present the model projections of potential species distribution for the Atlantic spotted dolphin in **Figure 2**. All 96 monthly (April-September) maps of potential species distribution based on the MaxEnt final SDMs, as well as the 34 maps for species richness are freely available online as raster grid files from the Pangaea database: https://doi.org/10.1594/PANGAEA.864511.

Baleen Whales

The spatio-temporal patterns of the four species in this group were quite variable, probably due to different dietary preferences, energetic requirements, and species migratory behaviors. Potential distribution for the minke whale (*Balaenoptera acutorostrata*) was essentially homogenous throughout the region and the period analyzed. The model for that species was chiefly driven by local variation in the night-time sea surface temperature and, at a much lower extent, by depth (**Table 3**). These results are in line with results reported by Silva et al. (2014) who did not find any apparent seasonal pattern for the species from stranding records. However, the model had the lowest AUC scores of all models and also one of the lowest TSS scores, and should be interpreted with reserve. Blue (*B. musculus*) and fin (*B. physalus*) whales' potential habitat differed seasonally with a strong latitudinal component, driven in great part by temporal variation in the primary productivity in the region, but also water temperature in the case of the fin whale. In contrast to the blue and fin whale models, the sei whale (*B. borealis*) model did not retain variables related to primary production (**Table 3**). In combination these results agree with previous work suggesting that the region may play different ecological roles for migrating baleen whales, being a foraging area for blue and fin whales but only a transit area for sei whales (Silva et al., 2013; Prieto et al., 2014). A more in-depth interpretation of the models for the blue, fin and sei whale is given in Prieto et al. (2016).

Sperm and Beaked Whales

Sperm (*Physeter macrocephalus*) and beaked whales are all deep diving cetaceans and are often considered to be essentially teutophagous (Mead, 2002). However, recent research has shown that beaked whales may show dietary plasticity (MacLeod et al., 2003). In the Azores, the diet of Sowerby's beaked whale (*Mesoplodon bidens*) is composed essentially of meso- and bathy-pelagic fish, with little contribution from cephalopods (Pereira et al., 2011). Night-time sea surface temperature was retained in the models of all species in this group and, apart from the sperm whale, was highly influential in the models consistent with a seasonal presence of beaked whales in the region (**Table 3**). From combined survey and stranding data Silva et al. (2014) report an almost year-round presence of *Mesoplodon* and Cuvier's (*Ziphius cavirostris*) beaked whales, with a peak in summer months. The same authors recorded the presence of the northern bottlenose whale (*Hyperoodon ampullatus*) only during the summer months. These results are in agreement with our results that show improving habitat conditions for all beaked whales with progression of the summer months. Beaked whales can be considered cryptic, as sightings of this group are heavily affected by sea conditions (e.g., Waring et al., 2008). The apparent improvement of habitat suitability with progression of the season predicted by the models can be an artifact of higher detectability during summer months. The model for the Cuvier's beaked whale had the largest drop in AUC mean value of test-SDM when compared with the AUC of the SDM_f (11.5%). Thus, predictions based on this model should be interpreted with some reserve.

The sperm whale model had the highest number of variables retained among all models (**Table 3**), indicating that their environmental niche in the region is dependent on the combination of several conditions, possibly related to different life-history requirements. The variable that contributed most to the sperm whale model was the time-lagged Chlorophyll-a local variation (2 months prior to sighting month), which may be an indication that they associate with oceanographic structures that enhance biological productivity. Chlorophyll concentration of the prior month to the sighting month was also included in the model. Other studies have found primary productivity to be a good predictor of sperm whale distribution, despite being a distal predictor due to large spatial and temporal lags between the onset of primary productivity and cephalopod presence (Jaquet, 1996; Jaquet and Gendron, 2002; Praca et al., 2009). Morato et al. (2008b) report that sperm whale sighting frequencies in the Azores were not influenced by distance to seamounts. In contrast, Waring et al. (2008) report that sightings of sperm whales made along the mid-Atlantic ridge in the summer of 2004, were usually made at the tops of seamounts and rises. This apparent contradiction may be due to the effect of differing feeding ecologies of male and female sperm whales. Most of the sperm whale sightings reported by Waring et al. (2008) were made north of 50° North, where only male sperm whales are supposed to occur (Whitehead, 2009). While female sperm whales feed mostly on cephalopods, males have a more catholic diet that may include large demersal fish (Whitehead, 2009). Our results are in agreement with those reported by Morato et al. (2008b), seamount presence was not retained in the sperm whale model

TABLE 3 | Functions and environmental variables used to build final SDMs, after model tuning, by species.

Species	Functional group	Functions used to fit models	Variable Permutation Importance (PI)								
			Depth	NSST	Chl-a	Distance to shore	d-Seamounts	Chl-a (−1 m)	Chl-a (−2 m)	V-Chl-a (−2 m)	V-NSST
Balaenoptera acutorostrata	Baleen whales	LQ	16.7	–	–	–	–	–	–	–	83.3
Balaenoptera borealis		LQ	–	49.8	–	27.6	–	–	–	–	22.6
Balaenoptera physalus		LQ	–	62.6	–	–	–	28.6	8.8	–	–
Balaenoptera musculus		LQ	–	–	–	13.9	–	47.2	24.4	–	14.5
Physeter macrocephalus	Sperm and beaked whales	LQP	10.5	5.4	–	16.2	13.7	13.3	–	40.9	–
Ziphius cavirostris		H	–	47.4	–	19.8	–	32.8	–	–	–
Hyperoodon ampullatus		LQ	55.5	39.2	–	–	–	–	5.3	–	–
Mesoplodon spp.		LQP	–	33.1	–	31.5	–	–	–	35.4	–
Tursiops truncatus	Small *Delphinids*	LQP	27.1	24.2	–	19.7	–	–	–	29	–
Stenella frontalis		LQP	–	41	–	10.7	6.7	7.3	–	34.3	–
Stenella coeruleoalba		H	–	–	–	32.1	–	25.8	–	31.3	10.8
Delphinus delphis		LQP	–	–	18.4	21.6	10.9	-	–	38.3	10.8
Orcinus orca	Large *Delphinids*	LQ	–	–	–	13.4	50.4	-	–	36.2	–
Grampus griseus		LQ	–	–	9.3	14.8	–	27.5	–	48.4	–
Pseudorca crassidens		LQ	36.6	–	–	41.7	–	21.7	–	–	–
Globicephala macrorhynchus		LQ	36.5	–	–	–	–	–	–	63.5	–
n			6	8	2	12	4	8	3	9	5
Mean PI score			30.5	37.8	13.9	21.9	20.4	25.5	12.8	39.7	28.4
Median PI score			31.8	40.1	13.9	19.8	12.3	26.7	8.8	36.2	14.5

The final permutation importance reported by MaxEnt for each variable (PI; please refer to Supplementary Material S1 for explanation) is presented, along with the number of models (n) using that variable and the mean and median variable PI values across models. Variables not selected in any model were not included in this table. Please refer to the main text for variable acronyms. Types of functions: linear (L), quadratic (Q), product (P), hinge (H).

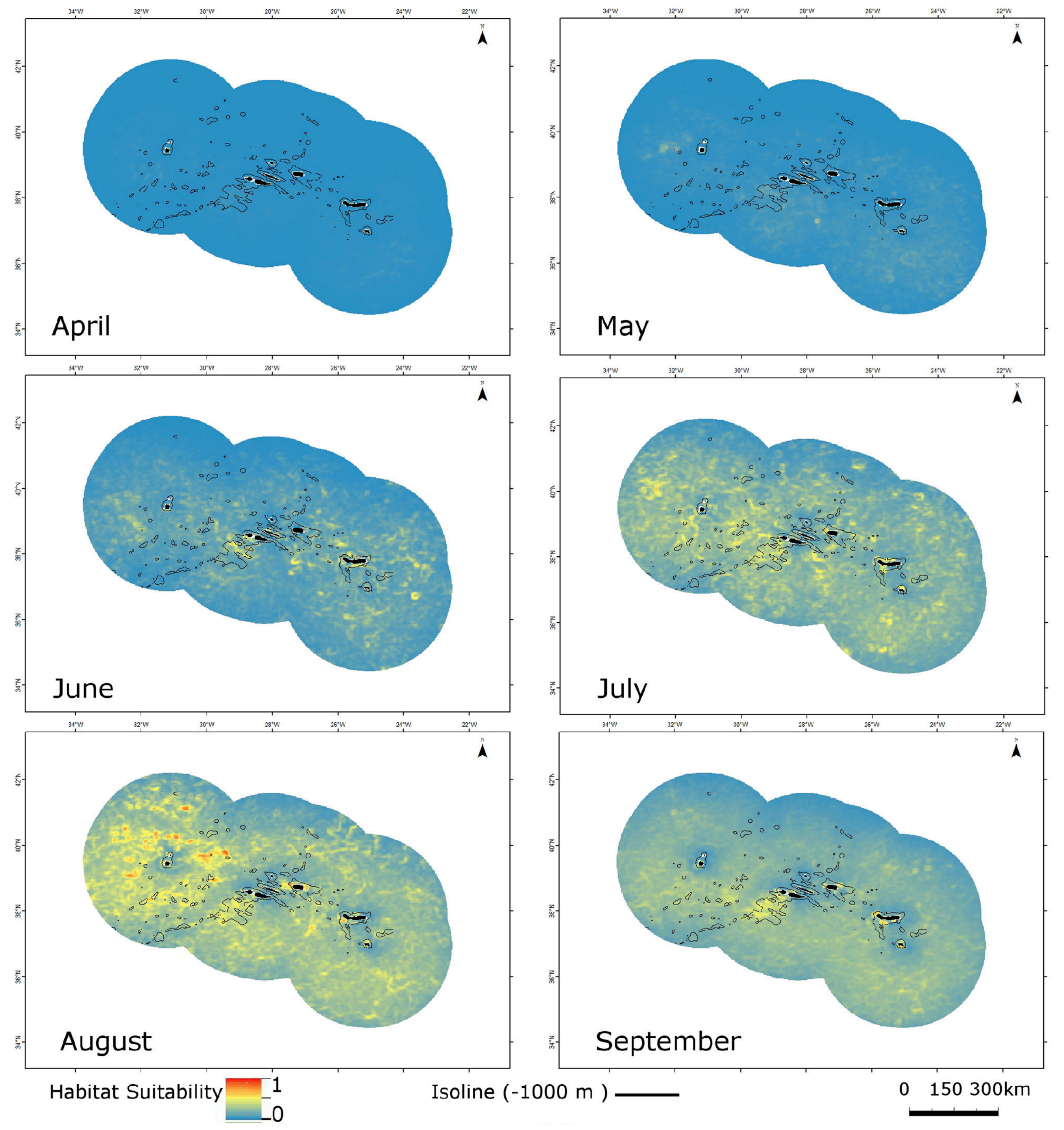

FIGURE 2 | Monthly potential distribution (April-September) of the Atlantic spotted dolphin (*Stenella frontalis*), from MaxEnt modeled habitat suitability. Warmer colors correspond to increased habitat suitability. The 1000 m isoline is indicated by the thin black lines.

(or in any other model for that matter). However, seamount density was retained in the model, with a reasonably high permutation importance (13.7; **Table 3**). In fact, the potential distribution maps for the sperm whale highlight some seamount complexes as preferential habitat, especially during spring and early summer months. One possible explanation for the retention of this variable in this and other models is that seamount density reflects increased topographic complexity that may be important at creating physical processes that aggregate enough productivity to attract visitors (Morato et al., 2015).

Small Delphinids

All models for the small dolphins retained distance to shore and time-lagged Chlorophyll-a local variation (**Table 3**). Our results highlight a succession pattern in the seasonality of the common (*D. delphis*) and spotted (*Stenella frontalis*) dolphins that had already been detected by Silva et al. (2014). Both species present a marked seasonality, but while the potential distribution of the common dolphin compresses with the progression of the summer, the potential distribution of the spotted dolphin expands. Silva et al. (2014) suggested that the phenomenon could be related with the effect of the warming water on prey distribution, or to strategies for reducing interspecific competition for prey. The retention of SST and Chl-a derived variables in both models does not allow to identify which of these mechanisms may be at play. As the season progresses the potential distribution of the common dolphin becomes restricted to some seamount complexes, indicating that seamounts may play an important role in maintaining conditions for the occurrence of the species in the region throughout the year. Morato et al. (2008b) report that the common dolphin was significantly more abundant in the vicinity of shallow seamounts, supporting our results.

The model for the striped (*S. coeruleoalba*) shows a strong variation of the potential habitat with season. Silva et al. (2014) report an almost continuous presence of the striped dolphin in the Azores, with higher encounter rates between May and July. Our results indicate that the distribution of the striped dolphin is strongly influenced by water temperature, as night-time sea surface temperature was the most important variable in that model (**Table 3**). This result might explain the higher encounter rates in early to mid-summer detected by Silva et al. (2014).

The bottlenose dolphin (*Tursiops truncatus*) model also indicates an effect of the season on the distribution of the species. As expected from the presence of resident animals near the islands (Silva et al., 2008), physiographic variables (distance to shore and depth) were influential in the bottlenose dolphin model, along with variables indicative of productivity distribution (**Table 3**). However, our model shows an expansion of the potential habitat to offshore areas up to August, and then a contraction in September.

Silva et al. (2008) report a complex pattern of residency for the bottlenose dolphin in the Azores, including residents, transients and temporary migrants. Despite a continuous presence in the region, Silva et al. (2014) reported that encounter rates with the bottlenose dolphin "varied greatly between months," and suggested that fluctuations in encounter rates might be caused by the temporary immigration of non-resident [transient] dolphins. According to Silva et al. (2008), resident bottlenose dolphins have small, near-shore, home-ranges in disagreement with the expansion of the potential habitat predicted by the model. However, large-scale movements among islands and to offshore banks were recorded for non-resident bottlenose dolphins (Silva et al., 2008). The study by Silva et al. (2008) could not test for an effect of season on the occurrence of large-scale movements but the authors hypothesized that these movements were a response to the low density and patchy distribution of prey. Seasonal immigration of transient bottlenose dolphins combined with wider ranging behavior by non-resident dolphins during part of the year could explain the fluctuations in the extent of potential habitat predicted by our model for the species.

Large Delphinids

The predictions for the four species in this group varied substantially. Based on their feeding ecology, the Risso's dolphin (*Grampus griseus*) and the short-finned pilot whale (*Globicephala macrorhynchus*) can be considered more similar to each-other, as they are both deep divers and prey preferentially on cephalopods (Baird, 2009a; Olson, 2009). On the other hand, the killer whale (*Orcinus orca*) and the false killer whale (*Pseudorca crassidens*) are both top predators with generalist diets that can include cephalopods, large fish and also marine turtles and other marine mammals (Baird, 2009b; Ford, 2009). The Risso's dolphin model indicates an expansion of the potential distribution up to June and then a contraction after that month. Coastal habitats, however, seem to be important during most of the period, which may be related to the presence of resident groups using these areas as foraging, calving and nursing habitats (Hartman et al., 2014, 2015). In contrast, the short-finned pilot whale model indicates a potential distribution that is spatially and temporally homogeneous. However, the short-finned pilot whale model had poor performance, based both on the AUC and TSS scores, and should be interpreted with reserve. Additionally, and despite our data quality control, it cannot be ruled out that some sightings attributed to this species are in fact of its sister species (*Globicephala melas*), that sometimes is seen in the region and is almost indistinguishable from the short-finned pilot whale at sea (Prieto and Fernandes, 2007). The killer whale model was chiefly influenced by seamount density and, to a much smaller extent distance to shore, with no temporal pattern being detectable. Based on combined sighting and strandings data, Silva et al. (2014) also failed to detect any temporal trend for this species. Finally, the false killer whale model shows a potential distribution highly influenced by the mid-Atlantic ridge and seamounts or seamount-like structures.

Cetacean Richness

When all species are considered together, the distribution of areas with increased relative species richness is somewhat diffuse, showing great spatial and temporal variation (**Figure 3**). This is not surprising taking into consideration the wide differences in trophic ecology and natural history among the 16 taxa and the fact that most species in this study have predominantly pelagic habits. Not surprisingly, since it was based in the same dataset, the encounter rates maps in Silva et al. (2014) also show a great heterogeneity in the distribution patterns of cetaceans in the region. However, our models show seasonal effects that could not be detected with the methodology utilized by Silva et al. (2014).

Pelagic habitats are a function of complex oceanographic processes that can be highly dynamic in space and time (Hazen et al., 2013; Scales et al., 2014). Pelagic features can be classified in three categories according to their predictability: static bathymetric, persistent hydrographic and ephemeral hydrographic features (Hyrenbach et al., 2000). Most marine top predators are known to track productivity associated with meso-

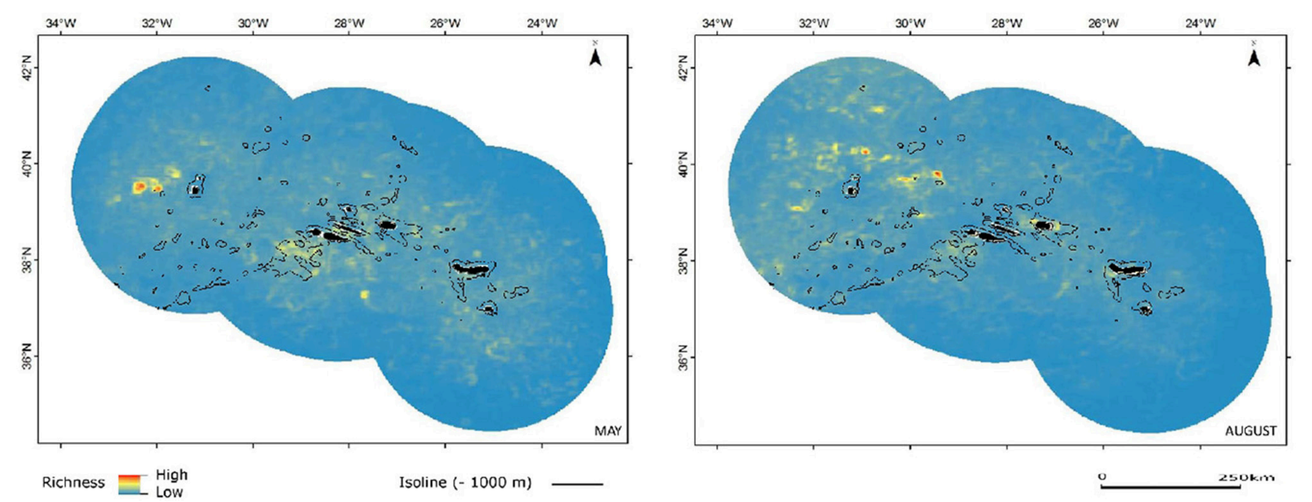

FIGURE 3 | Combined predicted cetacean richness in spring (May) and summer (August). Color shading indicates relative species richness, with warmer colors corresponding to increased richness.

and sub-mesoscale oceanographic structures (fronts, eddies, and filaments) that are often transient in nature (Tew Kai et al., 2009; Scales et al., 2014). However, static seabed features may influence and even originate persistent hydrographic features, which can lead to the creation of predator hotspots (Bouchet et al., 2015). That effect is apparent from our predictions, more notably for small and large dolphins, over the seamount complex located southwest of the central group of islands in the Azores, identifiable by the 1000 m isoline (**Figures 5**, **6**).

The richness maps organized by functional groups (**Figures 4–7**) offer a more focused perspective, helping to better interpret the results.

The relative species richness maps from all baleen whale models combined are marked by the strong latitudinal component from the individual blue and fin whale models. The combined predictions do not show any evident affinity of baleen whales as a group to specific oceanographic or topographic but the latitudinal progression of conditions is clearly seen when comparing predictions for spring and summer months (**Figure 4**).

The maps of relative species richness for small and large Delphinids show the likely influence of transient oceanographic structures, translated by temporary sites of increased richness with filamentous or circular configuration. However, for both groups the species richness is increased also in coastal zones of some of the islands and, as mentioned earlier, around and over seamount complexes, as in the case of the seamounts just southwest of the central group of islands, but also around other seamount and seamount-like structures (**Figures 5**, **6**).

Combined sperm and beaked whale richness seems to be also increased by transient oceanographic features, seen as temporary sites of increased richness with filamentous or circular configuration (**Figure 7**). There seems to be an apparent, although difficult to discern, effect of seamount complexes in increasing richness for this group (**Figure 7**). However, and unlike the results for most of the dolphins, the sperm and beaked whales models show lowest habitat suitability in the shallowest areas over seamounts and seamount-like structures, as well as coastal areas. Instead, the richness appears to increase in deeper waters, which is in agreement with the deep diving habits of the taxa in this group (**Figure 7**).

Overall, the relative species richness maps highlight the fact that cetaceans utilize large areas and actively seek dynamic oceanographic features believed to be associated with increased biological productivity, making the identification of delimited priority areas a complex task. However, our results do show areas that hold increased species richness, such as some seamount complexes and coastal areas around islands, deserving special treatment regarding management of human activities that may threaten cetaceans.

Performance and Caveats of Models

By choosing a modeling technique specifically designed to handle presence-only data (MaxEnt), carefully implementing a data quality control and tuning models for each species individually, we were able to build plausible habitat suitability models, using existing sighting data collected with a consistent methodology by an observer fisheries program (POPA).

Model evaluation metrics indicate that, overall, models had reasonable performance, and are useful both for ecological studies and to support decision making. The majority of the models showed moderate discrimination power (based on test-AUC values and the true skill statistic) and appropriate robustness (based on prevailing low SD in test-AUC values and small differences between AUC from the SDM_f and test-AUC). However, there is ample space for improvement in future revisions of these models.

Data quality control dictated that some models had to be fitted with low number of occurrences (<20). Although MaxEnt has been repeatedly shown to perform well at small sample

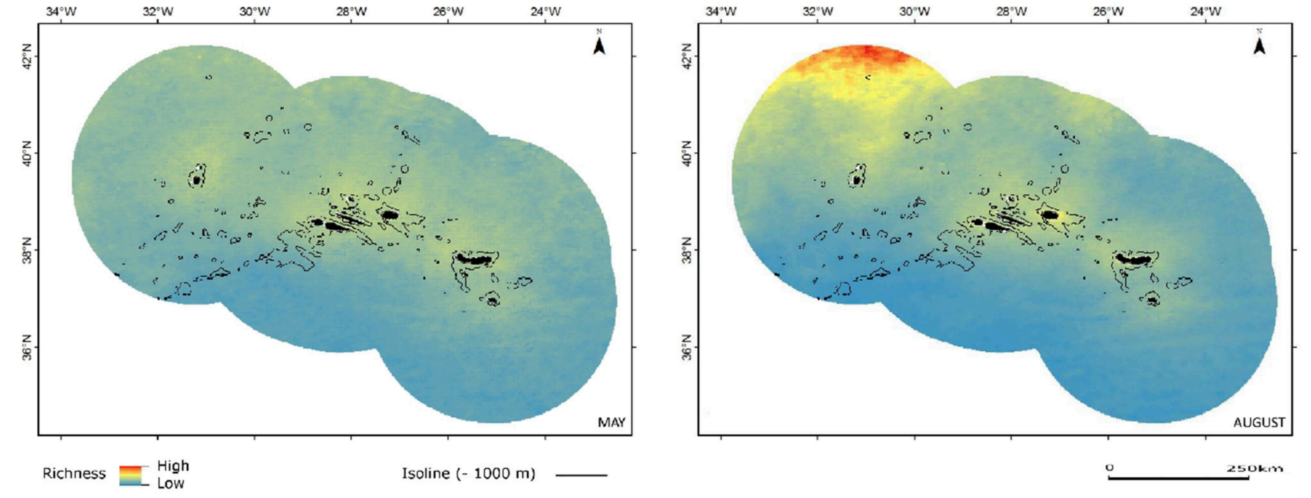

FIGURE 4 | Combined predicted richness of baleen whales in spring (May) and summer (August). Color scheme as in **Figure 3**.

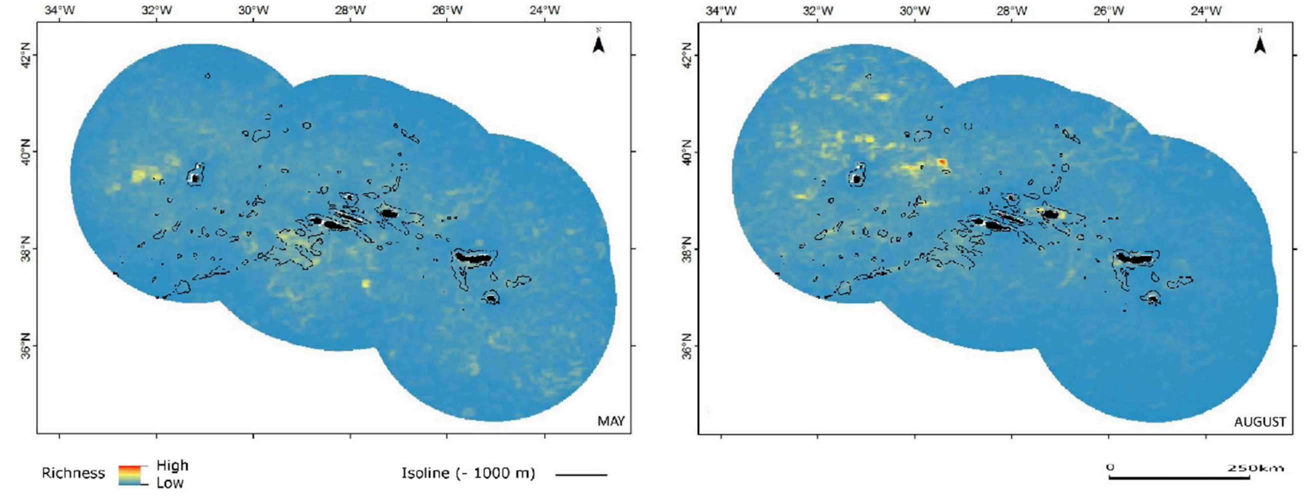

FIGURE 5 | Combined predicted richness of small dolphins in spring (May) and summer (August). Color scheme as in **Figure 3**.

sizes, models using few occurrences can yield inconsistent results (Wisz et al., 2008; Aguirre-Gutiérrez et al., 2013). Additionally, we could only carry out internal evaluations of performance as no independent dataset was available. Ideally spatially independent data should be used for evaluating model performance, since performance metrics are inflated by the effect of spatial autocorrelation between training and test data (Bahn and McGill, 2013). It is likely that the performance metrics we used are positively biased, by the combined effects of small sample size and the lack of an independent test dataset (Randin et al., 2006; Bean et al., 2012). We intend to address those issues in future revisions of the models.

An important, although subjective, part of model evaluation is visually examining fitted functions and mapped projections to detect unexpected model responses or predictions (Elith et al., 2010). As mentioned above, we carefully inspected fitted functions plots (partial dependence plots; Supplementary Material S2) as part of the tuning process (detailed in Supplementary Material S1) and evaluated the ecological coherence of the function plots for each variable and species. Despite some minor artifacts, the mapped projections did not produce any unrealistic patterns, improving our confidence on the models. Nevertheless, when creating the models we had to make some assumptions that may have affected the estimation of the relationships with environmental covariates, at least for some species. Due to small sample sizes, we could not subset the data to create seasonal models; instead we created a single model for each species and then projected that model onto the environmental conditions of different months. In doing so, we assumed that the habitat preferences of the species do not drastically change with

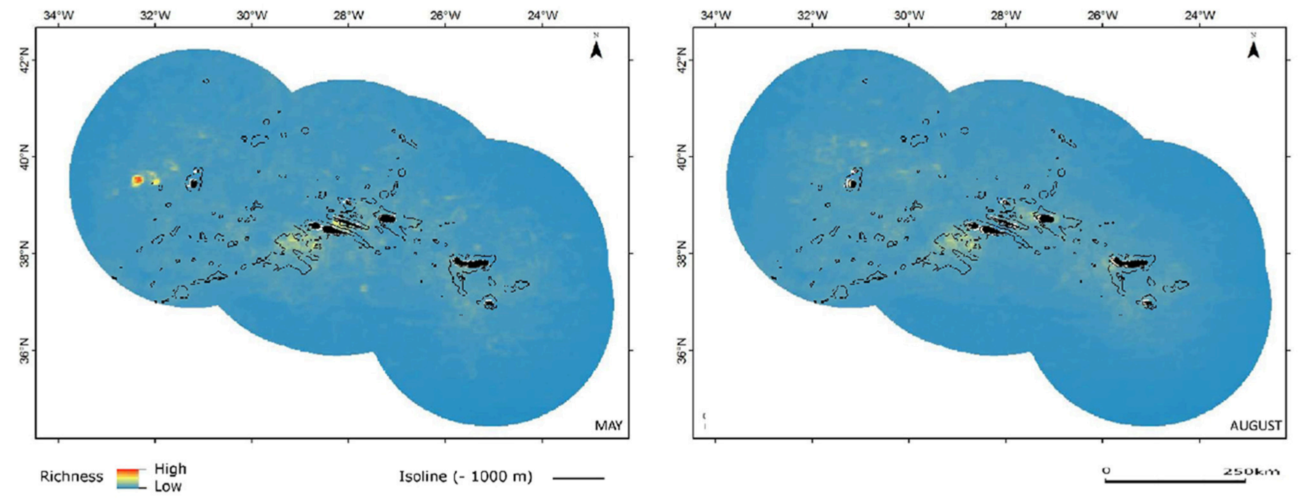

FIGURE 6 | Combined predicted richness of large dolphins in spring (May) and summer (August). Color scheme as in **Figure 3**.

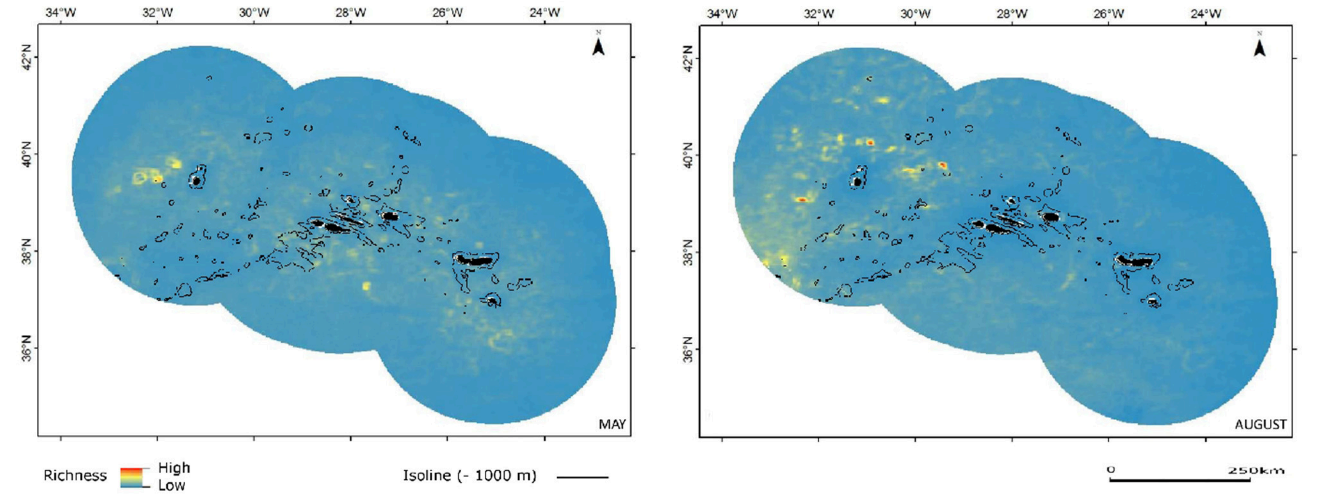

FIGURE 7 | Combined predicted richness of sperm and beaked whales in spring (May) and summer (August). Color scheme as in **Figure 3**.

time. If that assumption is not met the relationships estimated by the models may be biased. Granted more sightings are available, this issue can be investigated and addressed in the future by creating models for distinct seasons.

There may also be an effect of using climatologies to project the models that could potentially affect predictions. Since the data from dynamic variables used to fit the models were quasi-contemporaneous (same month) to the sightings, these data will present more variability than the climatologies used to project the models (which will smooth out interannual variability). In extreme cases that effect could be an issue because the predicted habitat suitability will tend to be underestimated (or overestimated). For example, if a variable was low for most of the years and high in 1 year, and if the species was present only in that particular year, the model would fit a relationship to that variable and depending on the modeled relationship the predictions could be unreasonable. The predictions could indicate that the habitat suitability for the species in the region is low (due to the smoothing effect of the climatologies), when in fact it would be high during years with more extreme conditions. This issue would be more concerning for species for which the Azores are positioned in the limits of their geographical range, such as the Bryde's whale (*Balaenoptera edeni*), the Fraser's dolphin (*Lagenodelphis hosei*) and the rough toothed dolphin (*Steno bredanensis*), all tropical species that are rare visitors to the region (Silva et al., 2014). However, we did not include species considered as rare visitors to the region in this work. We find highly unlikely that our models were fit to extreme values, because all species for which models were fit were present in multiple years.

To the best of our ability, we tried to follow the principle of using explanatory covariates that are reasonably proximal to the target species (Austin, 2002). For example, we included water temperature (NSST) as a covariate in our models because cetacean distribution is highly influenced by thermal preferences (MacLeod, 2009; Lambert E. et al., 2014). Additionally we implemented a methodology for eliminating variables with marginal predictive importance, in order to obtain the most parsimonious SDMs possible. However, we were limited by the currently available variables. Prey abundance and quality directly influence cetacean distribution, and as such should ideally be included in SDMs as proximal predictors (Guisan and Zimmermann, 2000; Young et al., 2015). However, that information was not available and it can take years before it will be. Instead, we used Chlorophyll-a (Chl-a) and the derived variables as proxies for prey distribution. These variables may have limited explanatory power due to potential large lags between oceanographic processes and biological response of cetacean prey, especially in the case of upper trophic level cetaceans (Lambert C. et al., 2014). In the future we intend to integrate prey data by fitting a 3-dimentional model for mid-trophic organisms to the Azores pelagic ecosystem conditions and then nesting it into our own SDMs (Lehodey et al., 2010; Lambert C. et al., 2014).

We also intend to include a wider range of dynamic covariates, once they are available, in order to identify areas of predictable or persistent oceanographic activity that are potentially important for cetaceans and that were not detected with our original set of covariates. For example, the inclusion of fine-scale information on circulation patterns derived from models tunned at the regional scale (e.g., Sala et al., 2015) could help interpreting some of the spatial patterns and variability shown by the models.

CONCLUSIONS

High-resolution species distribution data for marine taxa are still scarce but essential in ecosystem functioning research and to implement ecosystem-based management through marine spatial planning (MSP) (Beck et al., 2012; Shucksmith et al., 2014). Here we present the first SDMs for 16 cetacean taxa at the scale of the entire Azores archipelago up to 150 nautical miles from shore, at a fine spatial resolution. We also produced cetacean relative richness maps that may both inform MSP efforts by highlighting discrete important areas for cetaceans and help identify potential local processes influencing large-scale macroecological patterns (Belmaker and Jetz, 2011).

Species distribution models are valuable in identifying areas that can be effective in protecting marine predators (Pérez-Jorge et al., 2015; Young et al., 2015). Our models show areas (namely near or over seamounts) that appear to hold favorable conditions to the occurrence of some of the species investigated in this study, especially among dolphins. These areas should deserve special attention when considering MSP actions. Nevertheless, our results also highlight the fact that cetacean distribution can vary widely at relatively short periods of time as they track dynamic oceanographic structures. Any effort at protecting cetaceans and their habitats must take the temporal dimension into account. Dynamic ocean management (DOM) is a relatively recent concept that aims to refine the temporal and spatial scales of managed areas by integrating near-real time biological, oceanographic and socio-economic data (Maxwell et al., 2015). We acknowledge that DOM still faces several challenges for widespread application as it has only been tested on a few systems and for few species, and requires a large amount of resources (Maxwell et al., 2015; Mills et al., 2015). However, we argue that we must take steps in the direction of integrating DOM with more traditional MSP approaches if we are to effectively protect pelagic species with very dynamic distributions, especially in face of predicted effects of climate change (Fulton et al., 2015).

Our models provide a new baseline regarding the spatial and temporal distribution patterns of cetaceans in a vast area of the Azores marine ecosystem. However, they lack some essential information about species density and abundance. In the future, efforts should also be made to regularly collect data under conditions that enable the application of more sophisticated modeling techniques such as density surface modeling (DSM) and multi-species DSM (Kissling et al., 2012). Data for other seasons are also lacking and efforts should be made to fill that gap.

At the core of the SDMs presented here are the data collected by POPA. Despite not being designed as a cetacean monitoring program, POPA has two great advantages: it is a long-term dataset and follows a consistent methodology. As this work has shown, using data collected from fisheries observer programs such as POPA can be a cost-efficient way of developing robust SDMs. In the future, we also plan to explore the possibility of applying novel field and statistical methods to enable using POPA sighting data to provide reliable estimates of cetacean abundance and density (Williams et al., 2006; Paxton et al., 2011; Isojunno et al., 2012).

AUTHOR CONTRIBUTIONS

Conceived and designed the experiments: MAS, MT, RP. Performed the experiments: MT, RP. Analyzed the data: MT, RP, MAS Contributed with data: MM. Wrote the paper: MT, RP, MAS, MM.

ACKNOWLEDGMENTS

We thank the Azores Fisheries Observer Program (POPA), which is funded by the Azorean Regional Government, and acknowledge the collaboration of all the observers, captains, and crew members of tuna vessels. We are grateful to Inês Seabra, Irma Cascão, and Ricardo Medeiros for assistance with the POPA dataset and with the Geographic Information System. This work was supported by FEDER funds, through the Competitiveness Factors Operational Programme - COMPETE, by national funds, through FCT - Foundation for Science and Technology, under project TRACE (PTDC/ MAR/74071/2006), and by regional funds, through DRCT/SRCTE, under projects

MAPCET (M2.1.2/F/012/2011) and 2020 (M2.1.2/I/026/2011). We acknowledge funds provided by FCT to MARE, through the strategic project UID/MAR/04292/2013. RP is supported by an FCT postdoctoral grant (SFRH/BPD/108007/2015); MAS is supported by Program Investigator FCT (IF/00943/2013) and MT was supported by a research fellowship under the Exploratory project (IF/00943/2013/CP1199/CT0001) that also paid the fees for this open-access publication. IF/00943/2013 and IF/00943/2013/CP1199/CT0001 are funded by FSE and MCTES, through POPH and QREN.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2016.00202

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

DATA REPORT
published: 20 October 2016
doi: 10.3389/fmars.2016.00204

Seafloor Characteristics in the Azores Region (North Atlantic)

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Keywords: Azores, seafloor characteristics, bathymetry, deep sea, geomorphology, GIS dataset

Current European legislation such as the Marine Strategy Framework Directive (MSFD; 2008/56/EC) has highlighted the need for accurate maps on the geomorphology of Europe's maritime territory. Such information is notably essential for the production of habitat maps and cumulative impact assessments of human activities (Halpern et al., 2008) necessary for marine spatial planning initiatives (Gilliland and Laffoley, 2008) and assessments of the representativity/sufficiency of marine protected areas networks like Natura 2000. Broadscale satellite bathymetry presently allows the identification of all prominent geomorphic structures present on the seafloor with a high grade of accuracy. However, these datasets and maps still need to be more widely disseminated in the scientific community.

In this contribution, we provide an inventory of some important datasets related to the physical characteristics of the seafloor surrounding the Azores Archipelago. The objective is to ensure that our compilation is readily available for any researchers interested in developing species distribution models, or for the management and conservation of natural resources in the region.

In total, we produced and compiled 18 layers of seabed characteristics for the Azores region (**Table 1**), deposited at Pangaea, Data Publisher for Earth and Environmental Science (Perán Miñarro et al., 2016).

The Azores area is located in the North Atlantic Ocean between 28°00′ N – 49°00′ N, and 17°00′ W – 41°00′ W with an extension of approximately 8,051,544 km^2 that includes the Exclusive Economic Zone (EEZ) along with the Portugal's claimed extended continental shelf area around the archipelago (**Figure 1**).

Several seafloor geomorphic variables were produced through the different geoprocessing tools: Slope, Aspect, Northness, Eastness, Vector Ruggedness Measure (VRM), Plan Curvature, Profile Curvature, Total Curvature, Surface-area, Surface-ratio, Hillshading, MDOW-Hillshade (Multidirectional Oblique-Weighed) and broad/fine scale Bathymetric Position Index (BPI). All these bathymetric derivatives (**Table 1**) were based on the Global Bathymetry and Elevation Data at 30 Arc Seconds Resolution (SRTM30_PLUS; Becker et al., 2009) and computed in ArcGIS using a combination of two geoprocessing add-ons; Benthic Terrain Modeler (Wright et al., 2005) and Digital Elevation Model Surface Tools (Jenness, 2004).

Using SRTM30_PLUS (**Figure 1A**), we also provide a layer that delimits the depth-based biological zones proposed by Howell (2010). Four different biological zones were mapped: sublittoral (0.05% of the seafloor in our study area), upper slope (0.29%), upper bathyal (0.42%), mid bathyal (2.95%), lower bathyal (9.94%), and abyssal (86.28%).

The diversity of the different geomorphologic structures present in the study area (**Figure 1B**) was obtained through the recently completed digital Global Seafloor Geomorphic Features Map (GSFM; Harris et al., 2014).

In their study, Harris et al. (2014) present seafloor geomorphology as a hierarchy of base layers for the shelf, slope, abyss and hadal zones, which are further divided into classification layers and discrete feature layers, sometimes overlaying each other. The Azores area considered

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Specialty section:
This article was submitted to Deep-Sea Environments and Ecology, a section of the journal Frontiers in Marine Science

Received: *05 July 2016*
Accepted: *30 September 2016*
Published: *20 October 2016*

Citation:
Peran AD, Pham CK, Amorim P, Cardigos F, Tempera F and Morato T (2016) Seafloor Characteristics in the Azores Region (North Atlantic). Front. Mar. Sci. 3:204. doi: 10.3389/fmars.2016.00204

TABLE 1 | Layers on the characteristics of the seafloor in the Azores.

Layer	Description	Source	Processing tool
Bathymetry	Seafloor depth	SRTM30_PLUS	–
Slope	Maximum seafloor depth gradient	SRTM30_PLUS	DEM Tools
Aspect	Direction of maximum slope	SRTM30_PLUS	DEM Tools
Northness	Orientation of the slope (cosine of aspect)	SRTM30_PLUS	Benthic Terrain Modeler
Eastness	Orientation of the slope (sine of aspect)	SRTM30_PLUS	Benthic Terrain Modeler
Vector Ruggedness Measure (VRM)	Index reflecting the variability of slope and aspect in a single measure	SRTM30_PLUS	Benthic Terrain Modeler
Plan Curvature	Variable representing the concave, convex or linear profile of the substrate perpendicularly to the slope. A positive value indicates the surface is sidewardly convex at that cell, while negative values indicate the surface is sidewardly concave. A value of zero indicates the surface is flat across-slope. PlC emphasizes convergence and divergence of along-slope flows	SRTM30_PLUS	DEM Tools
Profile Curvature	Profile curvature is extracted along to the direction of the maximum slope. A negative value on a given cell indicates that the surface is upwardly concave. Instead, positive values indicate surfaces that are upwardly convex. A value of zero indicates that the surface is linear (i.e., slope does not change along-slope). PrC emphasizes the ridges, valleys and terraces on a surface. It is also an indicator of the acceleration and deceleration of gravitational flows, which influences erosion and deposition processes	SRTM30_PLUS	DEM Tools
Total Curvature	Total curvature or general curvature is the second derivative of the surface (or the slope-of-the-slope). It is extracted on a cell-by-cell basis taking into account its eight surrounding neighbors. It considers both plan and profile curvature together, permitting a more accurate understanding of flow patterns across a surface	SRTM30_PLUS	DEM Tools
Surface-area ratio	Seafloor topographic roughness/irregularity index calculated by dividing the surface area value of a gridcell (taking into account its slope gradient) by its planimetric area	SRTM30_PLUS	DEM Tools
Bathymetric Position Index (BPI) (Broad-scale)	The BPI is a measure of where a referenced location is relative to the locations surrounding it. The BPI is derived from an input bathymetric data set and itself is a modification of the topographic position index algorithm that is used in terrestrial environment. The Broad-scale BPI (inner radius of 25 and outer radius of 250) identifies larger features within the seafloor	SRTM30_PLUS	Benthic Terrain Modeler
Bathymetric Position Index (BPI) (Fine-scale)	The BPI is a measure of where a referenced location is relative to the locations surrounding it. The BPI is derived from an input bathymetric data set and itself is a modification of the topographic position index algorithm that is used in terrestrial environment The Fine-scale BPI (inner radius of 5 and outer radius of 25) identifies smaller features within the seafloor	SRTM30_PLUS	Benthic Terrain Modeler
Hillshading	Sun-illuminated relief representation computed using a single illumination angle	SRTM30_PLUS	DEM Tools
MDOW-Hillshade (Multidirectional Oblique-Weighled)	Advanced sun-illuminated relief representation computed using illumination simulations from multiple angles	SRTM30_PLUS	DEM Tools
Classified depth zones	Depth zones segmentation using Howell (2010) thresholds (littoral, upper slope, upper bathyal, mid bathyal, lower bathyal, abyssal)	SRTM30_PLUS	–
Geomorphic features	Delimitation of the different geomorphic structures present in the region (abyss, basin, canyon, escarpment, plateau, ridge, rift-valley, rise, shelf, through)	Harris et al., 2014	–
Substrate type	Seafloor substrate type	Multiple (see text)	–
Sediment thickness	Sediment thickness of the seafloor	Divins (2003)	–

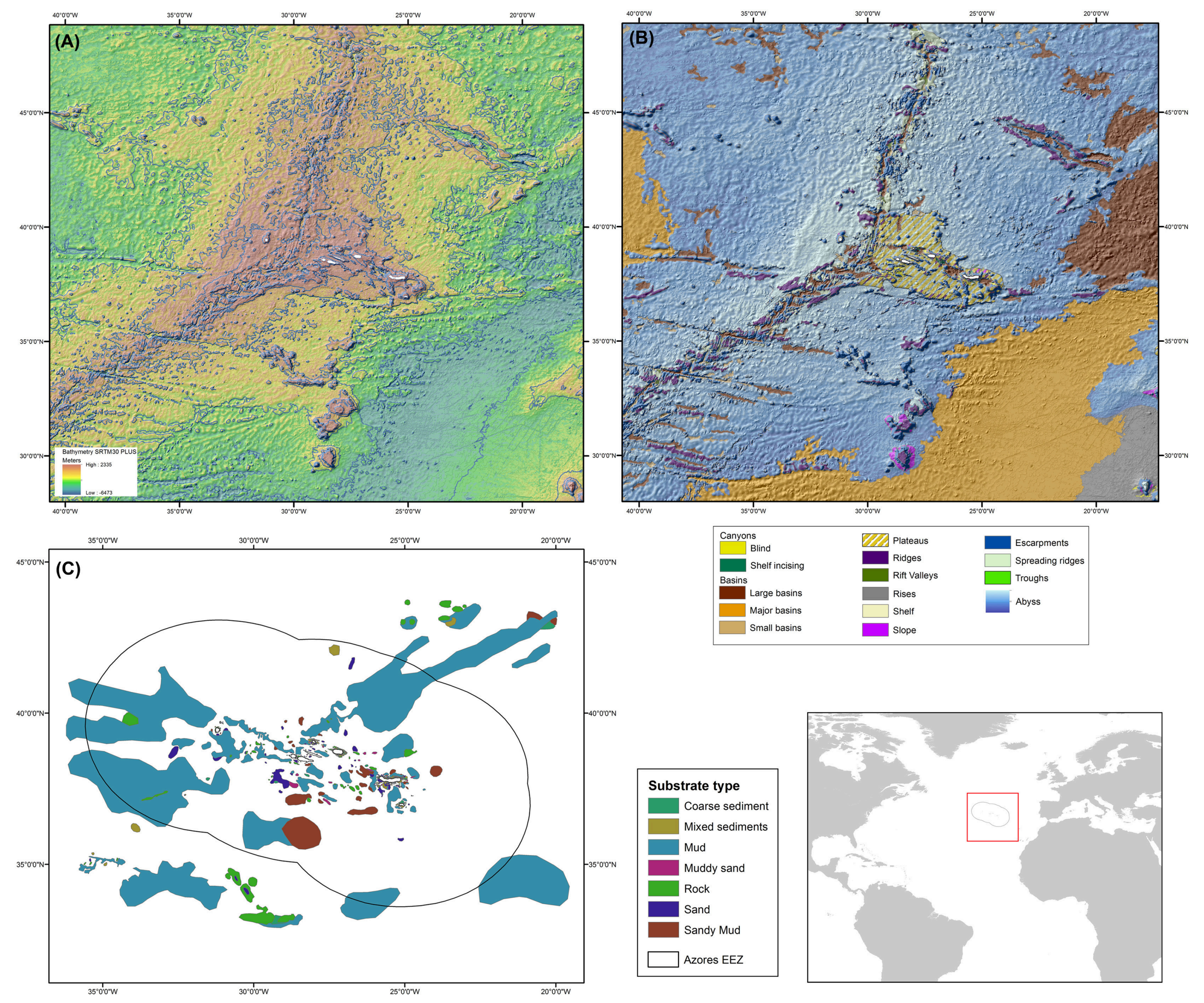

FIGURE 1 | (A) Bathymetry of the study area (SRTM30_PLUS) for which all the derivatives were based on; **(B)** geomorphologic structures of the seafloor based on Harris et al. (2014); **(C)** seabed substrate type.

in this study encompasses the following layers: the base layer abyss (representing 99.1% of the study area and subdivided into abyssal plains, abyssal hills and abyssal mountains) and the following discrete feature layers: basin (22.72%), canyon (0.14), escarpment (7.35%), plateau (2.91%), ridge (3.95%), rift-valley (0.63%), spreading ridges (3.4%), shelf (0.04%) and through (0.54%).

Seabed substrate type (**Figure 1C**) were based on different sources: multibeam backscatter and seismic surveys, point data digitized from up-to-date and historical nautical charts for the Azores and data provided by the World Seabed Data Browser, the Lamont-Doherty Earth Observatory and National Geophysical Data Center (NGDC). Since most of the information was available as sample point data, a geologic interpretation of seafloor type around the Azores was undertaken (collaboration with IEO researchers: José Luis Sanz Alonso and Dulce Mata Chacón) using the seafloor point data and bathymetry information. This approach was later complemented by statistical modeling (Multinomial regression models) using other terrain variables (e.g., Bathymetry, Slope, Eastness, Northness, Rugossity) to cover the uninterpreted areas left by the expert (Mata Chacón et al., 2013; Vasquez et al., 2015). The expert geological interpretation of seabed sampled points was given priority in the final mosaic of the substrate types for the Azores region. The output resulted in the compilation of the highest resolution seabed substrate data available: an interpreted and modeled substrate layer with a 250 m resolution. The area covered by the seabed substrate layer is more limited than the total area considered in this study.

A specific analysis of the sediment thickness characteristics of the Azores area was undertaken using the "Total Sediment Thickness of the World's Oceans and Marginal Seas, Version 2" (Whittaker et al., 2013), an updated dataset from the original global National Geophysical Data Centre (NGDC) sediment grid (Divins, 2003). The new total sediment thickness grid can be found at the National Geophysical Data Center's website (https://www.ngdc.noaa.gov/mgg/sedthick/index.html).

The compilation of the seabed characteristics for the Azores and surrounding areas in North Atlantic is part of a larger effort to assemble as much data on the environmental characteristics of this region (e.g., Amorim et al., in press), to improve our knowledge and facilitate the development of future integrated studies.

AUTHOR CONTRIBUTIONS

TM, CP, FC, and FT designed the study. PA, ADP, and FT collected and processed most of the data through GIS software. TM, CP, PA, and ADP performed most of the analyses. PA, ADP, CP, FC, FT, and TM wrote the paper.

FUNDING

This research received funding from Fundo Regional da Ciência, Tecnologia (FRCT), through the research project 2020-M2.1.2/I/026/2011 (Pro-Convergência), and the European Union Seventh Framework Programme (FP7/2007-2013) under the MIDAS project, grant agreement 603418 and Interreg project MeshAtlantic (AA-10/1218525/BF). The authors also acknowledge funds provided by the Fundação para a Ciência e a Tecnologia (FCT) through the strategic project (FCT/UID/MAR/04292/2013) granted to MARE. TM is supported by Program Investigador FCT (IF/01194/2013) and IFCT Exploratory Project (IF/01194/2013/CP1199/CT0002), PA is currently supported by a FCT Ph.D grant (SFRH/DB/103504/2014) and was previously co-financed by project MeshAtlantic (AA-10/1218525/BF), FT was supported by a post-doc grant from the FCT (ref. SFRH/BPD/79801/2011), ADP was partially supported by the Estagiar L program from the Government of the Azores, and FC was supported by IMAR and the European Marine Observation and Data Network through contract IMAR/EMODnet Biology/001-2014.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 12 December 2016
doi: 10.3389/fmars.2016.00245

Food-Web and Ecosystem Structure of the Open-Ocean and Deep-Sea Environments of the Azores, NE Atlantic

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The Marine Strategy Framework Directive intends to adopt ecosystem-based management for resources, biodiversity and habitats that puts emphasis on maintaining the health of the ecosystem alongside appropriate human use of the marine environment, for the benefit of current and future generations. Within the overall framework of ecosystem-based management, ecosystem models are tools to evaluate and gain insights in ecosystem properties. The low data availability and complexity of modeling deep-water ecosystems has limited the application of ecosystem models to few deep-water ecosystems. Here, we aim to develop an ecosystem model for the deep-sea and open ocean in the Azores exclusive economic zone with the overarching objective of characterizing the food-web and structure of the ecosystem. An ecosystem model with 45 functional groups, including a detritus group, two primary producer groups, eight invertebrate groups, 29 fish groups, three marine mammal groups, a turtle and a seabird group was built. Overall data quality measured by the pedigree index was estimated to be higher than the mean value of all published models. Therefore, the model was built with source data of an overall reasonable quality, especially considering the normally low data availability for deep-sea ecosystems. The total biomass (excluding detritus) of the modeled ecosystem for the whole area was calculated as 24.7 t km^{-2}. The mean trophic level for the total marine catch of the Azores was estimated to be 3.95, similar to the trophic level of the bathypelagic and medium-size pelagic fish. Trophic levels for the different functional groups were estimated to be similar to those obtained with stable isotopes and stomach contents analyses, with some exceptions on both ends of the trophic spectra. Omnivory indices were in general low, indicating prey speciation for the majority of the groups. Cephalopods, pelagic sharks and toothed whales were identified as groups with key ecological roles in the ecosystem. Due to concerns on the use of ecosystem models with low confidence in exploring management decisions and ecological theories, the current version of this model should only be use with caution until biomass estimates are validated with survey data or the model is fitted to time series.

Keywords: ecopath, ecosystem model, fisheries, Azores, trophic links

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Specialty section:
This article was submitted to Deep-Sea Environments and Ecology, a section of the journal Frontiers in Marine Science

Received: *01 July 2016*
Accepted: *11 November 2016*
Published: *12 December 2016*

Citation:
Morato T, Lemey E, Menezes G, Pham CK, Brito J, Soszynski A, Pitcher TJ and Heymans JJ (2016) Food-Web and Ecosystem Structure of the Open-Ocean and Deep-Sea Environments of the Azores, NE Atlantic. Front. Mar. Sci. 3:245. doi: 10.3389/fmars.2016.00245

INTRODUCTION

The European Union (EU) Marine Strategy Framework Directive (MSFD) defines the marine environment as "a precious heritage that must be protected, preserved and, where practicable, restored with the ultimate aim of maintaining biodiversity and providing oceans which are clean, healthy and productive (EU Directive 2008/56/EC)." The MSFD requires member states to adopt an ecosystem approach to management of human activities that puts emphasis on maintaining the health of the ecosystem alongside sustainable use of marine goods and services. MSFD encourages the implementation of an ecosystem-based approach to fisheries management that would take into account the environmental impacts of fishing. However, the EU's Common Fisheries Policy (CFP) still is a single-species based fisheries management policy, implementing total allowable catches for target species. It has been criticized for failing in delivering long-term sustainability of the fish stocks and reducing the adverse effects of fisheries on the whole ecosystem (Beddington et al., 2007; Khalilian et al., 2010; Villasante et al., 2012). Under the recent CFP reform (EU Regulation 1380/2013), ecosystem-based approaches are considered acceptable to address the specific problems of mixed fisheries but still seldom used.

Within the overall concept of ecosystem-based management, ecosystem models provide a holistic approach to address the various complexities and multiple drivers associated with marine ecosystems (Larkin, 1996; Espinoza-Tenorio et al., 2011; Link et al., 2012) and can be used to evaluate trade-offs between fisheries and conservation (Pikitch et al., 2004). However, modeling complex marine ecosystems with its associated human uses is very challenging and encompasses a degree of uncertainty (Fulton et al., 2003; Garcia et al., 2003; Plagányi and Butterworth, 2004; Pinnegar et al., 2005; Coll et al., 2009; Forrest et al., 2015). Nevertheless, the development of the Ecopath with Ecosim (EwE) modeling approach, based on Polovina (1984) and further developed by Christensen and Pauly (1992, 1993, 1995), opened the way toward holistic ecosystem modeling that describes the food-web structure and the functioning of marine ecosystems. EwE has proven to be a useful tool for quantifying a large array of ecosystem indicators (Christensen and Walters, 2004; Heymans et al., 2014; Shannon et al., 2014) necessary for assessing Good Environmental Status (GES) under the MFSD (Piroddi et al., 2015). A recent global overview of the applications of the EwE have demonstrated the use of this approach in a wide variety of ecosystems and to analyse wide range of research questions (Colléter et al., 2015).

Deep-water and open-ocean ecosystems are characterized by complex trophic links and are, with a few exceptions, data-limited. The low data availability and complexity of modeling deep-water ecosystems has limited the application of ecosystem models to few deep-water ecosystems (Heymans et al., 2011; Tecchio et al., 2013, 2015). Nevertheless, Heymans et al. (2011) concluded that in some ecosystems there are sufficient data available for developing ecosystem models for deep-sea ecosystem warning, however, for serious potential sources of uncertainties. Only if acknowledging such limitations, the ecosystem modeling approach can help our understanding of deep-water and open-ocean ecosystem functioning and exploring management scenarios and policy options.

The Azores is an oceanic archipelago in the mid North-Atlantic Ocean, between continental Europe and North America. The seafloor is mostly deep but a large number of seamounts, a fraction of the Mid Atlantic Ridge, and the slopes of the islands compose the shallowest parts (Perán et al., 2016). After the first expeditions to the open ocean and the deep-sea in the late nineteenth century, extensive scientific research based in the Azores has opened a window on the functioning of large oceanic, deep-sea and seamount ecosystems and the impacts of human activities in such ecosystems, making this region a good case study for ecosystem model of the deep-sea and open ocean. We therefore hypothesized that there is sufficient data to construct a deep-sea ecosystem model of the Azores. The overarching goal of this study was to develop an ecosystem model for the deep-sea and open ocean in the Azores exclusive economic zone (EEZ) to characterise the food-web and ecosystem structure of the open-ocean and deep-sea environments of the Azores.

MATERIALS AND METHODS

The Study Area: the Azores Archipelago

The Azores is a Portuguese archipelago composed of nine islands situated on the Mid-Atlantic ridge (**Figure 1**) with an extensive EEZ of about 1 million km^2. As a volcanic archipelago of recent origin, the islands have narrow shelves and steep slopes, and the surrounding waters have an average depth of 3000 m with only 0.8% of the EEZ being less than 500 m deep. The highly irregular submarine topography contains vast undersea mountain ranges, with around 100 large and 400 small seamounts-like features (Morato et al., 2008, 2013), deep-water coral gardens and reefs (Sampaio et al., 2012; Braga-Henriques et al., 2013; de Matos et al., 2014; Tempera et al., 2015), sponge grounds (Tempera et al., 2012, 2013), and hydrothermal vents (Cardigos et al., 2005; Cuvelier et al., 2009). In winter a deep mixed layer is present at 150 m and average sea surface temperature (SST) is about 15–16°C. During summer, a seasonal thermocline develops at 40–100 m and the average SST is typically 22–24°C (Amorim et al., in review).

The region is characterized by very complex ocean circulation patterns. Large scale circulation is dominated by the eastward-flowing Gulf Stream, which forms a current system with many unstable eddies and meanders, the cold North Atlantic Current in the north, and the warm Azores Current in the south (Santos et al., 1995; Alves and Verdière, 1999; Johnson and Stevens, 2000; Bashmachnikov et al., 2009). Various water masses are present around the Azores. North Atlantic Central Water occurs above a permanent thermocline, located at depths shallower than 700 m, North Atlantic Deep Water is the dominant water mass below 2000 m depths, and at intermediate depths, northern sub-polar waters and Antarctic Intermediate Water predominate, but Mediterranean Outflow Water can also occur (Santos et al., 1995; Johnson and Stevens, 2000; Mann and Lazier, 2006).

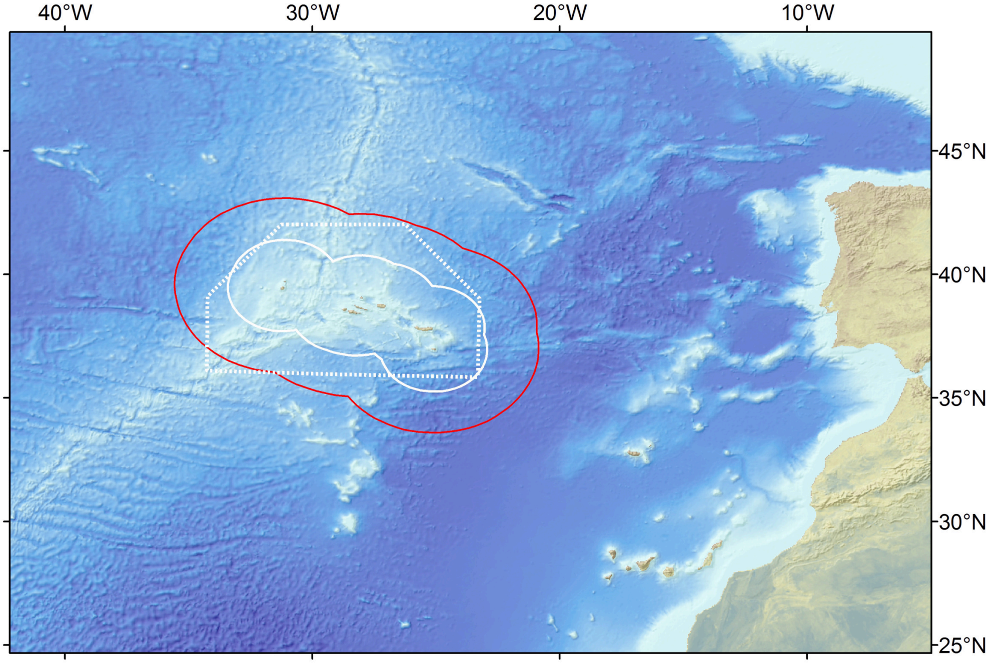

FIGURE 1 | Location of the study area in the Northeast Atlantic showing the Azores archipelago region, its exclusive economic zone (red line), 100 nm limit (straight white line) and the trawl ban area (dotted white line).

For this study, we confined the study area to the boundary of the EEZ, which covers an area of 954,563 km^2. The area includes the deep-sea, open-ocean, some seamounts, parts of the Mid Atlantic Ridge and island slopes (**Figure 1**). The reference year of 1997 was chosen as most of the data used to construct the base model (diet and growth parameters) originated from that year.

Fisheries Description

Marine resources are central to the Azores' local economy, but bottom fishing grounds are limited and scattered on the island slopes and seamounts (da Silva and Pinho, 2007; Diogo et al., 2015). The Azores fleet is dominated by a small-scale artisanal fishing fleet (Carvalho et al., 2011) with only 10–20% of the fleet being a large-scale, semi-industrial fishing fleet. An overview of the main fisheries in the Azores, their gear types, target species, fishing vessels and regulations was taken from Gaspar (2011). A total of 11 Azorean fisheries were included in the model: the deep-water bottom longline and handline fisheries targeting mostly deep-water demersal fishes such as blackspot seabream (*Pagellus bogaraveo*), wreckfish (*Polyprion americanus*), alfonsinos (*Beryx* spp.) and the blackbelly rosefish (*Helicolenus dactylopterus*); the Azores pelagic longline, Portuguese mainland pelagic longline, and the foreign pelagic longline fisheries targeting swordfish (*Xiphias gladius*) and blue shark (*Prionace glauca*); the pole and line tuna fishery (including the live-bait); the small-size pelagic fisheries targeting mostly blue jack mackerel (*Trachurus picturatus*) and chub mackerel (*Scomber colias*); the drifting deep-water longline targeting black scabbardfish (*Aphanopus carbo*) which is a recent fishery in the Azores (Machete et al., 2011); the commercial coastal invertebrates; the recreational fishing; the experimental bottom trawling; and the squid (*Loligo forbesii*) fisheries.

Modeling Approach

Ecopath with Ecosim (EwE) is a food-web modeling facility that can be used to build trophic static mass-balanced snapshots (Ecopath) and to create temporal dynamics (Ecosim) of an ecosystem (Christensen and Pauly, 1992; Walters et al., 1997, 2000; Pauly et al., 2000; Christensen and Walters, 2004; Christensen et al., 2008). EwE has been widely adopted all over the world (Colléter et al., 2015) and has led to some ground-breaking science (Pauly and Christensen, 1994; Pauly et al., 1998; Watson and Pauly, 2001; Branch et al., 2010; Smith et al., 2011; Irigoien et al., 2014). However, it should be used with caution to avoid common mistakes and pitfalls (Ainsworth and Walters, 2015). EwE has been described in detail elsewhere (e.g., ecopath.org; Christensen and Pauly, 1992; Walters et al., 1997; Christensen and Walters, 2004), with the best practice in Ecopath described recently (Heymans et al., 2016).

Ecopath models parameterization is based in two master equations, one describing the production term and the other the energy balance for each functional group. The first master equation ensures a mass balance between groups and expresses production as a function of the catch, predation, net migration, biomass accumulation and other mortality (Equation 1). The second master equation is based on the principle of conservation of matter within each group (Equation 2; Christensen and Walters, 2004). Each group is parameterised with its biomass (B, t·km^{-2}), production over biomass ratio or production rate (P/B, year^{-1}), consumption over biomass ratio or consumption rate (Q/B, year^{-1}), the prey-predator interaction in the form of a diet composition (DC) table, ecotrophic efficiency (EE_i), the biomass accumulation rate (BA_i, year^{-1}) and the net migration rate (E_i, year^{-1}).

$$B\left(\frac{P}{B}\right)_i = Y_i + \sum_j B_j\left(\frac{Q}{B}\right)_j DC_{ij} + E_i\, BA_i + B_i\left(\frac{P}{B}\right)_i (1 - EE_i) \qquad (1)$$

$$Consumption\ (Q_i) = production\ (P_i) + respiration\ (Ri) + unassimilated\ food\ (Ui) \qquad (2)$$

Model Construction and Parametrization

The current version of the Azores model was built upon previous models developed for this region and associated seamounts (Guénette and Morato, 2001; Morato and Pitcher, 2002; Morato et al., 2009). The present model focused mostly on intermediate and deep-water species present in the Azores ecosystem and used, when possible, recent and local data for model parameterization. Species with biological and ecological similarities were grouped into functional groups or biomass pools. Fish species lists were compiled from previous models, and completed with more recent biodiversity studies of the Azores (Supplementary Data Sheet 1). The present model took into consideration 387 fish species representing about 66% of the known marine fish biodiversity (WoRMS Editorial Board, 2016). Non-fish functional groups were defined based on a previous Ecopath model of the Azores (Guénette and Morato, 2001) and an Ecopath model for a hypothetical seamount in the North Atlantic (Morato et al., 2009). With the exception of marine mammals (16 most common species, representing 66% of the known biodiversity; Mónica Silva, pers. comm.), seabirds (8 most common species, 73% of reported nesting species; Verónica Neves, pers. comm.), and sea turtles (3 most common species, 60% of the reported species; Marco Silva, pers. comm.), most of the non-fish groups were poorly represented in the model due to the limited amount of information available. In this model, energy related parameters are expressed in t·km^{-2} of wet weight and the temporal unit is year^{-1}.

Input Parameters

Fish species present in the Azores EEZ were compiled based on a checklist of marine fishes of the Azores (Santos et al., 1997), an updated list of commercial species caught in the Azores for the period 1950–2010 (Pham et al., 2013), a list of fish species caught on fisheries research cruises (Menezes, unpublished data), a list of deep-pelagic fishes compiled during mesopelagic trawling surveys (Sutton et al., 2008), and a list of coastal species sighted during a sub-aquatic visual census program (Afonso, 2002). Of the 387 fish species complied, only 223 (representing 38% of the known fish biodiversity) were included in the model because of data limitations. All of the selected species were allocated stepwise to 29 functional groups after compiling a dataset with diet composition, asymptotic length and average habitat depth for each species, gathered from local studies and completed with Fishbase data (Froese and Pauly, 2015). In addition, some fish were separated into single species functional groups because of their commercial interest and/or to allow specific management simulations. These are: *H. dactylopterus, Conger conger, Pontinus kuhlii*, *Raja clavata*, *Phycis phycis*, *Pagrus pagrus*, *Beryx splendens*, *Beryx decadactylus*, *P. bogaraveo*, *Mora moro*, *L. caudatus*. The model presented here consisted of 45 functional groups: one detritus group, two primary producer groups, eight invertebrate groups, 29 fish groups, three marine mammal groups, one sea-turtle and one seabird group (Supplementary Data Sheet 1).

Model parameters, P/B, Q/B, and production of consumption ratio (P/Q, unitless) were estimated from the literature, with preference to studies within our area or from similar areas, or using empirical equations (Pauly, 1980; Palomares and Pauly, 1998). Habitat area fraction, which is the habitat area to total model area ratio, for each group was calculated using habitat depth ranges compiled from local studies (e.g., Menezes et al., 2006) and Fishbase, and converted into surface areas using bathymetric grid of the Azores. Details on the calculations or sources of these model parameters and the habitat area fraction are presented in Supplementary Data Sheet 1.

The model pedigree describing the origin and quality of each parameter was calculated and used to analyse our hypothesis that there is sufficient data to construct an ecosystem model of the Azores. This was done by comparing with the estimated pedigree values with the reported ranges in Colléter et al. (2015). The model pedigree is also used to assign confidence intervals to the data inputs (Pauly et al., 2000).

A diet matrix was assembled using preferentially local literature on stomach content analyses, completed with other literature and adapted using empirical knowledge (Supplementary Table 1). To constrain the model and due to a lack of direct biomass assessments, biomass expressed in tonnes of wet weight per square kilometer of species' habitat, was estimated empirically for the two primary producer groups, the detritus group, and four top predator groups. For the remaining groups, biomass was left to be estimated by the model, assigning different EE values to the different groups (Supplementary Table 1). To balance the model, diet compositions were modified, and for some fish groups, ratios of P/B were left to be estimated by the model, using empirical P/Q values as input.

Marine Catch Data

Total marine catch data was obtained from Pham et al. (2013). The dataset contains both official fishery statistics and estimated illegal, unreported, and unregulated catch (IUU) within the Azores EEZ. However, discards (fish returned to the sea), were not reported separately. Species catch data was assigned to the different fishing fleets and the functional groups. Catch data that could not be assigned to a specific functional group or fleet (e.g., unidentified marine species) were redistributed into the groups exploited by the various fleets. Catch data was constructed for the reference year 1997 (**Figure 2**; Supplementary Table 2) and then expressed in tonnes of wet weight per square kilometer of the model area. The tuna pole and line fishery is together with

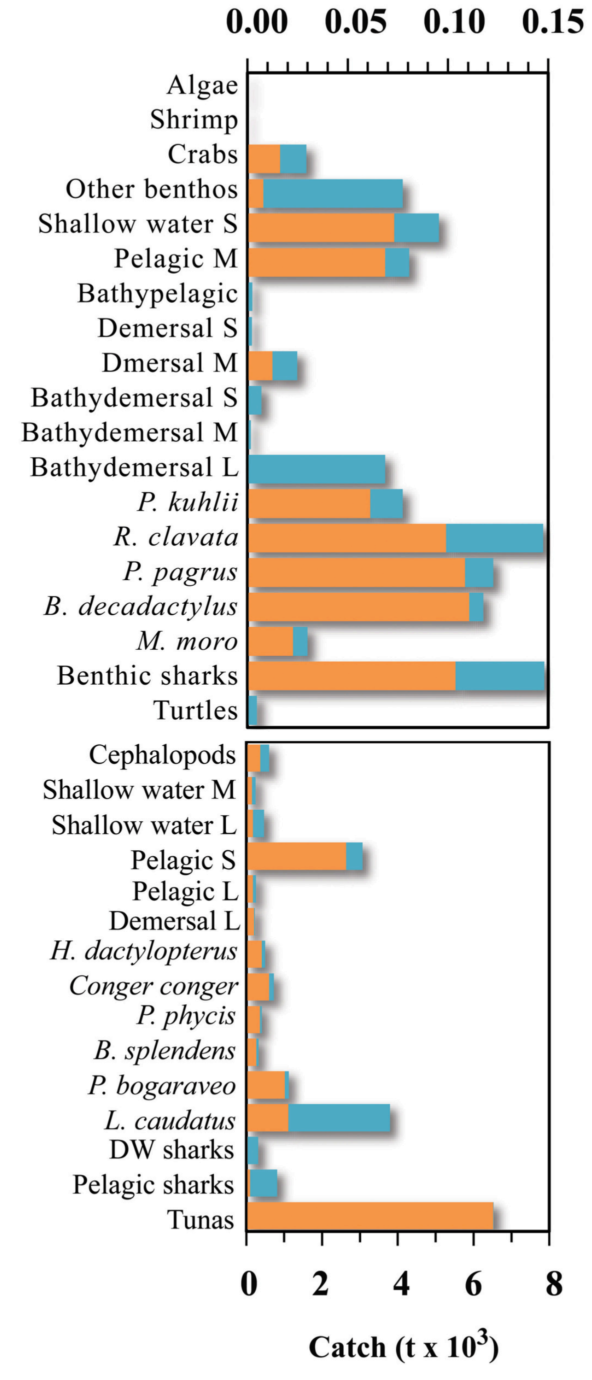

FIGURE 2 | Fisheries catch for the different groups included in the Azores ecosystem model, for the reference year 1997 (adapted from Pham et al., 2013). S, small-size; M, medium-size; L, large-size.

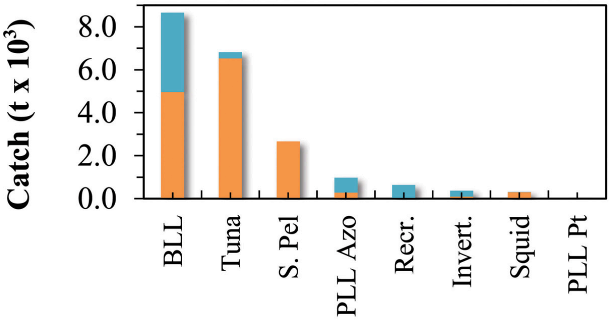

FIGURE 3 | Marine fisheries catch for the different fleets included in the Azores ecosystem model, for the reference year 1997 (adapted from Pham et al., 2013). BLL is deep-water bottom longline and handline fisheries, Tuna refers to the pole and line tuna fishery (including the live-bait catch), S. Pel refers to the small-size pelagic fisheries, PLL Azo is the Azores pelagic longline fisheries, Recr. is the recreational fishing, Invert. is the commercial coastal invertebrates fisheries, Squid is the squid (*L. forbesii*) fisheries, and PLL Pt refers to the Portuguese mainland pelagic longline fisheries.

the deep-water bottom longline and handline fishery accountable for the majority of the catch of marine resources in the Azores during the studied period (**Figure 3**). Before the prohibition of bottom trawling in a large part of the EEZ, some trawling experiments were performed in 2001–2002 and were responsible for a significant amount of catch (Melo and Menezes, 2002). The total marine production in the Azores currently stands at over 20,000 tonnes, corresponding to about € 60 million in landed value (Pham et al., 2013).

Network Analysis

After mass-balancing the model, a trophic network analysis was performed. For each functional group, a fractional trophic level (TL) was calculated based on the diet. An omnivory index, representing the trophic specialization of the predator (Christensen et al., 2008), was calculated for each consumer group. The "Keystoneness" index (KS), as defined by Libralato et al. (2006) was also calculated for each functional group. The KS allow the identification of the keystone species, i.e., relatively low biomass groups that have a structuring role in their food webs, in the given ecosystem. The mixed trophic impact (MTI) routine, developed by Ulanowicz and Puccia (1990), was applied to evaluate the impact of direct and indirect interactions on the static food web model. The routine was used to assess the theoretical impacts of increased biomass of a particular group on the biomass of the other groups, assuming that the trophic structure remains the same.

A selection of ecosystem indicators were calculated, allowing for a comparison of ecosystem properties with other models. Amongst others, the sum of all consumption, exports, respiratory flows, flows into detritus, and the ratio of total primary production/total respiration were calculated. The System Omnivory Index (OI), defined as the average OI of all consumers weighted by the logarithm of their consumption, was calculated. This index is a measure of the trophic specialization of the whole system. The Total System Throughput (TST) was calculated by totalling all biomass fluxes occurring in the system.

RESULTS

Azores Ecopath Model

The various parameters for the balanced Ecopath model of the Azores ecosystem are presented in **Table 1**. Additional to

TABLE 1 | Input parameters for Azores ecosystem model showing those estimated by the model in bold.

	Group name	Trophic level	Habitat (%)	Biomass in habitat (t/km^2)	Biomass (t/km^2)	P/B (year^{-1})	Q/B (year^{-1})	EE	P/Q	OI
1	Phytoplankton	**1.00**	100.00	2.9000	2.9000	576.29	0.00	**0.12**		**0.00**
2	Algae	**1.00**	0.03	2619.0480	0.9072	4.34	0.00	**0.02**		**0.00**
3	Zooplankton S	**2.00**	100.00	**4.5201**	**4.5201**	11.21	43.29	0.90	**0.26**	**0.00**
4	Zooplankton L	**2.58**	100.00	**3.5080**	**3.5080**	4.78	15.50	0.90	**0.31**	**0.29**
5	Shrimp	**2.77**	100.00	**2.2971**	**2.2971**	1.45	9.67	0.95	**0.15**	**0.41**
6	Cephalopods	**3.72**	100.00	**0.3247**	**0.3247**	3.28	12.29	0.95	**0.27**	**0.57**
7	Crabs	**2.26**	100.00	**2.0318**	**2.0318**	1.60	10.00	0.95	**0.16**	**0.27**
8	Benthic filter feed.	**2.05**	100.00	**2.2115**	**2.2115**	0.80	9.00	0.95	**0.09**	**0.05**
9	Benthic worms	**2.20**	100.00	**1.1815**	**1.1815**	2.28	11.40	0.95	**0.20**	**0.16**
10	Other benthos	**2.17**	100.00	**1.0604**	**1.0604**	3.00	10.00	0.95	**0.30**	**0.15**
11	Shallow-water S	**3.16**	0.14	**12.2571**	**0.0166**	**2.49**	8.31	0.95	0.30	**0.29**
12	Shallow-water M	**3.28**	0.14	**14.4711**	**0.0196**	**1.26**	6.30	0.95	0.20	**0.56**
13	Shallow-water L	**3.57**	0.14	**1.8744**	**0.0025**	**0.44**	4.42	0.95	0.10	**0.58**
14	Pelagic S	**2.99**	100.00	**0.5172**	**0.5172**	**2.84**	9.47	0.95	0.30	**0.39**
15	Pelagic M	**3.86**	100.00	**0.1231**	**0.1231**	**0.87**	4.33	0.95	0.20	**0.18**
16	Pelagic L	**4.47**	100.00	**0.0009**	**0.0009**	0.73	2.50	0.95	**0.29**	**0.22**
17	Mesopelagics	**3.35**	100.00	**0.9783**	**0.9783**	**2.59**	8.62	0.95	0.30	**0.23**
18	Bathypelagic	**3.90**	100.00	**0.6769**	**0.6769**	0.44	4.90	0.95	**0.09**	**0.33**
19	Demersal S	**3.56**	0.48	**14.0301**	**0.0672**	**2.23**	7.43	0.95	0.30	**0.11**
20	Demersal M	**3.83**	0.48	**4.2574**	**0.0204**	**0.93**	4.66	0.95	0.20	**0.34**
21	Demersal L	**4.32**	0.48	**1.0446**	**0.0050**	0.46	3.82	0.95	**0.12**	**0.33**
22	Bathydemersal S	**3.29**	99.39	**0.9906**	**0.9845**	**0.49**	4.95	0.95	0.10	**0.05**
23	Bathydemersal M	**3.83**	99.39	**0.0043**	**0.0042**	**0.33**	3.31	0.95	0.10	**0.23**
24	Bahtydemersal L	**4.39**	99.39	**0.0007**	**0.0007**	**0.35**	3.53	0.95	0.10	**0.24**
25	*H. dactylopterus*	**4.09**	0.56	**4.2684**	**0.0237**	**0.45**	4.57	0.95	0.10	**0.31**
26	*Conger conger*	**4.61**	0.52	**1.3758**	**0.0072**	0.13	2.99	0.95	**0.04**	**0.21**
27	*Pontinus kuhlii*	**4.00**	0.25	**0.4035**	**0.0010**	0.25	3.62	0.95	**0.07**	**0.26**
28	*Raja clavata*	**4.25**	0.19	**0.5037**	**0.0010**	0.29	4.10	0.95	**0.07**	**0.23**
29	*Phycis phycis*	**4.08**	0.24	**2.5017**	**0.0059**	0.22	4.50	0.95	**0.05**	**0.36**
30	*Pagrus pagrus*	**3.39**	0.12	**1.0900**	**0.0013**	0.32	4.73	0.95	**0.07**	**0.29**
31	*Beryx splendens*	**3.75**	0.51	**0.4971**	**0.0026**	0.39	3.58	0.95	**0.11**	**0.15**
32	*Beryx decadactylus*	**3.73**	0.70	**0.4070**	**0.0029**	0.26	2.74	0.95	**0.10**	**0.15**
33	*Pagellus bogaraveo*	**4.04**	0.48	**3.6039**	**0.0173**	0.31	4.68	0.95	**0.07**	**0.22**
34	*Mora moro*	**4.27**	99.39	**0.0012**	**0.0012**	0.17	2.69	0.95	**0.06**	**0.28**
35	*Lepidopus caudatus*	**4.32**	100.00	**0.0457**	**0.0457**	0.25	4.79	0.95	**0.05**	**0.13**
36	Rays and sharks	**4.16**	0.61	**0.4684**	**0.0029**	**0.31**	3.13	0.95	0.10	**0.46**
37	Deepwater sharks	**4.53**	99.39	**0.0037**	**0.0037**	**0.36**	3.57	0.95	0.10	**0.32**
38	Pelagic sharks	**4.30**	100.00	**0.0493**	**0.0493**	**0.27**	2.68	0.95	0.10	**0.15**
39	Tunas	**4.09**	100.00	**0.0886**	**0.0886**	0.36	3.03	0.95	**0.12**	**0.13**
40	Turtles	**3.63**	100.00	**0.0404**	**0.0404**	0.15	3.50	0.95	**0.04**	**0.04**
41	Seabirds	**4.15**	100.00	0.0001	0.0001	0.25	84.39	**0.23**	**0.00**	**0.18**
42	Dolphins	**4.31**	100.00	0.0019	0.0019	0.10	11.41	**0.38**	**0.01**	**0.15**
43	Baleen whales	**3.49**	100.00	0.0208	0.0208	0.06	5.56	**0.46**	**0.01**	**0.11**
44	Toothed whales	**4.64**	100.00	0.0560	0.0560	0.02	10.27	**0.14**	**0.00**	**0.06**
45	Detritus	**1.00**	100.00	1.0000	1.0000			**0.05**		**0.09**

P/Q is the production rate over biomass, Q/B is consumption rate over biomass, EE is ecotrophic efficiency, P/Q is production rate over consumption rate and OI is the omnivory index. S is small-size, M is medium size, and L is large-size.

those parameters, the Pedigree index was estimated to be 0.53 which although being similar to many other models (e.g., Corrales et al., 2015) showed that some input data should be improved. Due to the scarcity of biomass data, most of the ecotrophic efficiencies (EE's) had to be estimated based on expert knowledge. Nevertheless, EE of the top predator groups (group

40–43, **Table 1**) that were estimated by the balanced model were generally low, ranging from 0.13 (toothed whales) to 0.46 (baleen whales) and indicating that large fractions of the production of those groups is not being used in the modeled system. The EE's of phytoplankton and algae are 0.11 and 0.013, respectively; suggesting low utilization of primary production in the system.

The total biomass (excluding detritus) of the modeled ecosystem for the whole area was calculated as 24.7 t km^{-2} (**Table 1**). Primary producers form 15.4% of the total biomass (3.8 t km^{-2}) and fish biomass contributed to 14.8% (3.7 t km^{-2}). The largest part of the total ecosystem biomass, 17.1 t km^{-2} (69.3%), was composed by the invertebrate and zooplankton groups, while the non-fish groups occupying the higher trophic levels (seabirds, dolphins, baleen whales and toothed whales) contributed only to 0.5% of the total biomass (0.12 t km^{-2}). The trophic spectra of the ecosystem is shown in **Figure 4**.

The Azores ecosystem model included five trophic levels with toothed whales and *C. conger*, presenting the top predators in the ecosystem with TL of 4.64 and 4.61, respectively. Other functional groups with a TL > 4 included the deepwater sharks, large-size pelagic fish, large-size bathydemersal fish, *L. caudatus*, large-size demersal fish, dolphins, pelagic sharks, *M. moro*, *R. clavata,* rays and other sharks, seabirds, tunas, *H. dactylopterus*, *P. phycis*, *P. bogaraveo*, and *P. kuhlii*. The remaining fish groups have a TL ranging from 2.99 (small-size pelagic fish) to 3.90 (bathypelagic fish). Invertebrate functional groups were estimated to have a TL between 2.05 (benthic filter feeders) and 2.77 (shrimps), with the exception of cephalopods who were estimated to have a TL of 3.72. Zooplankton functional groups have a TL of 2.00 (small-size) and 2.58 (large-size and gelatinous). The food web and flow diagram demonstrated the complex structure of the ecosystem (**Figure 5**).

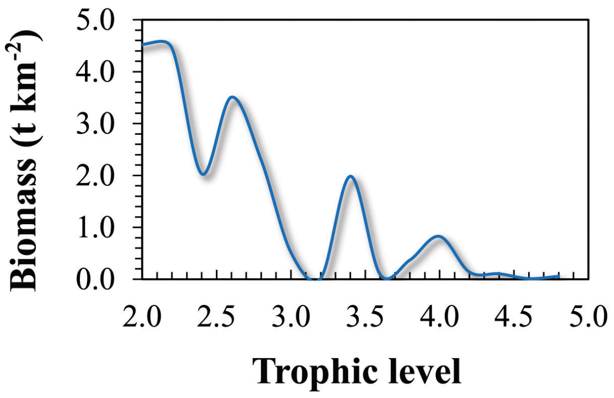

FIGURE 4 | Trophic spectra of the Azores ecosystem model for the reference year 1997.

The mean trophic level for the total marine catch of the Azores (**Figure 6**) was estimated to be 3.95, matching the trophic level of the bathypelagic and medium-size pelagic fish groups, but situated below the trophic levels of most of the top predators in the system. Drifting deepwater longline and the pelagic longline showed the highest values of 4.40 and 4.34 respectively, approximating the trophic levels of some top predator groups. Bottom logline and handline fishery showed a trophic level of 4.19, while the small-size pelagic fisheries showed the lowest trophic level of 2.99.

The Omnivory Index (**Table 1**) showed that most groups were feeding on few trophic levels. The OI ranged from 0.04 to 0.58, with shallow-water large-size fish, cephalopods, shallow-water medium-size fish, and rays and other sharks showing the highest index and sea turtles, benthic filter feeders, small-size bathydemersal fish and toothed whales showing the lowest values of OI.

The Mixed Trophic Impact (MTI) analysis (**Figure 7**) revealed the direct and indirect impact of an increase/decrease in biomass of an impacting group or fisheries catch on an impacted group or fishery. The MTI indices ranged from 1.8, representing a strong positive effect of cephalopods on toothed whales, to

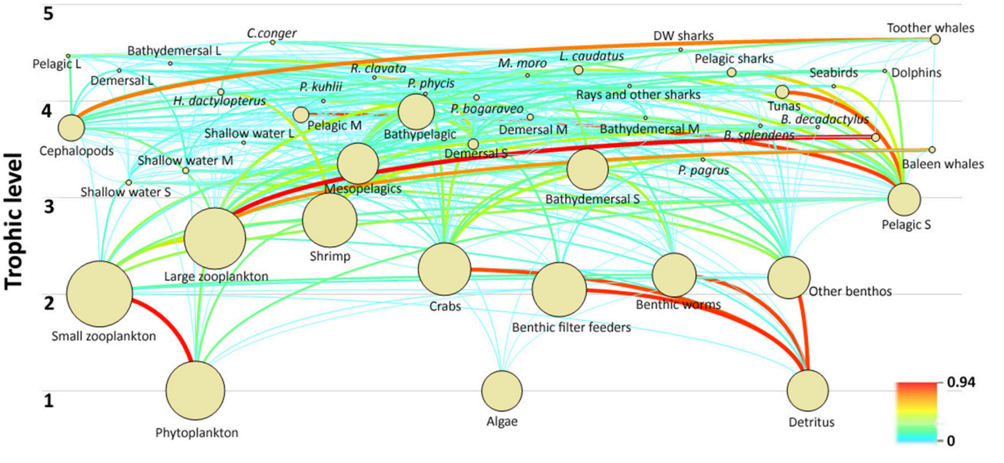

FIGURE 5 | Diagram of the food web and trophic flows of the Azores ecosystem model for the reference year 1997. The circles are dimensional representations proportional to the logarithm of group biomasses and the lines indicate the trophic links among functional groups.

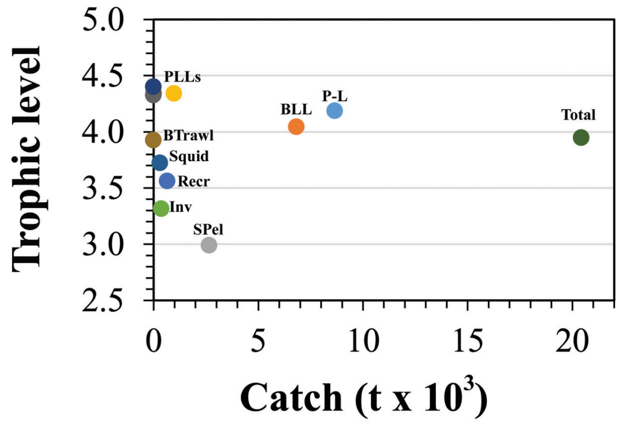

FIGURE 6 | Mean trophic levels of the catch for all fishing fleets included in the Azores ecosystem model for the reference year 1997. BLL is deep-water bottom longline and handline fisheries, P-L refers to the pole and line tuna fishery (including the live-bait catch), SPel refers to the small-size pelagic fisheries, PLLs refers to all pelagic longline fisheries, Recr is the recreational fishing, Inv is the commercial coastal invertebrates fisheries, Squid is the squid (*L. forbesii*) fisheries, and BTrawl is the bottom trawling experimental fishing.

−2.0, revealing a strong negative effect of toothed whales on its main prey. The MTI analyses showed the influence of toothed whales, pelagic sharks, cephalopods and small-size pelagic fish in the ecosystem, having both strong positive and negative impacts in many components of the ecosystem. For example, toothed whales had a strong negative impact on their main prey (e.g., cephalopods) but also had a positive impact on other groups or species (e.g., large-size pelagic fish or *Beryx* spp.), through mixed trophic links such as removal of their predators (**Figure 7**). On the other hand, small-size pelagic fish had a strong positive impact on its predators (e.g., Seabirds or tuna) and a negative impact though complex trophic links (e.g., toothed whales). Most groups will have a positive impact of their fisheries while most fisheries showed a strong negative effect on its target species (**Figure 7**). However, some groups had a negative impact on some fisheries as for example, toothed whales and cephalopods were shown to have a negative impact on the pole and line and pelagic longline fisheries. Dolphins were found not to have a significant impact on any type of fisheries.

The Keystoneness index calculated according to Libralato et al. (2006) were highest for pelagic sharks (#38, KS = 0.66), toothed whales (#44, KS = 0.64) and cephalopods (#6, KS = 0.61; **Figure 8**). These groups also showed the highest relative total impact, highlighting their importance in the ecosystem structure. The groups of the small-size pelagic fish and bathypelagic fish (group #14 and #18) also showed high keystoneness (KS = 0.39 and 0.30, respectively) indicating an important role as prey in the food web.

Ecological summary characteristics of the system are represented in **Table 2**, along with general ecosystem statistics for other deep-sea models. The ratio of total primary production/total respiration (Pp/R) was 8.2 while the total primary production/total biomass ratio (Pp/B) was 67.7. The total transfer efficiency of the system was estimated to be 18.8%.

DISCUSSION

An ecosystem model for the Azores EEZ using 1997 as the reference year was built using various data sources. This reference year seemed appropriated for the purpose of the study since it will allow for model validation with data collected afterwards, but it represents a snap-shop of the ecosystem state. Ecological groups were chosen so that the model could address deep-water and open ocean related research questions, as compared to the Azores ecosystem model presented in Guénette and Morato, 2001, where coastal, shallow water fish groups were overrepresented. Total marine fishery catch data from Pham et al. (2013), including illegal, unreported and unregulated catch for the Azores EEZ, is assumed to be of high confidence. However, many input parameters such as biomass, diet composition, P/B and Q/B were often estimated from other regions, from other models or even guesstimated, leading to a decreased quality and higher uncertainty associated with the model, and inconsistencies in the estimation of the biomass, P/B, Q/B and P/Q ratios. Nevertheless, the model pedigree (0.53) was similar to the value reported for the deep-sea ecosystem (0.54) in the NW Mediterranean Sea (Tecchio et al., 2013) and higher than the overall mean (0.47; range between 0.14 and 0.74) of the pedigree index recorded for 34 models (Colléter et al., 2015). Therefore, the model was built with source data of an overall reasonable quality, especially considering the normally low data availability for deep-sea ecosystems (Heymans et al., 2011).

The model construction highlighted the lack of valued information for some of the groups of the ecosystem. Especially biomass estimates for the Azores EEZ were lacking and providing those biomass estimates from stock assessments seem to be the key to enhance the model quality and accuracy. Biomass was calculated empirically for the primary producer groups and some top predator groups to constrain the model within total biomass boundaries, and to deal with the issue of migrating species. Migration was accounted for by estimating the average annual biomass for these top predator migrating groups. The biomass of other species were estimated by the model and found comparable to the estimates presented in the previous ecosystem model for the Azores (Guénette and Morato, 2001). Estimated biomasses for three commercially important fish species, representing the only single-species groups in the previous model (*H. dactylopterus*, *Pagellus bogaraveo* and *P. phycis*), were similar between the two models. Other groups that showed large differences in estimated biomasses were the large-size pelagic (two orders of magnitude lower in the current model), small-size demersal fish (one order of magnitude higher), and large-size demersal fish and turtles groups (one order of magnitude lower). Biomass estimates presented by Guénette and Morato, 2001 were either estimated by the model, or derived empirically by the authors, so whether these inconsistencies are improvements or deteriorations in model quality remains unclear.

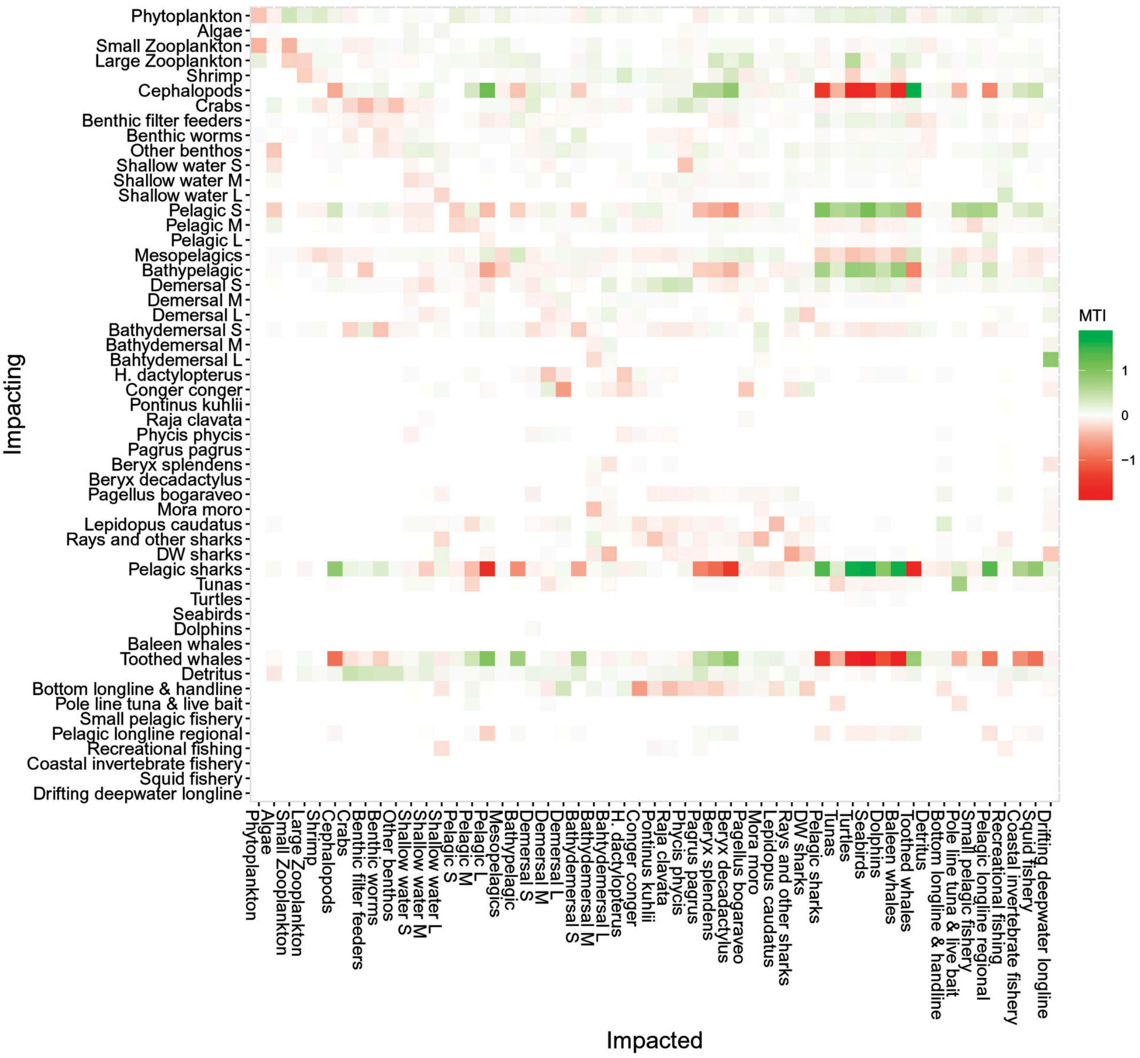

FIGURE 7 | Mixed trophic impact analysis of the Azores ecosystem model for the reference year 1997. The figure shows positive (green), negative (red), or no (white) impacts. Impacting groups are shown on the vertical axis, and impacted groups on the horizontal axis. S, small-size; M, medium-size; L, large-size; DW, deep-water.

Trophic level estimates for the single species fish groups were found similar to those TL estimated by stable isotope analyses at the Condor seamount in the Azores EEZ (Colaço et al., 2013) and a stomach content analysis of demersal fish in the Azores (Morato-Gomes et al., 1998); i.e., trophic levels within the range of ±0.2 TL from reported values. The only exceptions were *C. conger* and *R. clavata* where the model estimated a TL of 0.4 and 0.3 higher, respectively. Also some non-single species groups (deepwater sharks, shrimps and crabs) was compared and showed similar TL between the model the stable isotopes estimates (Colaço et al., 2013). This could indicate that the diet composition data of those groups is of reasonable quality, and that only the diet input for *C. conger* and *R. clavata* should be reassessed, even though the diet composition information for these last species was taken from stomach content analyses from within the Azores EEZ (Morato et al., 1999, 2003). The surprisingly high TL of the cephalopod group may be related to findings that some deep-sea cephalopod are top predators (Cherel et al., 2009; Fanelli et al., 2012). On the other hand, the trophic levels of low TL groups such as small- and large- size zooplankton, and benthic worms may be underestimated compared to published estimates from stable isotopes (Fanelli et al., 2011a,b, 2013), revealing once again the limited information available for these groups in the Azores. Adjusting the diet composition of low trophic level groups to increase their TL didn't have an impact in the model estimated parameters, rather than producing an overall overestimation of the TLs of all other groups in the model.

Omnivory indices were overall low, indicating prey speciation for the majority of the groups. This is contrary to the perception that deep-sea species are opportunistic feeders, feeding on a wide range of prey species (Gage and Tyler, 1991; Anastasopoulou et al., 2013; Gale et al., 2013; Mueller et al., 2014; Bernal et al., 2015; Hoving and Robison, 2016). Recent studies, however, have shown specialized feeding strategies in some deep-sea organisms (e.g., Romeu et al., 2016). Nevertheless, in the Azores there is still limited knowledge concerning the diet composition of most deep-sea species, highlighting the difficulty to quantify opportunistic feeding (e.g., scavenger behavior) in deep-sea environments.

The functional groups identified as keystone, were also those that had the highest impact in the mixed trophic impact analysis. A keystone group has a disproportionally large impact on other groups in the system, in spite of having a relatively low abundance (Paine, 1995). Cephalopods are one of these keystone groups that play a major role in the marine ecosystem (Rodhouse and Nigmatullin, 1996; Fanelli et al., 2012), however their exact trophic relationships in the Azores deep-sea environment remains unclear. They are proven to be important prey species for large-size predators (e.g., sperm whales), but far less is known about their diets (Clarke, 1996). The top predators pelagic sharks and toothed whales also showed a high keystoneness, in accordance to what has been found in other regions (Libralato et al., 2006).

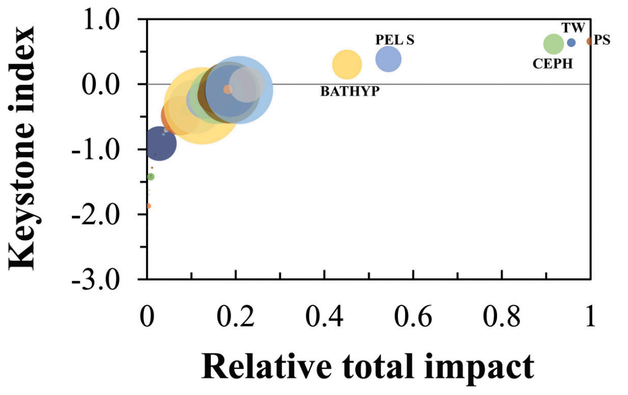

FIGURE 8 | Keystoneness analysis for each functional group, according to Libralato et al. (2006), of the Azores ecosystem model for the reference year 1997. The keystoneness index is shown on the vertical axis, the relative total impact on the horizontal axis. BATHYP is bathypelagic fish, PEL S is small pelagic fish, CEPH is cephalopods, TW is toothed whales, and PS is pelagic sharks.

Future versions of this model should focus on finding an improved ecological grouping that better differentiates between deep, intermediate and shallow water species, and by including feeding guilds (e.g., according to feeding type). This will be paramount mainly for lower trophic levels where the available information is most limited. Additionally, future models should also consider grouping animals according to their larval dispersal distances, since this has been demonstrated of paramount importance for marine conservation (Baco et al., 2016). The use of multistanza (size-age structured species groups) for certain commercial species could also increase the later policy simulation options. Dealing with migrating species is another important issue for improving the model quality, but is complicated due to EwE's inherent limitation for dealing with migration (Christensen and Walters, 2004). And finally providing biomass estimates for a number of groups will greatly improve the model quality.

Heymans et al. (2016) raised serious concerns on the use of ecosystem models with low confidence in exploring management decisions and ecological theories. Therefore, the current version of the ecosystem model should be used with caution until biomass estimates are validated with survey data or the model is fitted to time series. Since the Azores fishing industry is dominated by hook and line gears (Carvalho et al., 2011), and since hook and lines have been demonstrated not suitable for

TABLE 2 | Summary ecosystem statistics calculated for the present model of the Azores exclusive economic zone (Azores EEZ, 2016), with statistics reported for other deep-sea ecosystem dominated models: Azores EEZ (Guénette and Morato, 2001), North Atlantic sea theoretical seamount (Morato et al., 2009), Catalan margin (Tecchio et al., 2013), Barents Sea (Blanchard et al., 2002), New Zealand Southern Plateau (Bradford-Grieve et al., 2003).

	Azores EEZ		N Atlantic	Catalan margin	Barents sea	Southern Plateau, NZ	Units
	(2016)	(2001)	(2009)	(2013)	(2002)	(2007)	
Sum of all consumption	365.27	1106.44	1119.90	51.36	2400.61	610.00	t/km^2/yr
Sum of all exports	1470.90	1611.03	1465.80	20.09	37.29	0.97	t/km^2/yr
Sum of all respiratory flows	204.27	435.08	610.50	20.19	1062.77	264.00	t/km^2/yr
Sum of all flows into detritus	1554.47	1825.44	1623.70	65.84	1700.77	251.00	t/km^2/yr
Total system throughput	3587.91	4977.98	4820.00	157.48	5201.00	1136.00	t/km^2/yr
Sum of all production	1763.11	2314.75	2361.00	14.83	1920.00	451.00	t/km^2/yr
Mean trophic level of the catch	3.95	3.80	4.08		4.11	4.48	
Calculated total net primary production	1675.16	2046.10	2076.00		1100.04	265.00	t/km^2/yr
Total primary production/total respiration	8.20	4.70	3.40		1.04	1.00	
Net system production	1470.90	1611.03	1466.00	−20.19			t/km^2/yr
Total primary production/total biomass	67.73	57.72	19.30	0.00	9.26		
Total biomass/total throughput	0.01	0.01	0.02	0.02	0.02	0.01	
Total biomass (excluding detritus)	24.73	35.45	107.60	3.93	118.81	6.22	t/km^2
System Omnivory Index	0.22	0.21	0.23	0.29	0.23		
Ecopath pedigree index	0.53			0.54			

total biomass estimates, fitting the model to relative abundances from survey data might be a way forward toward model validation. In addition, comparing the estimated biomasses across taxa and trophic levels as suggested by Link (2010) and reiterated in Heymans et al. (2016) will point to areas where better biomass estimates are needed.

However, this model is an important step toward the ecosystem-based management that is needed under the MSFD and CFP to address ecosystem-based related management questions. To assess GES of marine waters, criteria for 11 descriptors of the MSFD have been adopted but there is still a substantial need to develop additional scientific understanding to determine appropriated ecosystem metrics. Food-web models such as the one developed here, have been shown to be useful in obtaining appropriated indicators of GES (Shannon et al., 2014; Kleisner et al., 2015; Coll et al., 2016; Reed et al., 2016).

AUTHOR CONTRIBUTIONS

TM and TP designed the study. TM, EL, GM, CP, JB, and AS collected and processed most of the data. TM, EL, TP, and JH preformed most of the analyses. All authors contributed to writing the paper.

FUNDING

This research received funding from Fundo Regional da Ciência, Tecnologia (FRCT), through the research project 2020-M2.1.2/I/026/2011 (Pro-Convergência), and from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 633680, DiscardLess project. The authors also acknowledge funds provided by the Fundação para a Ciência e a Tecnologia (FCT) through the strategic project (FCT/UID/MAR/04292/2013) granted to MARE. TM is supported by Program Investigador FCT (IF/01194/2013).

ACKNOWLEDGMENTS

Building an Ecopath model is a very data intensive and time consuming task, involving many colleagues and collaborators. With a high probability of not mentioning all collaborators, the authors would like to acknowledge the important contributions from Ricardo Santos, Miguel Machete, João Gil Pereira, Pedro Afonso, Fernando Tempera, Filipe Porteiro, Ana Colaço, Mónica Silva, Verónica Neves, Maria Magalhães, Jorge Fontes, Natacha Carvalho, Rui Prieto, Helena Krug, João Gonçalves, Gilberto Carreira, Marina Carreiro-Silva, Ricardo Medeiros, Hugo Diogo, Frederic Vandeperre, Alexandra Rosa, Eva Giacomello, Dália Reis, ngela Canha, Carla Dâmaso.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2016.00245/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 07 February 2017
doi: 10.3389/fmars.2017.00025

Persistent Enhancement of Micronekton Backscatter at the Summits of Seamounts in the Azores

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OPEN ACCESS

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Specialty section:
This article was submitted to Deep-Sea Environments and Ecology, a section of the journal Frontiers in Marine Science

Received: *31 March 2016*
Accepted: *23 January 2017*
Published: *07 February 2017*

Citation:
Cascão I, Domokos R, Lammers MO, Marques V, Domínguez R, Santos RS and Silva MA (2017) Persistent Enhancement of Micronekton Backscatter at the Summits of Seamounts in the Azores. Front. Mar. Sci. 4:25. doi: 10.3389/fmars.2017.00025

Knowledge of the dynamics of micronekton at seamounts is critical to understanding the ecological role of these ecosystems. Active acoustic techniques are an effective tool to monitor the distribution and movements of pelagic organisms. We carried out several day- and nighttime active acoustic surveys over a 3-year period (2009–2011) to characterize the spatial and temporal distribution of micronekton backscatter on two seamounts (Condor and Gigante) in the Azores and in the surrounding open-waters. The highest mean volume backscattering strength (MVBS) was consistently found in the water column over the seamount summits, regardless of the season and diel period. MVBS over the summits was 14–26 times higher than over the slopes, and 10 times higher than in open-waters. Diel variations in backscatter intensity were more pronounced in open-waters and in Gigante seamount, with higher values during the day in open-waters, and at night over the summits and slopes of Gigante. Over Condor seamount, diel changes in backscatter intensity were small, but MVBS was generally higher at night than during the day, as in Gigante. Persistence of strong acoustic backscatter over the summits of Condor and Gigante seamounts is a key finding of this study and may be explained by the presence of a seamount-associated micronekton community and by the retention of vertically migrating micronekton. The latter hypothesis is consistent with observed day-night differences in backscatter, suggesting that nocturnal migrants may be passively transported or actively swim above seamount summits and slopes. Possible physical mechanisms leading to the observed patterns in micronekton distribution are discussed. This study contributes to a better understanding of how seamounts may influence the spatial and temporal dynamics of micronekton assemblages.

Keywords: micronekton, acoustic scatterers, seamount, spatial and temporal dynamics, Azores

INTRODUCTION

Sound-scattering layers (SLs) are dense aggregations of planktonic and nektonic organisms that reflect sound in water and can be observed acoustically. Scattering layers of micronekton are taxonomically diverse, consisting of small (mostly 2–20 cm long) pelagic crustaceans (adult euphausiids, decapods, and mysids), cephalopods (namely sepiolids, pyroteuthids, and enoploteuthids) and fishes (mainly mesopelagic and juvenile stages of pelagic species) (Barham, 1966; Brodeur and Yamamura, 2005).

Micronekton SLs are abundant worldwide and form a substantial biomass in oceanic waters (Atkinson et al., 2009; Irigoien et al., 2014). The organisms that make these layers are critical components of oceanic food webs: they consume large quantities of phytoplankton and small zooplankton (e.g., copepods) and serve as primary prey for higher trophic levels, including charismatic and endangered marine mammals and seabirds, as well as commercially harvested fishes and squids (Harrison and Seki, 1987; Pauly et al., 1998; Watanabe et al., 2009). Most micronektonic taxa undergo diel vertical migration (DVM), residing in deeper waters during the day and swimming toward the surface to feed at night (Sutton, 2013). Extensive diel horizontal migrations between oceanic and slope waters have also been documented in some areas (Benoit-Bird and Au, 2006). Thus, micronekton SLs also play an important role in the transport of carbon and nutrients between mesopelagic and epipelagic environments (Hudson et al., 2014), and between oceanic and neritic systems (Benoit-Bird and Au, 2004).

Like other topographic features, seamounts can shape the aggregation of pelagic organisms and many seamounts support unusually high biomass of micronekton SLs compared to the surrounding ocean (e.g., Boehlert, 1988; Johnston et al., 2008; Letessier et al., in press). Various non-exclusive mechanisms may explain increased micronekton biomass over seamounts. The abrupt topography of seamounts can interact with background ocean circulation promoting a range of physical processes (e.g., deflection of impinging currents, rectification of internal tides, amplification of internal waves, and formation of Taylor columns) that intensify flow over the summit and upper slopes of the seamount (Genin, 2004). This, in turn, enhances the flux of food particles and plankton over these areas, attracting micronekton foraging on surface layers during the night, and increasing the horizontal advection of migrating and non-migrating micronekton (Koslow, 1997; Porteiro and Sutton, 2007; Morato et al., 2009). Vertically migrating micronekton swept onto seamounts by prevailing currents may also become trapped over the seamount summit and upper slopes (Isaacs and Schwartzlose, 1965). Finally, seamounts may provide calm suitable shelter at the benthic boundary layer for some micronekton (Genin, 2004). Therefore, micronekton may conserve energy by taking advantage of this quiescent habitat during non-feeding intervals, whereas in open-waters they must swim constantly.

The effectiveness and magnitude of each of these mechanisms in increasing or aggregating micronekton biomass will depend on a range of factors, including the topography of the seamount, the extent, and depth of the summit and plateau, the distance to the continental shelf and to other bathymetric features, the hydrographic conditions, and the community composition (Porteiro and Sutton, 2007). For instance, bottom trapping will only be effective for seamounts shallower than the daylight depth of micronekton organisms (Genin, 2004; Martin and Christiansen, 2009; Denda and Christiansen, 2014). Moreover, because different organisms migrate to different daylight depths, the deeper the seamount summit, the fewer the species retained and the lower the biomass (Genin and Dower, 2007). Strong variability in impinging currents leading to instability of Taylor columns can also impact the retention potential over seamounts and affect concentration of micronekton organisms (Diekmann and Piatkowski, 2004). In addition, micronekton may suffer increased predation from benthopelagic predators inhabiting the seamount or they may actively avoid seamount shallow topographies (Pusch et al., 2004).

In fact, not all seamounts appear to hold high SL densities. Denda and Christiansen (2014) found no significant differences in zooplankton biomass at Ampère and Senghor seamounts (summits of 55 and 90 m, respectively) relative to open-waters. Reduced zooplankton biomass was found above the summits of Sedlo (750 m) and Seine (170 m) seamounts compared to the slope and far-field sites (Martin and Christiansen, 2009). Abundance and biomass of mesopelagic organisms was also lower above the summits of Cross seamount (330 m; De Forest and Drazen, 2009; Drazen et al., 2011) and over the summits and slopes of the Great Meteor (330 m) (Pusch et al., 2004).

While most of these studies suggest some kind of effect of seamounts on micronekton communities, they provide only limited information about the spatial and temporal dynamics of SLs around seamounts. Prior research on seamount pelagic communities has largely been based on trawl sampling. Trawl surveys sample only specific depth layers at discrete locations and because they are expensive and time-consuming, usually a small number of samples are obtained from each area. Thus, trawl catches provide a snapshot of the pelagic community living at seamounts. In contrast, active acoustics provide continuous measurements of organisms' abundance and depth distribution and are increasingly used to assess the density and study the movements of fish and zooplankton at various spatial and temporal scales (Benoit-Bird and Au, 2003). Acoustic studies on a wide range of seamounts, especially in different ecological settings, can contribute to our understanding of the dynamics of micronekton communities and provide insights into the underlying forcing mechanisms.

We conducted several day- and night-time active acoustic surveys over a 3-year period (2009–2011) to characterize the spatial and temporal dynamics of micronektonic backscatter at two seamounts in the Azores archipelago. This region has one of the highest densities of seamounts in the Northeast Atlantic (Morato et al., 2013). Several of these seamounts host commercially valuable pelagic and demersal fish species important for local fisheries (Morato et al., 2008b; Menezes et al., 2013) and act as foraging posts for sea turtles, seabirds, marine mammals, and large pelagic fishes (Santos et al., 2007; Morato et al., 2008b; Silva et al., 2013; Afonso et al., 2014b; Tobeña et al., 2016). However, with few exceptions (e.g., Hargreaves, 1975; Martin and Nellen, 2004), previous studies on acoustic backscatter distribution in the Azores have focused only in open ocean areas (e.g., Moore, 1950; McElroy, 1974; Smailes, 1976; Wade and Heywood, 2001). Here we compare the distribution of micronekton backscatter in open ocean waters and at two seamounts with different physical properties to (i) investigate the influence of seamounts in driving distribution patterns of acoustic scatterers, (ii) determine how this effect varies over diel and seasonal scales, and (iii) discuss physical and biological processes controlling dynamics of micronekton in the study areas.

METHODS

Study Area

Acoustic surveys were conducted in Condor and Gigante seamounts in the Azores archipelago and in adjacent open-waters (**Figure 1**). Morato et al. (2008a) classified both seamounts as "large seamount-like features," i.e., seamounts rising more than 1000 m from the surrounding seafloor.

Condor seamount (38°33′N, 29°02′W) is located approximately 17 km to the WSW of Faial Island and 100 km east of the Mid-Atlantic Ridge (MAR) (**Figure 1**). Condor is an elongated feature about 26 km long and 7.4 km wide at the 1000-m depth contour. It is a shallow-intermediate seamount with two major peaks: the main summit 182 m depth on the western side, and a secondary peak 214 m deep on the eastern side of the seamount. The summit at the 300-m depth contour is nearly flat, with a total surface area of 11.6 km^2 (**Figure 2A**). The nearest large seamount is at 39 km to the south, while the nearest small seamount (200 m $\leq$ height $<$ 1000 m) is 23 km to the SSE (Morato et al., 2008a). Tempera et al. (2012) describe in great detail the geomorphological structures on Condor seamount. Condor is characterized by peculiar multi-scale dynamics involving localized upwelling–downwelling patterns, enhanced mixing, and pronounced closed circulation structures over the seamount (Bashmachnikov et al., 2013).

Gigante seamount (38°59′N, 29°53′W) is situated about 98 km to the WNW of Faial Island and 6 km east from the MAR (**Figure 1**). It is approximately 16 km long and 6–13 km wide at the 1000-m depth contour. It is a shallow seamount, reaching 161 m depth, and the summit has a small surface area of 0.7 km^2 at the 300-m depth contour (**Figure 2B**). The nearest large seamount is located 31 km to the south, while the nearest small seamount is 15 km to the SW with a deep summit of 787 m (Morato et al., 2008a). The distance between Condor and Gigante seamounts is about 80 km. No hydrographical data are available for the Gigante area.

In addition to the seamounts, surveys were carried out at an open-water far-field site (38°30′N, 29°13′W), with depths ranging from 1770 to 1900 m (**Figure 2A**). This station was located 7 km west of Condor seamount (at the 1000-m depth contour; ∼10 km from the summit of Condor) and 35 km to the WSW of Faial Island (**Figure 1**).

Data Collection

Acoustic backscatter data were collected using a split-beam Simrad EK500 scientific echosounder system aboard R/V *Arquipélago*, operating at 38 and 120 kHz frequencies. Both elliptical transducers had approximately 7° beam widths (38 kHz: 7.2° along and 6.8° athwart; 120 kHz: 7° along and 7.1° athwart). They were set to operate with 1.024 and 0.256 ms pulse durations at 2000 and 1000 W transmit power for the 38 and 120 kHz frequencies, respectively. These settings allowed for 1000 and 300 m sampling depths for the 38 and 120 kHz frequencies, respectively. The transducers were calibrated every year prior to the first survey using a 60-mm-diameter copper sphere for 38 kHz and 23-mm sphere for 120 kHz, according to standard procedures (Demer et al., 2015). To exclude unwanted scatterers, such as plankton and other smaller organisms, the minimum threshold for the mean volume backscattering strength (S_v, hereafter designated as MVBS) was set to -70 dB re 1 m^{-1}. While this threshold level may exclude some scattering from low-density micronekton, -70 dB was selected based on known aggregative behavior of micronekton (Saunders et al., 2013) and to exclude backscatter from larger zooplankton.

Acoustic surveys on Condor and Gigante seamounts and at the control site were conducted during the day and at night in spring (March), summer (June–August), and autumn (September and November) from 2009 to 2011. Surveys followed a systematic design, and acoustic backscatter data were collected continuously along a pre-defined transect. Acoustic surveys over seamounts covered nine transects: five transects perpendicular to seamounts (each 11.11 km) and four transects along seamounts (each 5.56 km), totaling 77.78 km (**Figure 2**). Sampling in open-waters followed a single transect 18.52 km long (**Figure 2A**). Survey speed varied between 7 and 8 knots, depending on sea conditions.

In 2010, trawl surveys were conducted concurrently with acoustic surveys to determine the contribution of different species or taxa to the acoustic backscatter and to estimate the abundance of organisms sampled acoustically. Twenty-five oblique tows were made in open-waters and around Condor using an Isaacs Kid Midwater Trawl (3-m IKMT). Unfortunately, these surveys failed to capture meaningful samples of micronektonic organisms (average of 2.3 fishes captured/tow, no zooplankton or cephalopods were captured), preventing groundtruthing of acoustic data.

Data Analysis

Data Processing

Acoustic backscatter data were recorded using Movies + software (Ifremer) and then processed using Echoview software (Myriax Pty Ltd, Hobart, Tasmania). Data were pre-processed to avoid unreliable backscatter in the analysis. First, the surface layer (0–10 m depth) was excluded to avoid surface bubbles, noise, and near-field effects of the transducers. Then, each echogram was visually inspected to remove bottom echoes and acoustic or electrical noise from the sampled water column.

Only the 38 kHz data were used in this study to characterize the spatial and temporal distribution of acoustic scatterers, since the maximum penetration depth of the 120 kHz echosounder was

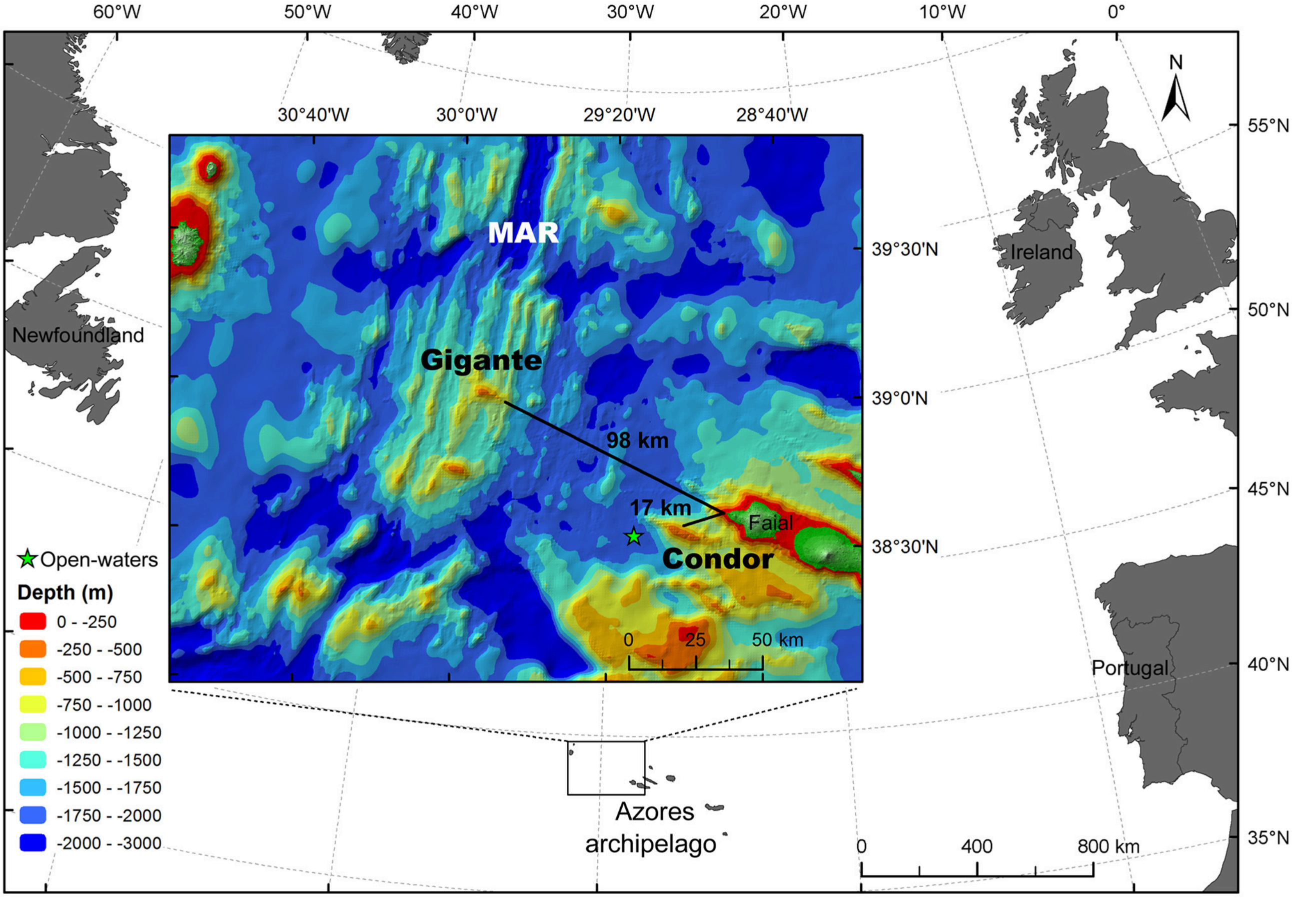

FIGURE 1 | Study area. Map of the study area indicating the locations where acoustic surveys were conducted: Condor seamount, Gigante seamount, and open-water far-field site (green star). MAR: Mid-Atlantic Ridge. Azores bathymetry data credits: (Lourenço et al., 1998).

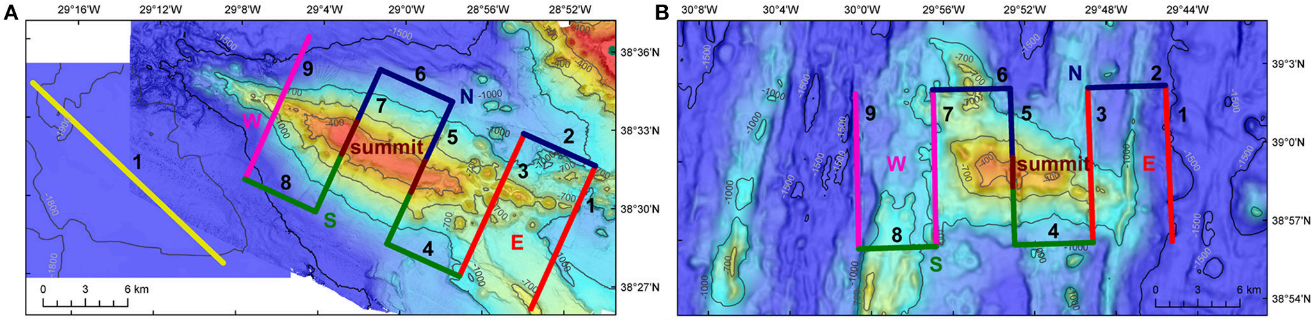

FIGURE 2 | Acoustic surveys. Surveys to collect acoustic data on Condor seamount **(A)**, Gigante seamount **(B)** and in open-waters **(A)**. Surveys at seamounts were composed of nine transects, while surveys in the open-waters followed a single transect. Condor and Gigante's transects were categorized into five regions: summit, East (E), North (N), South (S), and West (W). Warmer colors indicate shallower depths. On Condor seamount, transect 7 runs across the main summit (182 m deep) and transect 5 crosses the second peak (214 m deep). On Gigante seamount, transect 5 runs across the shallowest peak of 161 m depth. Bathymetry data credits: Open-waters—MeshAtlantic, IMAR-DOP/UAz; Condor—EMEPC, DOP/UAz, Project STRIPAREA/J.Luís/UAlg-CIMA; Gigante—EMEPC, IMAR-DOP/UAz.

only 300 m and, therefore, unable to capture the full vertical range of the deep scattering layer (∼400–700 m depths). At the 38 kHz frequency, acoustic backscatter is dominated by organisms with gas-filled structures (Kloser et al., 2009; Davison et al., 2015). Many epipelagic and mesopelagic fishes possess a gas-filled swimbladder that present a high density contrast with seawater, making them the most significant contributors to acoustic backscatter at the 38 kHz (Davison et al., 2015). Conversely, large crustaceans, squids and non-gas bearing fishes, are relatively weak scatterers at this frequency (Lavery et al., 2002; Kang et al., 2005) and their importance to total backscatter in this study was likely small. Gelatinous organisms with pneumatophores may also be important sources of scattering at 38 kHz (Warren et al., 2001). Bongo net catches indicate that pteropods, siphonophores, and salpids are not abundant in the surface waters around Condor and at a nearby open-water site (Carmo et al., 2013), and their scattering would have been masked by the much stronger scattering of the dominant swimbladdered fish. Thus, acoustic backscatter patterns reported in this study are likely to be primarily attributed to gas-bearing swimbladder fish.

Since most acoustic scatterers were aggregated in schools or layers, single-target echoes could not be identified. Therefore, acoustic density of micronekton fish was estimated by calculating the MVBS (dB re 1 m^{-1}). We initially calculated MVBS over 10-m deep by 100-m long bins. These data were used to construct variograms to determine the extent and scale of spatial autocorrelation in the acoustic observations (Rivoirard et al., 2000). Analysis of the variograms indicated that data were no longer correlated at distances >1 km. MVBS was recalculated for the entire water column (from 10 m depth to the sea floor) by 1-km long bins.

Day- and night-time acoustic data were examined separately, excluding crepuscular data from the analysis (1 h before and after sunrise and sunset) to avoid migratory periods of the sound scattering organisms. The sunrise and sunset times for the Azores were acquired from the U.S. Naval Observatory Astronomical Applications Department database. Echograms were visually inspected to ensure no migratory periods were included.

Statistical Analysis

Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs) were used to investigate spatial and temporal differences in MVBS in the study areas, and to assess the influence of physiographic variables. Latitude and longitude were strongly collinear (0.96) and were therefore not included in the analysis. We also tried to model the spatial distribution of backscattering strength using transect as a covariate, but these models provided a poor fit to the data. Instead, MVBS was compared between locations (open-waters, Condor, Gigante) and between seamount regions (summit, East, North, South, West) identified based on their orientation relative to the summits (**Figure 2**). Bottom depth at sampling locations was derived from *in situ* measurements of the echosounder, and slope values were extracted from a Digital Terrain Model created from depth data using ArcGIS$^{\text{TM}}$ Spatial Analyst tools. Possible effects of physical and biological variables other than physiography, such as currents, temperature, salinity, or chlorophyll-*a*, were not investigated because spatial and temporal resolution of those variables was too coarse to compare with backscatter data.

Prior to analysis, normality of the data was verified by plotting histograms and normal Q-Q plots of all variables, and boxplots were used to detect extreme values and outliers in the data. Boxplots, coplots and lattice graphs were used to inspect the relationship between covariates and the response variable, and pairplots were used to assess collinearity among covariates.

The GLM approach was inappropriate for our dataset since the relationship between MVBS and bottom depth was non-linear. Thus, backscattering data were modeled using GAMs with a Gaussian distribution and an identity link function, using the "*mgcv*" R package. Two different models were fitted to investigate the effect of bottom depth, slope, diel period, and season in MVBS in seamounts (summits and slopes) and open-waters (Model 1), and to compare MVBS and its diel pattern between the slopes of each seamount (Model 2):

$$\begin{aligned}\text{Model 1}: \text{MVBS} = {} & \alpha + \text{Location} \times \text{Diel} + \text{Location} \times \text{Season} \\ & + f(\text{Bottomdepth}) \times \text{Location}_{\text{O}} \\ & + f(\text{Bottomdepth}) \times \text{Location}_{\text{C}} \\ & + f(\text{Bottomdepth}) \times \text{Location}_{\text{G}} + f(\text{slope}) \\ & \times \text{Location}_{\text{O}} + f(\text{slope}) \times \text{Location}_{\text{C}} \\ & + f(\text{slope}) \times \text{Location}_{\text{G}} + \varepsilon_i\end{aligned}$$

where MVBS was the response variable, α the intercept, f the smoothing function for predictor variables, and ε_{i} the residuals. The model contained three categorical explanatory variables: location (open-waters—Location$_{\text{O}}$, Condor—Location$_{\text{C},}$ and Gigante—Location$_{\text{G}}$), diel (day and night) and season (spring, summer, and autumn). Bottom depth and slope were fitted as smoothing functions, and the model allowed for a different smoother at each location.

$$\text{Model 2}: \text{MVBS} = \alpha + \text{Region} \times \text{Diel} + f(\text{Bottomdepth}) + \varepsilon_i$$

where region had four levels corresponding to seamount sides (East, North, South, and West), and diel and bottom depth were fitted as in the previous model. Bottom depth was included as a covariate to account for differences in topography between seamount regions. A separate model was built for Condor and Gigante.

A backward stepwise selection procedure was used to identify the best fitting model based on the Akaike Information Criterion (AIC) value and analysis of deviance. The adequacy of the best fitting model was inspected using normal Q-Q plots, histograms of the residuals, and plots of residuals and observed values versus fitted values (Supplementary Figures 1, 2).

Maps of predicted MVBS were produced to visualize the distribution of acoustic scatterers in the study areas. As differences in MVBS between seamount slopes were small and not significant (see Results below), maps were generated using the best fitting Model 1. A 1 × 1 km spatial grid was created for the study area and values for the variable bottom depth were extracted at the mid-point of each grid cell. MVBS and respective standard errors were predicted for each grid cell, diel period, and season. Standard errors of predicted MVBS were also mapped to visualize regions of model uncertainty (Supplementary Figures 3, 4).

TABLE 1 | Summary of the acoustic surveys.

Year	Season	Date	Condor		Gigante		Open-waters	
			Day	Night	Day	Night	Day	Night
2009	Summer	15/06–18/06	9	9	9	9	1	1
	Summer	10/08–13/08	9	9	9	9	1	1
	Autumn	03/11–04/11			7	9		
	Autumn	25/11–27/11	9	9			1	1
2010	Spring	29/03–31/03	8	9				1
	Summer	05/07–10/07	9	8	9	9	1	1
	Autumn	14/09–18/09	9	9	9	9	1	1
2011	Spring	15/03–16/03					1	1
	Spring	19/03–20/03			9	9		
Total transects			53	53	52	54	6	7
Total distance covered (km)			402	419	422	434	108	122

Number of transects carried out in each location (Condor and Gigante seamounts, and in open-waters) per diel period and season.

TABLE 2 | Results from the best GAM of MVBS in open-waters and seamounts.

Parametric terms	*df*	*F*	*p-value*
Location	2	17.360	**<0.001**
Diel	1	4.839	**0.028**
Season	2	2.685	0.069
Location×Diel	2	19.958	**<0.001**
Location×Season	4	26.538	**<0.001**
Smooth terms	***edf***	***F***	***p-value***
s(Bottom depth)×Location$_O$	1.000	0.509	0.476
s(Bottom depth)×Location$_C$	4.837	146.345	**<0.001**
s(Bottom depth)×Location$_G$	5.862	60.386	**<0.001**

Deviance explained = 48.7% $n = 1918$
R-sq. (adj) = 0.48 AIC = 10089.51

Significant terms ($p < 0.05$) are shown in bold. Location$_O$, open-waters; Location$_C$, Condor seamount; Location$_G$, Gigante seamount.

RESULTS

Over 3 years, nine acoustic surveys were completed in 29 days, totaling 1907 km surveyed (**Table 1**). Similar sampling effort was achieved at Condor (821 km) and Gigante (856 km) seamounts, whereas in open-waters 230 km of acoustic surveys were carried out. The day-night sampling was equally distributed at each study location, but there were considerable differences in sampling between seasons. Most of the survey effort was conducted in summer due to favorable weather conditions, followed by autumn and spring. Sampled bottom depths around Condor seamount ranged between 182 and 1604 m, at Gigante between 161 and 1609 m, and in open-waters between 1774 and 1904 m. Seamounts had steeper slopes (Condor: 0.05°–73.08°; Gigante: 0.16°–51.30°) than open-waters (0.02°–3.94°).

Distribution of Acoustic Scatterers: Open-Waters vs. Seamounts

Acoustic scatterers were observed throughout the study area in all seasons and diel periods. Overall, the highest MVBS was found in the open-water site (−73.50 ± 2.47 dB), followed by Condor (−75.20 ± 5.19 dB) and Gigante (−75.74 ± 4.40 dB). MVBS was significantly related to seamounts bottom depth (**Table 2**). In Condor and Gigante seamounts, the highest MVBS was found over the shallowest areas. Backscattering strength then decreased rapidly with increasing seafloor depths with the lowest values occurring in areas 800–1100 m deep (**Figures 3A,B**). Conversely, in open-waters, MVBS decreased linearly but only moderately with depth (**Figure 3C**). Average backscattering strength above the summits of Condor (−63.28 ± 4.71 dB) and Gigante (−63.59 ± 6.76 dB) was 18 times higher the MVBS measured over the slopes (Condor: −75.90 ± 4.29 dB; Gigante: −76.04 ± 3.88 dB) and about 10 times higher MVBS in open-waters (**Figure 4**).

There was also a significant interaction between location and diel period, and between location and season (**Table 2**). In open-waters, the highest backscattering occurred during the day, while the reverse pattern was observed in Gigante. Diel differences in acoustic backscatter were small in Condor (**Figure 5A**, Supplementary Table 1). In Condor, MVBS peaked in spring, decreasing substantially in summer (ΔMVBS = 1.52 dB) and autumn (ΔMVBS = 5.27 dB) (**Figure 5B**, Supplementary Table 1). In contrast, mean backscatter was slightly higher in summer than in the other seasons in Gigante and open-waters.

Distribution of Acoustic Scatterers between Seamount Slopes

Model 2 was built to investigate differences in MVBS and its diel pattern between the slopes of Condor and Gigante seamounts. The best fitting models for each seamount explained 15.7–18.3% of the deviance (**Table 3**). The interaction between region and diel period, and the main term region had no significant effect on MVBS in any of the seamounts. Little variation was observed in MVBS between seamount flanks and the differences were not consistent between seamounts (**Figure 6**). Slightly lower values of MVBS were found on the eastern (−77.50 ± 3.87 dB) and northern (−75.58 ± 4.38 dB) slopes of Condor, and on the southern (−76.53 ± 4.10 dB) and northern (−76.27 ± 4.15 dB) slopes of Gigante.

Predicted Spatial Density of Acoustic Scatterers

The predictions of MVBS for Condor and Gigante seamounts and for the open-water site for each diel and season from the best fitting model (48.7% of deviance explained; **Table 2**) are shown in **Figures 7**, **8**. The maps highlight the spatial heterogeneity in backscattering strength around seamounts related to the depth gradient. The model predicted the highest MVBS over the summits and upper slopes of Condor and Gigante seamounts, irrespective of the season and diel period. Acoustic density decreased drastically along the seamount slopes, reaching the minimum values at the base of both seamounts. A slight enhancement in backscatter was predicted toward deeper waters

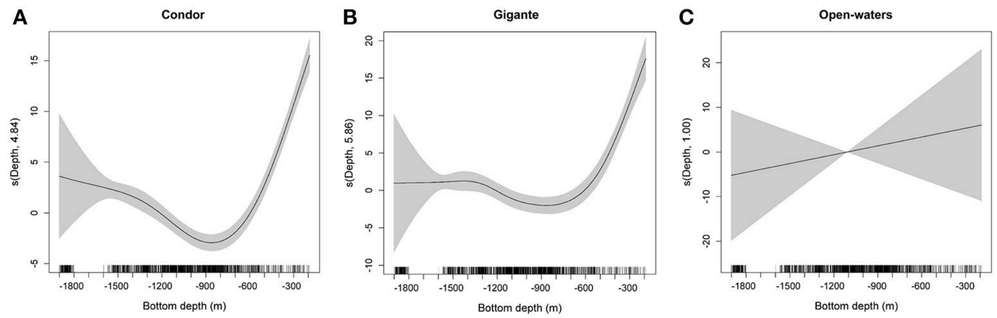

FIGURE 3 | Response curves for the GAM of MVBS relative to bottom depth for seamounts and open-waters. Fitted smoothing function (solid line) for bottom depth for Condor seamount **(A)**, Gigante seamount **(B)**, and open-waters **(C)** obtained by the best GAM. Estimated degrees of freedom (edf) are displayed on the y-axes. Tick marks on the x-axis show sample values. Shaded areas denote the approximate 95% confidence bands.

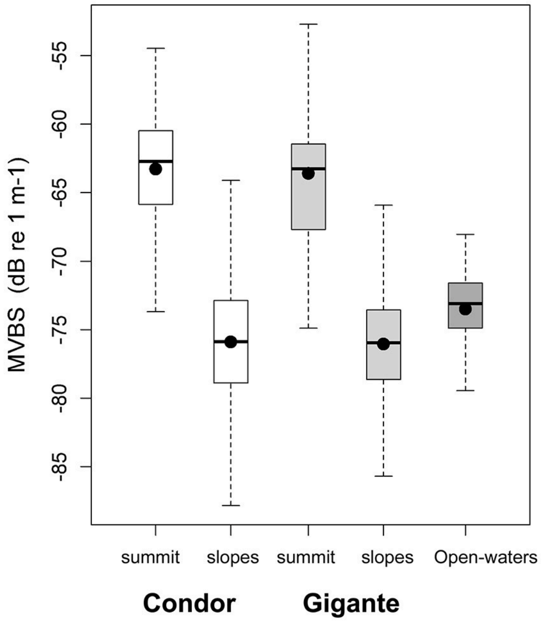

FIGURE 4 | Backscatter in seamount summits and slopes, and in open-waters. Box plots of MVBS for the summits and slopes of Condor seamount (white), Gigante seamount (light gray) and in open-waters (dark gray). Black dots represent the mean; black bars the median; boxes the 25 and 75% quartiles; whiskers extend 1.5 times the interquartile range (spread) from the box edges or indicate the most extreme values of the spread.

away from Condor and Gigante seamounts and in the open-water site. Average MVBS predicted for the open-water site was 3% higher (ΔMVBS = ~2.4 dB) than MVBS in seamount slope areas but 15% lower (ΔMVBS = ~10 dB) than MVBS predicted for Condor and Gigante summits.

Whilst the acoustic scatterer's hotspot over the Condor summit was a consistent feature in all seasons it decreased in size from spring to autumn (**Figures 5B**, **7**). Still, it was in autumn that the spatial gradient in acoustic density was more evident because of lower backscatter over the slopes and in areas farther away from the seamount. Compared to Condor and to the open-water site, diel differences in MVBS were much more pronounced in Gigante (**Figures 5B**, **8**) with consistently higher nighttime MVBS over the summit and slopes.

DISCUSSION

Our results clearly show that Condor and Gigante seamounts significantly affected the spatial and temporal distribution of micronekton, and this effect could be detected up to ~7 km from the seamount summit. Even though the two seamounts differ in a number of physical characteristics (e.g., size, shape, flatness of the summit, and distance to other topographic features), patterns and estimates of acoustic density were similar between them. Strong sound-scattering aggregations were a permanent feature above the summits of Condor and Gigante in all seasons, both during the day and at night. This contrasted with the reduced scattering in the water column above the seamount flanks, which was even lower than that measured in open ocean waters just a few kilometers away. Also, differences in scattering strength between seamount slopes were generally small, providing no evidence for micronekton concentrations at the upstream or downstream side of the seamounts. Finally, on seamount summits and slopes, acoustic backscatter increased during the night, while the opposite diel pattern was observed in open-waters.

Aggregations of micronekton are taxonomically diverse and include fish, cephalopods, and crustaceans but acoustic observations at the 38 kHz frequency used in this study are dominated by air-filled swimbladder fish (Kloser et al., 2009; Davison et al., 2015). Therefore, we assume that variations in backscattering strength mostly reflect changes in the relative density of micronekton fish, although occasional contribution of large nekton fishes cannot be completely ruled out. Still, the sound scatter produced by organisms depends not only on their numerical density but also on their morphological, physiological and behavioral characteristics (Godø et al., 2009; Davison, 2011; Davison et al., 2015). While it is impossible to identify species from acoustic scattering alone, the acoustic properties of micronekton fish, together with information on micronekton composition from studies in Condor and at other

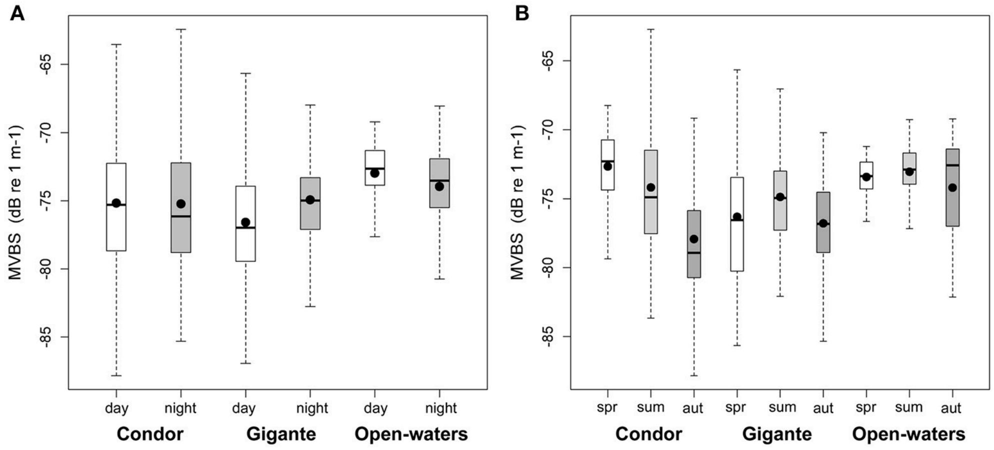

FIGURE 5 | Diel and seasonal patterns in backscatter in seamounts and open-waters. Box plots of MVBS for: **(A)** day (white boxes) and night (gray boxes) and **(B)** seasons—spring (white boxes), summer (light gray boxes) and autumn (dark gray boxes). MVBS for seamount summits and slopes were pooled into an overall value. Black dots represent the mean; black bars the median; boxes the 25 and 75% quartiles; whiskers extend 1.5 times the interquartile range (spread) from the box edges or indicate the most extreme values of the spread.

TABLE 3 | Results from the best GAM of MVBS between seamount slopes.

	Condor			Gigante		
Parametric terms	***df***	***F***	***p-value***	***df***	***F***	***p-value***
Diel				1	43.21	**<0.001**
Smooth terms	***edf***	***F***	***p-value***	***edf***	***F***	***p-value***
s(Bottom depth)	4.216	31.26	**<0.001**	4.189	20.91	**<0.001**
	Deviance explained = 18.3% R-sq. (adj) = 0.18 AIC = 4279.48 *n* = 769			Deviance explained = 15.7% R-sq. (adj) = 0.15 AIC = 4577.78 *n* = 849		

Significant terms (p < 0.05) are shown in bold.

seamounts in the Atlantic, may provide clues about the identity of sound scatterers and help explain the patterns documented here.

Midwater trawls conducted over the slopes of Condor and at a far-field station (located very close to our open-water site) captured 46 taxa but only a few species/families were numerically important (Porteiro et al., 2011). *Cyclothone* spp. represented 66% of the total catches in number, followed by myctophids (18%), the stomiids *Stomias boa ferox* and *Chauliodus sloani* (8%), and the sternoptychid *Argyropelecus hemigymnus* (2%). The majority of fishes ranged from 20 to 80 mm, well within the size range of micronekton.

Slope samples were dominated by species that also occurred in open-waters (Porteiro et al., 2011). Mid- and deep-water (400–800 m) catches were largely dominated by *Cyclothone* spp., a group of non-migratory mesopelagic fish very abundant worldwide (Nelson, 2006). Most *Cyclothone* species are strong scatterers at the 38 kHz frequency (Peña et al., 2014; Ariza et al., 2016) and this group likely was the major source of the day and nighttime backscatter over seamount slopes and in open-waters. Another important contributor to the backscatter outside the summits may be *A. hemigymnus*, also known to reside at depth all day long (Peña et al., 2014). Myctophids (especially *Lobianchia dofleini*, *Diaphus rafinesquei, and Lampanyctus pusillus*) were the second most abundant group overall but the first in shallow waters at night (Porteiro et al., 2011), consistent with their well-known DVM (Sutton, 2013). Catches were dominated by species with functional swimbladders as adults (Davison, 2011) which are strong scatterers. However, swimbladder resonance of myctophids and other mesopelagic fishes seems to increase with depth depending on swimbladder size, potentially biasing estimates of backscatter in deeper waters (Kloser et al., 2002; Godø et al., 2009; Yasuma et al., 2010). The effects of this bias in our estimates will be discussed below. In contrast to the former taxa, the two stomiids possibly contributed little to acoustic scattering because they lack air-filled swimbladders.

Unfortunately, a single nighttime trawl was conducted over the summit of Condor, capturing 3 fish specimens (myctophids *D. rafinesquei* and *S. boa ferox*; Porteiro et al., 2011). Video images from a baited lander (Fontes and Menezes, 2011) and from remotely operated vehicles (ROV) (Porteiro et al., 2013) showed that, during the day, the pelagic fish fauna on Condor summit was dominated by dense swarms of small sized zooplanktivorous fishes, including the seaperches (*Anthias anthias* and *Callanthias ruber*), the snipefish (*Macrorhamphosus scolopax*) and the blue jack mackerel (*Trachurus picturatus*), with occasional records of unidentified myctophids (Porteiro et al., 2013). Care must be taken, however, as ROV observations may be biased due to the known avoidance behavior of some micronekton fishes, including myctophids (Porteiro et al., 2013). Most zooplanktivorous fish were absent from the slopes of Condor and the few species present below 300 m depth had densities 20 times lower than those observed at the summit (Porteiro et al., 2013).

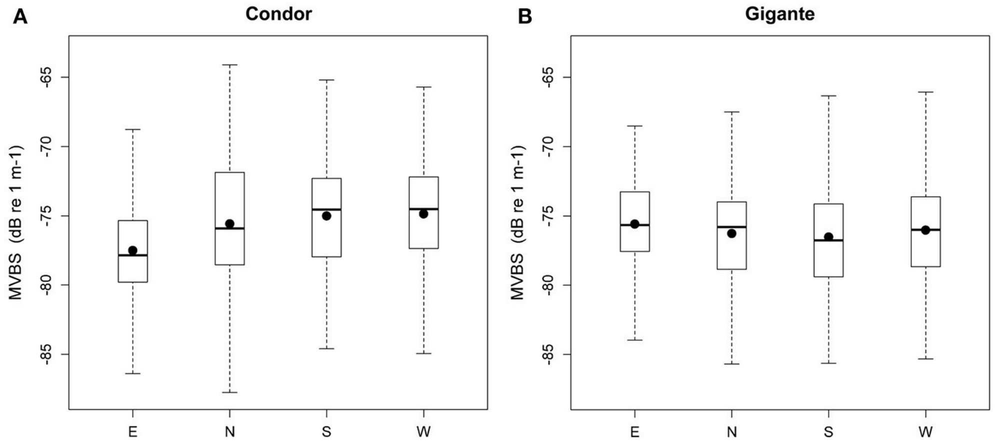

FIGURE 6 | Backscatter in seamount slopes. Box plots of MVBS for the slopes in Condor seamount **(A)** and Gigante seamount **(B)**. Black dots represent the mean; black bars the median; boxes the 25 and 75% quartiles; whiskers extend 1.5 times the interquartile range (spread) from the box edges or indicate the most extreme values of the spread.

These and other zooplanktivorous fish may well be part of the permanent micronekton community inhabiting the summits and upper slopes of Condor, and possibly Gigante, as reported in other shallow and intermediate seamounts in the subtropical Northeast Atlantic (see Morato and Clarke, 2007). Most of these fishes are good sound reflectors and possibly accounted for a significant part of the enhanced backscatter above the summits of Condor and Gigante in all seasons and diel periods. Seamount-associated micronekton fishes live a benthopelagic lifestyle, feeding in the water column above the seamount when conditions are right and resting at the benthic boundary layer (Boehlert, 1988; Genin, 2004). Presence of a resident micronekton community implies the existence of an abundant and predictable supply of prey. While there is no information on the oceanographic conditions or biological communities in Gigante, physical processes at Condor may be responsible for concentrating prey for resident micronekton fish. Condor is characterized by a quasi-persistent anticyclonic cap located 50–60 m above the summit, possibly generated by tidal forcing and/or a steady impinging flow (Bashmachnikov et al., 2013). Taylor caps penetrating into the euphotic zone can locally enhance primary production by bringing nutrient-rich waters to the surface (Genin, 2004). In the case of Condor, however, trapping induced by the Taylor cap occurs mostly below 170 m depth (i.e., below the seasonal pycnocline) (Bashmachnikov et al., 2013) and is unlikely to boost primary production. In addition, changes in water circulation and mixing result in periodic shedding of the Taylor cap lasting from weeks to months (Bashmachnikov et al., 2013). Thus, presence of the Taylor cap will hardly cause a persistent enrichment in primary productivity over Condor. Consistent with these findings, there is no evidence of increased phytoplankton concentrations in the top 100 m above the summit and slopes of Condor (Santos et al., 2013). Rather, the Taylor cap may retain sufficient concentrations of autochthonous or allochtonous prey above the seamount to enable self-sustainability of the resident micronekton (Genin, 2004; Genin and Dower, 2007). Alternatively, or in combination with this mechanism, the seamount micronekton community might rely on vertically migrating zooplankton that becomes trapped above the seamount summits.

Similar DVM behavior by mesopelagic fishes would add to the backscatter from the seamount resident community, amplifying the contrast between summits and slopes and causing diel changes in backscatter above the summits. Mesopelagic fish ascending from deeper waters in the vicinity and above the seamount flanks could be attracted to the summits to feed on concentrations of zooplankton created by physical forcing or topographic blockage. Despite being strong swimmers, micronekton may also be passively advected onto the summits by currents (Kaartvedt et al., 2009). The seamounts' shallow topography aggregates these fishes in near-surface waters at night and possibly retains part of this community during the day (Genin, 2004). Obviously, this would result in fewer fishes returning to bottom waters at the seamount flanks. The effect of topographic blockage should be more pronounced in Condor than in Gigante, because the smaller plateau of Gigante likely is less efficient at blocking the fish descent. We believe this is one of the reasons for the much clear day-night differences in backscattering intensity in Gigante, as opposed to Condor where diel changes were small. Although video imagery and net sampling provided only limited evidence of the presence of vertically migrant fishes on the Condor plateau (Porteiro et al., 2011, 2013), topographic blockage has been suggested as one of the mechanisms responsible for the increased nighttime micronekton abundance at other shallow/intermediate seamounts (Boehlert, 1988; Johnston et al., 2008).

As a result of the interaction of the local flow field with the seamount topography, distribution of micronekton fish often exhibits small-scale spatial variability, with enhanced biomass or densities on the downstream flanks of seamounts. At Southeast Hancock Seamount, micronekton fish moving into waters above the seamount on a diel basis were usually displaced by strong

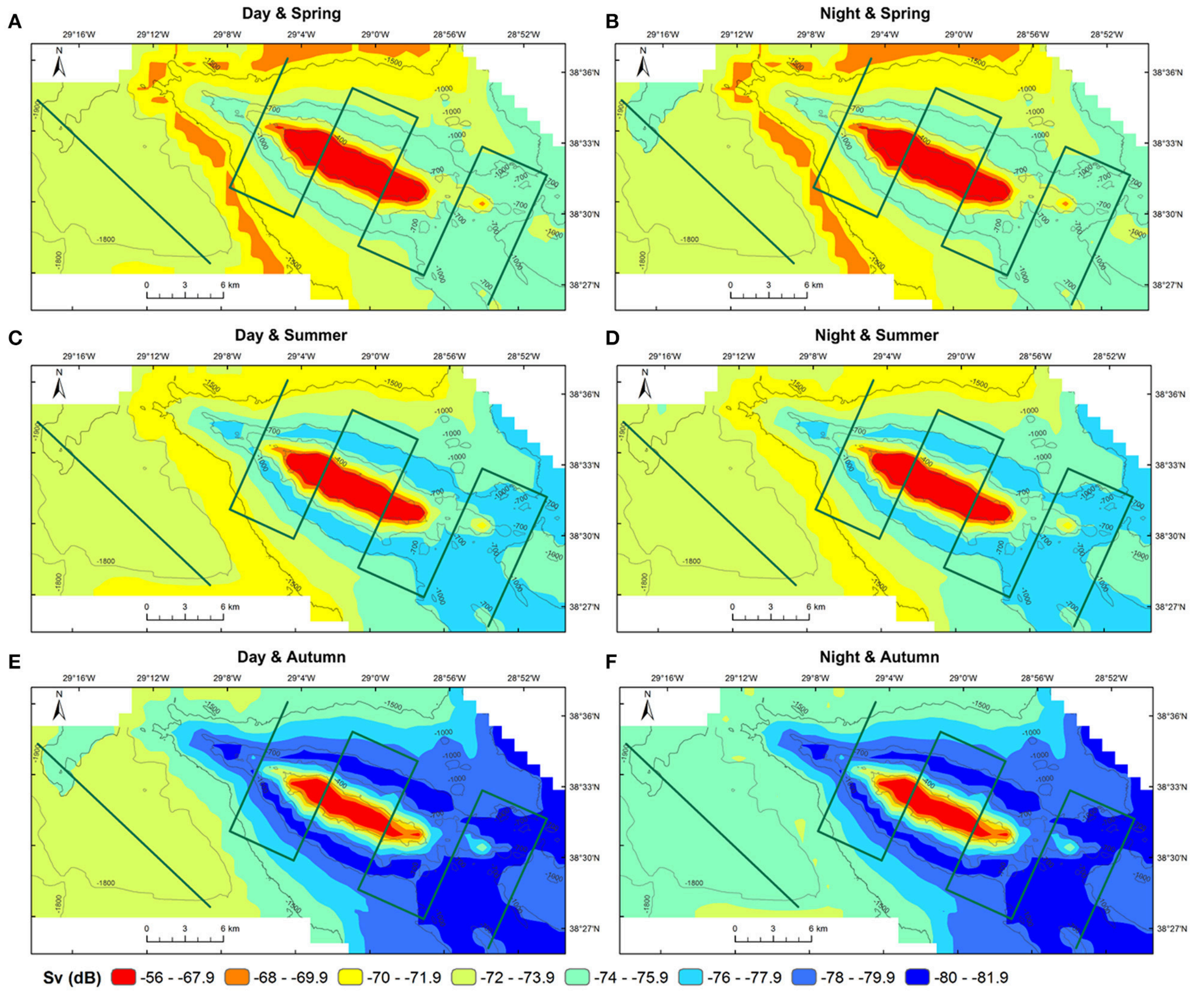

FIGURE 7 | Predicted backscatter in Condor seamount and in open-waters. Predicted MVBS obtained from the best GAM (Model 1) for each diel period (day—left; night—right) and season (spring—top; summer—middle; autumn—bottom). Warmer colors indicate higher S_V. Green lines illustrate transect surveys.

currents to the downstream side of the summit by the end of the night (Wilson and Boehlert, 2004). Porteiro et al. (2011) reported lower abundance and biomass of midwater fishes on the northern slope (upstream) of Condor when compared to the southern slope (downstream), consistent with the northern-southerly direction of the upper ocean current (Bashmachnikov et al., 2013). Since Gigante is under the influence of the same regional current, we assumed that acoustic density would be higher on the southern slope of the two seamounts. Against our expectation, total backscatter and its diel patterns were similar upstream and downstream the seamounts. In the case of Condor, it is possible that the effects of the anticyclonic vortex prevail over the background oceanic flow (Bashmachnikov et al., 2013), trapping micronekton fish and their prey and preventing them from being advected downstream the summit. Nonetheless, the presence of a Taylor cap has not been documented in Gigante and the potential retention of such mechanism in Condor is unknown. Concurrent acoustic and oceanographic observations will help understanding how different physical processes shape micronekton distribution at the scale of the seamounts.

Another interesting finding of this study is the reduced acoustic density above the seamount slopes in comparison to open-waters. As already mentioned, samples from midwater trawls conducted over the slopes and off the seamount were similar (Porteiro et al., 2013), suggesting that differences in species composition are unlikely to be responsible for backscattering variations between those regions. Assuming identical composition of scatterers, then a difference in mean backscattering strength of 2.4 dB indicates that density of micronekton above the slopes was nearly half of that found in the open ocean (Simmonds and MacLennan, 2005). Such difference may result from: (i) the retention at summit of part of the population of migrant fishes that never return to their daytime depths above the slopes, and (ii) the upward migration

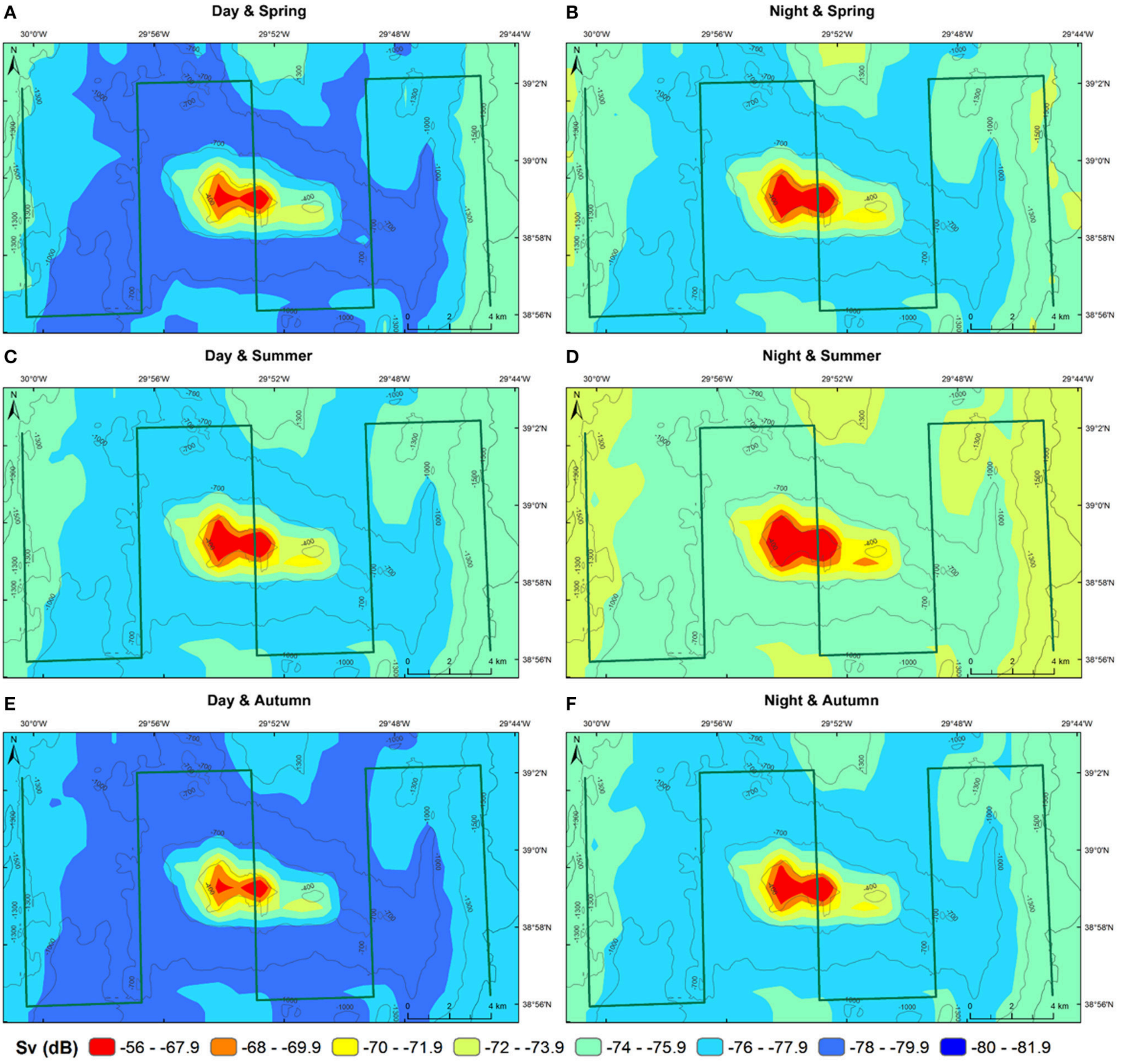

FIGURE 8 | Predicted backscatter in Gigante seamount. Predicted MVBS obtained from the best GAM (Model 1) for each diel period (day—left; night—right) and season (spring—top; summer—middle; autumn—bottom). Warmer colors indicate higher S_V. Green lines illustrate transect surveys.

in open-waters of some mesopelagic species from depths beyond the seamount base (∼1000–1200 m depth).

Contrasting with the diel pattern at seamounts (more evident in Gigante), backscatter measured in open-waters was consistently higher during the day. Different behavioral processes and physical mechanisms may explain this pattern. On one hand, the upward migration of taxa from depths beyond >1000 m; i.e., outside the range of the 38 kHz (Domokos, 2009) should contribute to greater nighttime backscattering. This could be offset by the effects of the horizontal movements of micronekton and of swimbladder resonance. During the day, myctophids occur in discrete, dense patches, but at night they tend to disperse horizontally and vertically in the upper water column (Benoit-Bird and Au, 2006). As the horizontal range of myctophids increases, estimates of volume backscattering strength decrease. Swimbladder resonance increases acoustic backscatter from fishes and such effect is more pronounced at greater depths (>300 m) (Godø et al., 2009; Yasuma et al., 2010). Consequently, bias from swimbladder resonance mainly affects daytime acoustic observations, when mesopelagic fish occur deeper in the water column. At present, it is impossible to know to what extent resonance may have overestimated daytime backscatter measurements. Future studies examining the vertical distribution of micronekton may help elucidating the role played by each of these factors.

We found a well-defined seasonal pattern in acoustic density at Condor seamount, with an evident peak in spring, lower backscatter in summer and the lowest values in autumn. In comparison, seasonal variations were not so clear in Gigante and in open-waters. In Condor, maximum concentrations of chlorophyll-*a* occurred in spring, associated with the well-mixed water column and lower surface temperature, whereas minimum values were recorded in summer with stratified, warmer waters (Santos et al., 2013). Zooplankton develops rapidly following the onset of the phytoplankton bloom, with the highest abundances recorded from spring to early summer (Carmo et al., 2013). More importantly, increased prey availability likely attracts greater numbers of micronekton fish to the seamount. As zooplankton becomes scarcer in upper layers in late summer and autumn, due to the decline in primary production and to predation, but also because some species descend to mid-waters to overwinter, several mesopelagic fishes, including myctophids, restrain from migrating to the surface at night (Dypvik et al., 2012 and references therein). Density of migrant micronekton fish above the seamount summits will therefore decrease, following the decrease in zooplankton biomass after the spring-early summer peak. In addition to prey distribution, life history patterns of seamount fishes may also contribute to seasonal peaks in backscatter. While several species are year-round residents at seamounts, others aggregate at seamounts periodically for spawning (e.g., *M. scolopax, Capros aper*) (Morato and Clarke, 2007). Arrival of high-density spawning aggregations at seamounts (Jorgensen et al., 2016) could potentially explain seasonal variations in acoustic density, although we have no way of confirming this hypothesis.

Acoustic sampling is a powerful method to estimate the distribution and biomass of micronekton fish but it has its own limitations, uncertainties and potential bias, which ultimately constrained interpretation of some of the findings of this study. First, our study area is certainly inhabited by many micronekton species not visible in the echograms, either because they are non-resonant at the 38 kHz frequency or because their weak signal is masked by dominant sound reflectors. Second, acoustics does not allow direct taxonomic identification of sound scatterers nor does it provide certain quantitative data (e.g., size and weight of organisms) necessary to estimate absolute density or biomass. In this study we did not attempt to convert MVBS into biomass; instead, MVBS was interpreted as a proxy for the relative density of micronekton. We also didn't assume equal composition of scattering layers within the study area or across the water column but tried to support our findings on available (albeit limited) knowledge about local pelagic communities. As an example, we avoided comparisons between Gigante and Condor because we lacked information on possible scattering layer constituents in Gigante. Future studies should consider using multi-frequency acoustics to better discriminate sound scatterers, providing insights into the relative composition and density of micronekton layers. Another constraint of this study is that acoustic data were not integrated with oceanographic observations to determine how bio-physical parameters influenced the distribution of sound-scattering micronekton fish. The only data available on sea surface temperature or chlorophyll-*a* were weekly averages at 4-km resolution which was judged too coarse considering the size of the seamounts, the duration of the surveys and the spatial variability of the SL. Therefore, we chose to use static seabed features (bottom depth and slope), as well as spatial (location and region) and temporal (diel and season) variables. Future work will be necessary to refine these analyses by including more biological-relevant environmental variables. Despite these shortcomings, this work fills an important knowledge gap of micronekton, the "missing link" between lower and higher trophic levels, and provides some clues to the mechanisms responsible for the variation in micronekton distribution across and within seamounts, contributing to our growing understanding of the functioning of seamount ecosystems.

SUMMARY

Through a series of acoustic surveys conducted over a 3-year period, this study provides the first comprehensive view of the distribution and temporal dynamics of micronekton at seamounts in the Azores. Our work showed that presence of seamounts affected the horizontal distribution of acoustic scatterers, contributing to the formation of persistent higher MVBS in near-surface waters over the summits, which contrasted with lower acoustic density in the water column above the slopes and in the open ocean. The dynamics of micronekton around seamounts likely result from a combination of behavioral and physical mechanisms acting over different spatial and temporal scales. The DVM brings huge concentrations of mesopelagic fishes to surface waters to feed under the cover of darkness. Fishes may actively seek seamounts to take advantage of prey aggregated around the top by the Taylor cap (Bashmachnikov et al., 2013). Micronekton fishes may also be advected from upstream the summit and become entrained in the circular flow generated by the Taylor cap (Pitcher and Bulman, 2007). Fishes present in the water column immediately above the plateau could then be trapped at the seamount when trying to descend the next dawn. In addition to vertically migrant fishes, we suggest these seamounts support an abundant community of year-round or seasonal residents.

The dynamics of micronekton likely has profound effects on the structure and function of seamount ecosystems, and on their linkages to other pelagic or coastal systems. Stable isotopes analysis showed that the food chain on Condor seamount is composed of five trophic levels, and that mesopelagic organisms play a crucial role in the trophic web, linking the epipelagic environment to benthic, and benthopelagic organisms (Colaço et al., 2013). Increased micronekton abundance at seamounts likely supports important biomasses of benthic fishes and attracts numerous pelagic visitors (Morato et al., 2008b). Studies conducted in the Azores have shown that several benthic and benthopelagic fish species rely on SL constituents for food (Gomes et al., 1998; Morato et al., 2001; Colaço et al., 2013) and that the vertical distribution of these fishes at seamounts is driven by the dynamics of the SL (Afonso et al., 2014a).

Large pelagic predators, such as tuna, seabirds, and marine mammals, feed on various micronektonic organisms (Choy et al., 2016). The effect of seamounts at aggregating micronekton may play an important role in the feeding success of these top predators, especially in oligotrophic environments, where food is often scarce and too patchy to be efficiently exploited. Indeed, several of these predators are known to intensively use and forage at seamounts (Awkerman et al., 2005; Garrigue et al., 2015; Jorgensen et al., 2016). In the Azores, several dolphin species preferentially distribute in areas with high density of seamounts (Tobeña et al., 2016) and baleen whales instrumented with satellite tags spent days to weeks apparently foraging around seamounts (Silva et al., 2013). Preliminary analyses of long-term acoustic recordings from hydrophones deployed at Condor and Gigante showed that dolphins use these seamounts nearly every day (Silva and Cascão, 2011). By concentrating micronekton prey in near-surface waters, these seamounts likely provide increased foraging opportunities for shallow divers.

AUTHOR CONTRIBUTIONS

Conceived and designed the acoustic surveys: IC, ML, MS. Executed data collection: IC. Performed data analyses: IC, RéD, MS. Wrote the paper: IC, MS. Reviewed the manuscript and approved the final version: IC, ML, RéD, VM, RuD, RS, MS.

FUNDING

This research was supported by FEDER funds, through the Competitiveness Factors Operational Programme - COMPETE, QREN European Social Fund, by national funds, through FCT - Foundation for Science and Technology, under project TRACE (PTDC/MAR/74071/2006), EEA Grants Financial Mechanism—Iceland, Liechtenstein, and Norway, through research CONDOR (PT0040). We acknowledge funds provided by FCT to MARE, through the strategic project UID/MAR/04292/2013. MS was supported by POPH, QREN European Social Fund and the Portuguese Ministry for Science and Education, through an FCT Investigator grant (IF/00943/2013). IC was supported by an FCT doctoral grant (SFRH/BD/41192/2007). The FCT Exploratory project (IF/00943/2013/CP1199/CT0001) paid the fees for this open-access publication.

ACKNOWLEDGMENTS

The authors are grateful to the crew of the R/V *Arquipélago*, João Medeiros, Yves Cuenot, and colleagues from the Oceanography group, especially Alexandre Medeiros and Sergio Gomes, for their support during data collection. Special thanks to Alexandre Morais for providing technical assistance on the EK500 echosounder and Yorgos Stratoudakis for hosting IC at IPMA for technical support on Movies+ software. We thank the reviewers for the fruitful discussions that significantly improved the original manuscript. This study is an output of research project TRACE (PTDC/MAR/74071/2006)—Cetacean-habitat associations in oceanic ecosystems: an integrated approach.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2017.00025/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 13 February 2017
doi: 10.3389/fmars.2017.00037

The Azores Confluence Zone

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The goal of this study is to characterize the meteorological and oceanographic conditions affecting the Azores Archipelago, and explore their biological implications. The Mid-Atlantic region of the Azores Archipelago is under the permanent influence of the Azores high pressure system, thereby providing sustained Ekman transport that facilitates the convergence in regional oceanography. The west and central island groups are affected by incoming meanders and filaments originating in the Gulf Stream, whereas the east island group is most affected by westward propagating eddies pinching-off from the Azores Current. Output from the European Centre for Medium-Range Weather Forecasts are combined with altimetry data to study the dynamic oceanographic processes affecting the archipelago. Satellite-derived sea surface temperature and sea surface chlorophyll data are used as proxies to examine the biological enrichment processes. Climatological data analysis permits differentiation of the oceanographic systems that reach the west vs. those that affect the east island groups. This is the first study to document the Azores as an oceanic confluence zone and demonstrate the associated biological impacts.

Keywords: gulf stream, ekman transport, eddy-corridor, mesoscale eddies, wake, Sverdrup model

OPEN ACCESS

Edited by:
Mónica Almeida Silva,
MARE–Marine and Environmental Sciences Centre, Portugal

Reviewed by:
Irina Rypina,
Woods Hole Oceanographic Institution, USA
Ana Aguiar,
Met Office, UK

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Specialty section:
This article was submitted to Deep-Sea Environments and Ecology, a section of the journal Frontiers in Marine Science

***Received:** 01 April 2016*
***Accepted:** 30 January 2017*
***Published:** 13 February 2017*

Citation:
Caldeira RMA and Reis JC (2017) The Azores Confluence Zone. Front. Mar. Sci. 4:37. doi: 10.3389/fmars.2017.00037

INTRODUCTION

The oceanographic conditions in the Mid-Atlantic Ridge (MAR) region adjacent to the Azores Archipelago has been the subject of many scientific studies (e.g., Gould, 1985; Mailly et al., 1997; Alves and Verdière, 1999; Pingree et al., 1999; Alves et al., 2002; Juliano and Alves, 2007; Søliland et al., 2008; Barbosa et al., 2011; Lázaro et al., 2013). Fewer studies however, center on the oceanographic processes affecting the Azores Islands *per se*. Lafon et al. (2004) focused on the optimal processing of Sea Surface Temperature (SST) data derived from the National Oceanic and Atmospheric Administration's (NOAA) Advanced Very High Resolution Radiometer (AVHRR) for highly contaminated cloud regions such as the Mid-Atlantic, where the Azores islands are located (36°–39° N; 25°–31°W). Applying the methodology of Lafon et al. (2004), Bashmachnikov et al. (2004) used limited SST fields (2001–2002) to show that the Azores Current influences SST south of the archipelago. A significant isotherm tilt representing a sub-tropical frontal region was mentioned, but not subjected to further analysis.

Most recently, Silva et al. (2013) studied the seasonal differences of the nearshore phytoplankton communities and their probable relationship with a "southward intrusion of cold water," and with a "northward incursion of sub-tropical warm water." Nonetheless, there were no attempts to relate these different observations to the regional ocean circulation patterns.

To the best of our knowledge, Sala et al. (2015) was the most recent work attempting to link the island-induced biological productivity (particles/larvae) to the regional oceanographic phenomena of the NE Atlantic. An ocean circulation model, partially validated with ARGO data, was used to study the transport of particles in the upper 500 m of the water column. The study focused on the ability of the archipelago to capture the particles and organisms transported by the incoming currents and eddies. The regional oceanographic patterns were characterized using historical analysis of altimetry (Eddy Kinetic Energy—EKE) and Lagrangian Coherent Structures (LCSs). Results suggested that the west group of islands was mostly affected by north and eastward flow i.e., Gulf Stream; whereas the east group was strongly affected by a westward propagating flow. The latter is hypothesized to be the westward propagating eddies pinching-off from the Azores Current (previously reported by Pingree et al., 1999; Sangrá et al., 2009; Barbosa et al., 2011).

Building on the findings of Sala et al. (2015), our study dissects the predominant meteorological and oceanographic conditions affecting the Azores Archipelago. The island chain, in this perspective, is located in between two confluent systems that render the region rich in turbulent ocean features such as filaments and eddies. Thus, the islands act as natural "sieves" to these (far-field) incoming features, which can also contribute to the enhancement of local productivity. The methodology used in the study is presented in section Methods and Data Analysis; in section Results and Discussion the results are discussed; while the main conclusions and future work are detailed in section Conclusions.

METHODS AND DATA ANALYSIS

Volume Transport Calculation

Climate reanalysis data (ERA-Interim) from the European Center for Medium-Range Weather Forecasts (ECMWF), was used to characterize the seasonal wind conditions affecting the Azores Archipelago (Dee et al., 2011). A 10-year dataset (January-2004–December-2014) with a horizontal resolution of about 14 km (0.125°) was considered. The sea level pressure and the "u" and "v" wind components were extracted from the daily means before calculating the seasonal averages. Mean surface wind stress (τ_{wind}) was calculated as:

$$\tau_{wind} = \rho_{air} C_D U_h^2 \tag{1}$$

where, ρ_{air} is the density of the air (1.2 kg m^{-3}), C_D is a dimensionless quantity representing the wind-drag coefficient (0.0013) and U_h is the wind speed at 10 m above the sea surface (Gill, 1982). Considering the wind stress, one can compute the horizontal components of the total mass transport integrated over the oceanic Ekman Layer. The Ekman transport (M_{ek}) was calculated according to Smith (1968) and Bakun (1973):

$$M_{ek} = \frac{1}{\rho_{sw} f} \tau_{wind} \times \hat{z} \tag{2}$$

where τ_{wind} is the wind stress, $\hat{z}$ is a unitary vector and f is the Coriolis parameter; ρ_{sw} represents the reference seawater density (1024 kg m-^{3}).

A useful dynamical quantity is the vertical motion associated with the curl of the wind (Ekman pumping velocity):

$$w_{ek} = \frac{1}{\rho_{sw} f} \nabla \times \tau_{wind} \tag{3}$$

where $\nabla \times \tau_{wind}$ is the curl of the wind stress vector (Smith, 1968).

Under Sverdrup (1947) dynamics (ignoring islands), the predicted meridional transport is:

$$M_y = \frac{\nabla \times \tau_{wind}}{\beta \rho_{sw}} \tag{4}$$

whereas the zonal transport is found from the continuity equation. Integrating the meridional divergence from the eastern boundary (EB) westward we can estimate M_x:

$$M_x = \int_{EB}^{x} \frac{\partial M_y}{\partial y} dx' = -\frac{1}{\beta\rho} \int_{EB}^{x} \frac{\partial \left[\nabla \times \tau_{wind}\right]}{\partial y} dx' \tag{5}$$

Thus, the Sverdrup transport was calculated with similar formulae used by Kessler and Gourdeau (2006); where $\beta = \partial f/\partial y$; and the volume transport is in units of Sverdrup (1 $Sv = 10^6\ \mathrm{m}^3\ \mathrm{s}^{-1}$). Positive / negative sign means northward / southward or eastward / westward transports, respectively. Considering that the Sverdrup Transport represents the total transport in the wind-influenced layer, including both Ekman (M_{ek}) and Geostrophic transports (M_G), one can roughly estimate M_G, by subtracting M_{ek} from the Sverdrup transport.

Sea Surface Currents

Sea surface currents were characterized using NOAA's Ocean Surface Current Analysis—Real Time product (OSCAR). OSCAR combines geostrophic and Ekman transport components derived from the combination of altimetry and scatterometer wind data (Lagerloef et al., 1999) and is partially validated by global drifters and moored buoys. A 5-day mean product for a 10-year period (2004–2014) with a horizontal resolution of about 37 km, was used to compile the mean and seasonal surface currents. **Figure 1** shows the overall mean sea surface circulation patterns for the region.

Mesoscale Eddies Reaching the Azores

Most recently, Chelton and Schlax (http://wombat.coas.oregonstate.edu/eddies/) used a nonlinear methodology (Williams et al., 2011) to produce an updated eddy tracking dataset from the newly released AVISO, Mean Sea Level Anomaly fields (DT-2014 MSLA). The altimetry data reprocessing included new sensor-specific instrumental and atmospheric corrections, new inter-calibration of the various altimeters, a new tide model and a longer reference period of 20 years for mean sea level (Pujol et al., 2016).

A total of 459 mesoscale eddies were detected in the Azores sub-region (dashed box surrounding the archipelago of **Figure 4**) between 1992 and 2012 (20-years). On the new DT-2014 SSH fields, the trajectories are available at 1-day time steps and interpolated directly to a ¼° grid. Thus, all 1-day eddies (or older)

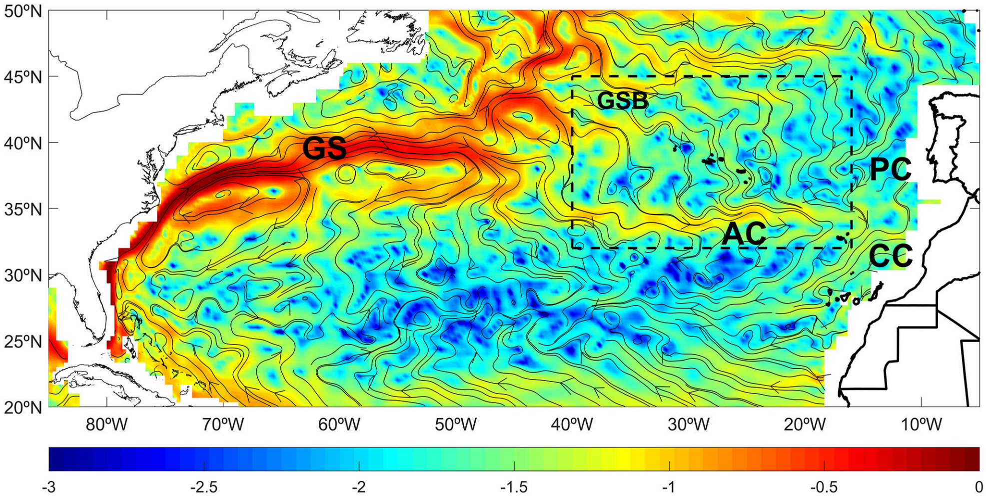

FIGURE 1 | Large-scale circulation of the North-Atlantic depicted by OSCAR-derived mean (2004–2014) sea surface currents are represented as isolines over $\log_{10}$ of the current velocity in order to improve the representation of the extremes. The known ocean circulation currents are marked: GS, Gulf Stream; GSB, Gulf Stream Bifurcations; AC, Azores Current; PC, Portugal Current; CC, Canary Current; the dashed-line box is centered around the Azores and depicts the region where most of the historical analysis were carried out.

were considered, and eddies had larger amplitudes, smaller radii and higher rotational speeds when compared to the previous analysis. They were also more nonlinear and had a higher eddy kinetic energy than those detected in previous datasets (Chelton et al., 2011). Statistically, the eddies in the new dataset have longer lifetimes and propagate over greater distances. These differences from the eddy characteristics in the previous datasets are mostly attributable to the changes in the new AVISO processing schemes used to produce the DT-2014 MSLA dataset (http://wombat.coas.oregonstate.edu/eddies/).

Sea Surface Temperature and Chlorophyll Enrichment

Sea surface temperature data was extracted from a merged satellite data product, the "Multi-scale Ultrahigh Resolution SST" (MUR SST). With a daily temporal frequency, and an original horizontal resolution of 1 km. MUR fills the gaps left by high cloud density using a "Battle-Lemarie" wavelet technique without statistical synthesis of the wavelet coefficients. That is, all coefficients are derived from the SST data in order to avoid data contamination with the interpolation (Chin et al., 1998).

Chlorophyll-a concentration is from weekly Moderate Resolution Imaging Spectroradiometer (MODIS) data installed onboard the Aqua satellite and processed by the "CoastWatch processing scheme" using the SeaWiFS Data Analysis System (SeaDAS) software (Fu et al., 1998). An atmospheric correction was applied to the data to yield a measurement of water leaving radiance (Shettle and Fenn, 1979; Gordon and Wang, 1994). These radiances are processed to obtain chlorophyll-a concentration using the NASA OC3M algorithm (described in O'Reilly et al., 2000). This algorithm is analogous to the OC4v4 algorithm used in the processing of SeaWiFS data, but is adjusted for the specific bands available on the MODIS sensor. Validation of the processing schemes is accomplished by comparison with *in situ* ocean color measurements gathered by buoys as part of the Marine Optical Characterization Experiment (MOCE). The data are mapped to an equal angle grid with a resolution of about 6 km (0.05 × 0.05° longitude) using simple arithmetic means to produce composite images of various durations (8-day in this particular case).

Water Masses and Nutrient Profiles

Taking profiles of temperature and salinity data from the World Ocean Atlas (WOA) 2013 (Locarnini et al., 2013; Zweng et al., 2013), and accounting for the weak seasonal variability of the ocean's interior, the annual water mass distribution for each island group was represented on a Theta-S diagram.

Nutrient profiles for the Azores were extracted from the WOCE Global Climatology (Gouretski and Koltermann, 2004). The WOCE Global Hydrographic Climatology has been derived using World Ocean Atlas data 1998. Data quality checks, cruise bias corrections, averaging on isopycnal surfaces, and optimal interpolation on 45 standard levels was used to determine the climatologies and error estimates of salinity and temperature and a suite of nutrients (Gouretski and Koltermann, 2004).

RESULTS AND DISCUSSION

Figure 1A summarizes the mean sea surface ocean circulation system of the NE Atlantic composed of: (i) the Gulf Stream (GS) and Gulf Stream bifurcations (GSB). As the Gulf Stream moves northward, it veers to the right due to the Coriolis effect. As it weakens, it meanders and bifurcates and several of these bifurcations reach the Azores from the northwest, north and northeast; (ii) the Azores current (AC), south of the archipelago, moves eastward but is populated with eddies—most of which propagate westward (WE). For completeness, the Portugal (PC) and Canary Currents (CC) are also represented in **Figure 1**.

The sea-surface currents represented herein are consistent with the sub-tropical Gyre circulation of the North Atlantic discussed in depth in Dohan and Maximenko (2010). The basin-scale Gyre circulation comprises an intense western boundary current (Gulf Stream) with a set of narrower and weaker re-circulation cells (bifurcations) populated by eddies, filaments and other turbulent features (see also Bryden et al., 2014; Elken, 2016). The Azores is affected by these filaments and eddies that converge at the archipelago. Whereas, the global wind patterns drive the basin-scale circulation, the local winds are expected to force local Ekman currents, surface waves, and turbulent features (Elken, 2016).

A schematic representation of the local sea surface circulation is shown in **Figure 2**. Westward propagating eddies from the Azores Current converge at the Azores and meet eddies and filaments from the Gulf Stream. As is apparent from **Figures 2**, **3**, the archipelago is bounded northward by incoming eddies and meanders originating in the Gulf Stream and southward by the westward propagating eddies pinching-off from the Azores Current. Simultaneously, the leeward side of the islands has weaker currents. The analysis also suggests a convergence of several incoming systems windward of the archipelago, particularly north of the Central group. In agreement with Sala et al. (2015), altimetry data analysis of the mean eddy kinetic energy ($EKE = \frac{1}{2}\left[u^2 + v^2\right]$) bracketed the archipelago with two regions of intense EKE activity: the Gulf Stream (GS), northward; and the Azores Current (AC), southward (**Figure 2**).

Regarding the eddy distribution, the analysis of the Chelton and Schlax North Atlantic dataset revealed the pathway of 459 eddies, of which 140 came to the Azores from afar ("far-field") and 319 were generated inside the Azores confluence zone ("near-field"). The far-field eddies were the largest (∼80 km radius) and longer-lived (∼51 days); whereas younger near-field eddies, lived between 2 and 10 days and reached slightly smaller (mean) sizes (70 km radius). From the total number of eddies 46% were cyclonic whereas 54% were anticyclonic. As expected, most eddies (403) propagated westward. In general, westward propagating eddies lived longer and reached larger sizes when compared to their eastward propagating counterparts.

From the 140 eddies that reached the archipelago from abroad: 32 entered from the north and 31 from the northeast; 14 entered from the south, 6 from the southeast and 1 from the southwest; 50 eddies entered at the eastern boundary; and only 6 entered at the western boundary; thus we hypothesize that most of the incoming eddies reaching the Azores followed either the Gulf Stream southward path (entering through the north / west quadrants, see **Figure 1**) or via the Azores Current propagating flow (entering the east / south quadrants). About 70% of the eddies entering the confluence zone lose their identity either through dissipation, by merging with other eddies or simply breaking down into smaller eddies. In fact, confluence zones are typical merging spots for meanders, eddies and filaments. At any given time, there could be tens of mesoscale eddies interacting with each other as well as with other sub-mesoscale eddies. Much research is going into the study of these high energy turbulent mixing zones, but it is still early to fully understand the "transforming nature" of these mesoscale processes (see e.g., Tikinaga et al., 2005).

Table 1 summarizes the physical characteristics of the far-field eddies that reached the archipelago. Although the eddy characteristics compare well with those calculated by Barbosa et al. (2011), the Chelton and Schlax dataset has higher spatial (1/4°) and temporal resolution (daily) when compared with the 1 × 1° results that are calculated every 4-days by Barbosa et al. (2011). This resulted in the visual detection of 152 "loopers" (eddies), using Lagrangian drifters for a period of 18 years in

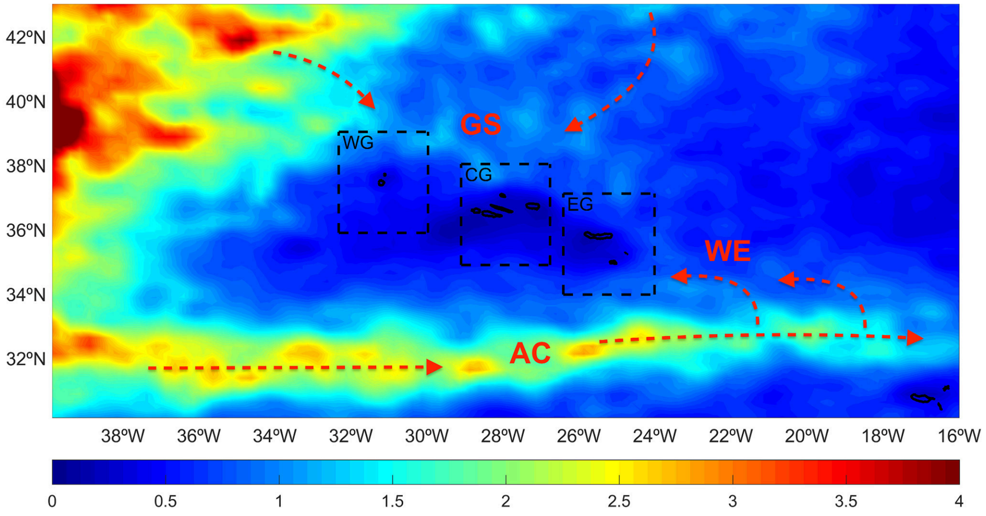

FIGURE 2 | Overall mean (2004–2014) of Eddy Kinetic Energy (EKE) emphasizing the main regional oceanographic processes: AC, Azores Current; WE, Westward propagating Eddies; GS, Gulf Stream. EKE in cm^2 s^{-2}.

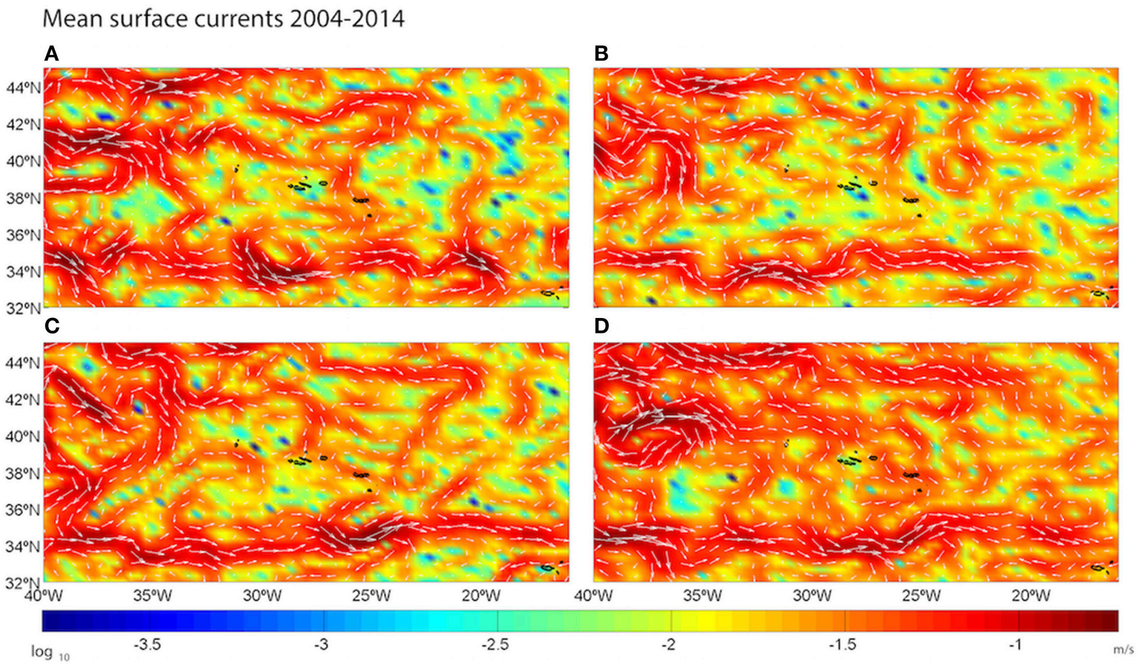

FIGURE 3 | Seasonal mean surface currents for the Azores sub-region (2004–2014) extracted from OSCAR data for (A) spring; **(B)** summer; **(C)** autumn; **(D)** winter. Color scale represent $\log_{10}$ of current speed and white-arrows the current vectors.

TABLE 1 | Physical characteristics of the far-field eddies that reached the Azores Archipelago between 1992 and 2012 (dashed box in Figure 4).

	Cyclones	Anticyclones
Nº of eddies	211	248
Mean duration (days)	26.51	21.01
Radius (km)		
min	33.59	31.47
max	171.24	167.25
mean	74.18	74.31
Swirl velocity (cm s^{-1})		
min	4.56	4.43
max	31.53	22.47
mean	10.63	9.61
Translation velocity (cm s^{-1})		
min	0.15	0.09
max	6.83	6.97
mean	2.44	2.63
Rossby number (Ro)		
min	0.05	0.03
max	0.44	0.45
mean	0.36	0.38
EKE (cm^2 s^{-2})		
min	10.39	9.81
max	497.07	252.45
mean	56.50	46.18

a much broader region (Barbosa et al., 2011), compared with 459 eddies that reach the Azores detected using the newly processed altimetry data (Chelton and Schlax). Nevertheless, the Barbosa et al. (2011) Lagrangian analysis (1990–2008) can be considered as a representative sub-sample of the altimetry data (1992–2012) since it overlaps in time (16 years) and in space.

From the 459 eddies that reached the Azores, 211 were cyclones (C) and 248 were anticyclones (AC). Their mean duration was approximately the same (C 26.51; AC 21.01 days). Their radius and, therefore, their diameter was also very similar and of the same order of magnitude of that calculated by Barbosa et al. (2011). Contrary to Barbosa et al. (2011), however, Cyclonic eddies rotated and also propagated faster than anticyclones. As in Barbosa et al. (2011), the local "vortex Rossby number" (Ro) was calculated as a function of ζ/f redefined by Lazar et al. (2013) as $Ro = V_{max}/f r_{max}$; where ζ is the vortex core vorticity; f is the Coriolis parameter; V_{max} is the maximum "swirl velocity" of the eddy; and r_{max} is the radius corresponding to the maximum velocity. Rossby numbers were slightly higher but of the same order of magnitude as of those previously reported, indicating a strong influence of planetary rotation (Barbosa et al., 2011). However, using the altimetry dataset the maximum EKE was much higher for cyclones (497 cm^{-1} s^{-2}), than it was for anticyclones (252.45 cm^{-1} s^{-2}). By contrast, in Barbosa et al. (2011) they had indistinguishable EKE values.

Figure 4 shows the trajectories of the eddies that reach the Azores coming from afar. The main patterns are similar to the representation of all eddies, however this filter substantially reduced the "chaotic" trajectories of the locally born ones. The far-field eddy trajectories remained unchanged with the filtering. As expected, two main pathways have emerged: (i)

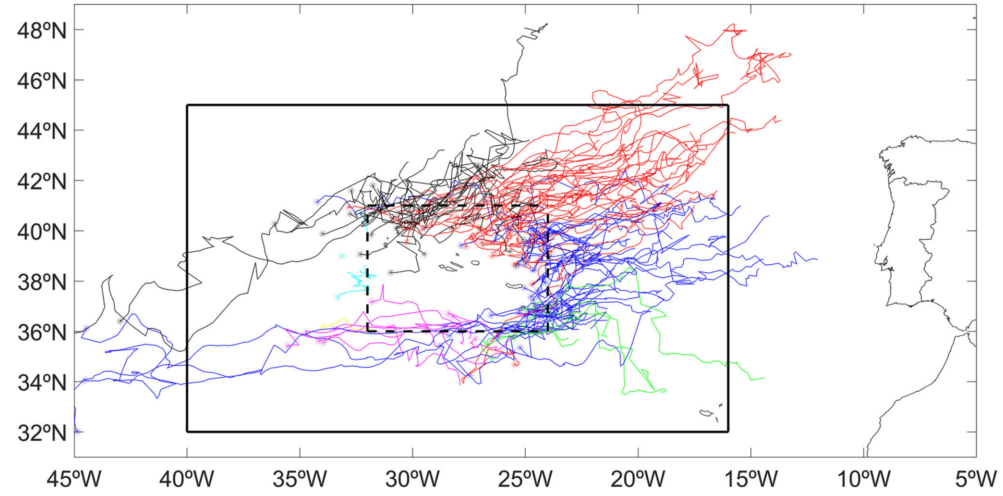

FIGURE 4 | Eddy trajectories from Chelton and Schlax 20-year dataset (1992–2012; http://wombat.coas.oregonstate.edu/eddies/). All far-field eddies (140) that reached the Azores Archipelago (box with dashed line) were considered. Asterisks (*) represent the final position of the eddies. Locally generated eddies were filtered out.

eddies that reach the Archipelago from the north and northwest (Gulf Stream pathways); and (ii) eddies that reach the islands from the east. Only one eddy (considering the full dataset) entered the Azores sub-region from the west. South-entering eddies are expected to have the same dynamical origin as the ones entering at the eastern boundary i.e., westward-propagating eddies pinching off from the Azores Current.

We hypothesize that local wind-induced transport is responsible for the confluence of these regional mesoscale processes in the Azores region. The characteristic of the confluence in the Azores is not so much the merging of intense surface currents, such as in the Brazil-Falklands region, but rather the confluence of eddies, meanders and filaments originating from different ocean regions, with different dynamical qualities.

The predominant meteorological patterns are depicted in **Figure 5**, highlighting the dominance of the Azores high pressure system. The strongest pressure gradients occur during summer (**Figure 5B**) and winter **(Figure 5D**). Due to its positioning over the archipelago, the west group of islands are often under the influence of eastward winds, whereas at the east group (34° N; 20°W) the wind veers northward. These wind patterns result in different Ekman transport regimes affecting west and east island groups. These Ekman transport patterns can also contribute to the tendency of Gulf Stream bifurcation filaments and eddies to veer south and/or east toward the Azores, whereas the westward-propagating eddies pinching off the Azores Current are advected westward throughout the year. The analysis also shows that on the leeward (southwest) side of the archipelago, the wind, and therefore the Ekman transport, is very weak i.e., wind wake. This is also a region with weak EKE and very few eddies detected. In general, the southward Ekman transport is stronger during the winter months (DJF; **Figure 5D**), whereas the northward Ekman transport is stronger during the summer (JJA, **Figure 5B**), in alignment with the wind stress gradient.

Although it is hard to measure *in* situ the influence of wind stress gradient in influencing and steering fields of eddies, numerical models have documented the role of wind stress in generating surface-intensified eddies in other regions. Calil et al. (2008) has shown that sufficient wind forcing is important in reproducing the observed mesoscale vortices in the lee of the Hawaiian Archipelago. Subsequently, Yoshida et al. (2010) noted that the eddies observed in the southwest section of Hawaii were generated by the local wind stress curl associated with the blocking of the trade winds by the island. Kersalé et al. (2011) emphasized the need to consider the use of high resolution wind products, i.e., QuikSCAT, in conjunction with accurate representation of the regional currents and topography in an ocean circulation model of the Hawaiian Archipelago. Couvelard et al. (2012) studied the generation and confinement of mesoscale eddies in the lee of Madeira Island. Sea surface EKE also responds to wind forcing. Most recently, Hogg et al. (2015) showed a decadal increase in EKE most likely due to the continuing increase in wind stress over the Southern Ocean. Moreover, the authors showed that the Antarctic Circumpolar Current transport correlates well with wind stress on interannual timescales.

The Ekman vertical velocity calculation is shown in **Figure 6**. Here the negative values represent downward velocities ("Ekman pumping") and positive values represent surface divergence i.e., "Ekman suction." Ekman pumping is strongest during spring (−0.08 Sv) and weaker during winter months (north of the archipelago). By contrast, Ekman suction is strongest (0.1 Sv) during winter and weaker during spring.

Figure 7 shows the result of the Sverdrup transport calculation for the Azores sub-region, overlaid onto the instances when eddies reached the archipelago (red vertical lines, as identified

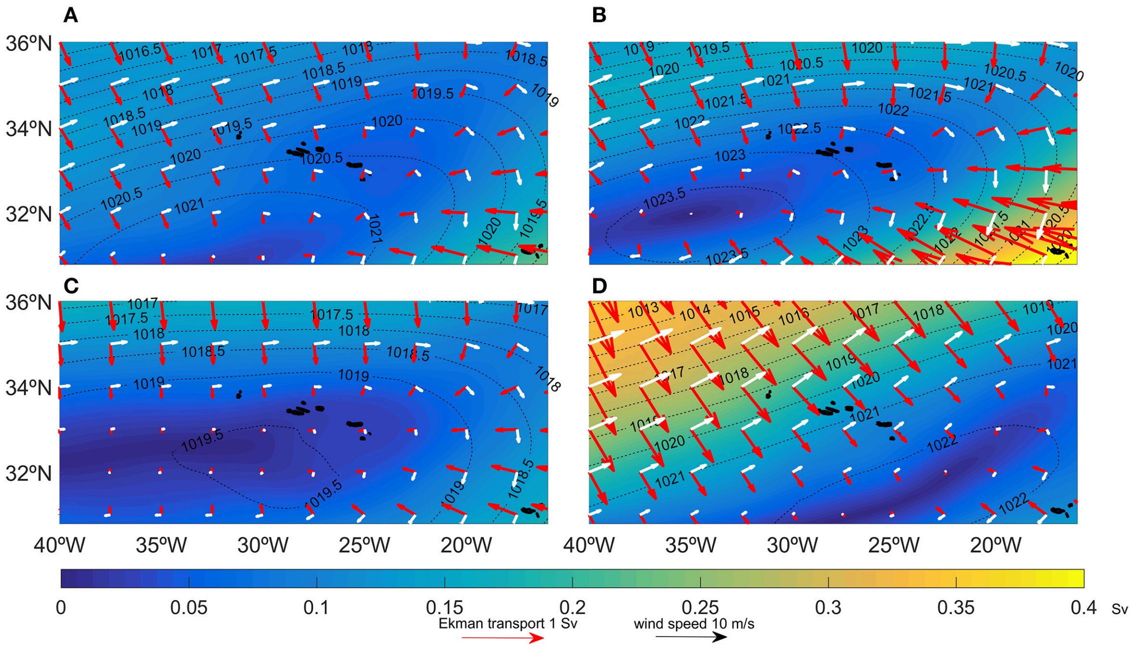

FIGURE 5 | Representation of the mean seasonal variability of the sea surface pressure (mb) (2004–2014); (A) spring (MAM: March; April; May); **(B)** summer (JJA: June; July and August); **(C)** autumn (SON: September; October; November); **(D)** winter (DJF: December; January and February). Wind vectors are represented as white arrows; calculated Ekman transport is represented as red arrows (1 $Sv = 10^6$ m^3 s^{-1}). The color legend shows wind stress (N m^{-2}); reference vectors are also shown.

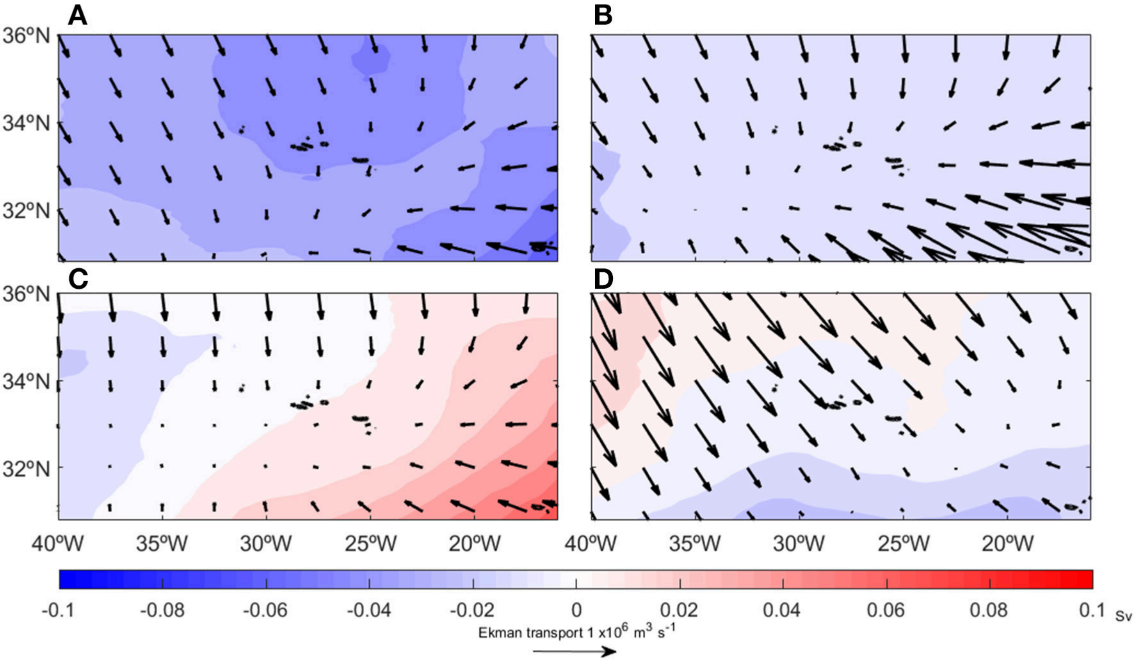

FIGURE 6 | Calculated seasonal mean Ekman transport divergence (2004–2014); (A) spring; **(B)** summer; **(C)** autumn; **(D)** winter. Ekman transport arrows are represented as black arrows. Reference vector included.

in Chelton and Schlax dataset). Meridional (My; **Figure 7A**) and zonal (Mx; **Figure 7B**) transport components are shown separately. The meridional transport, which is integrated over the whole of the northern boundary (~1200 km wide), shows a dominant geostrophic transport mostly toward the north (positive) and a southward Ekman transport (negative). Zonally,

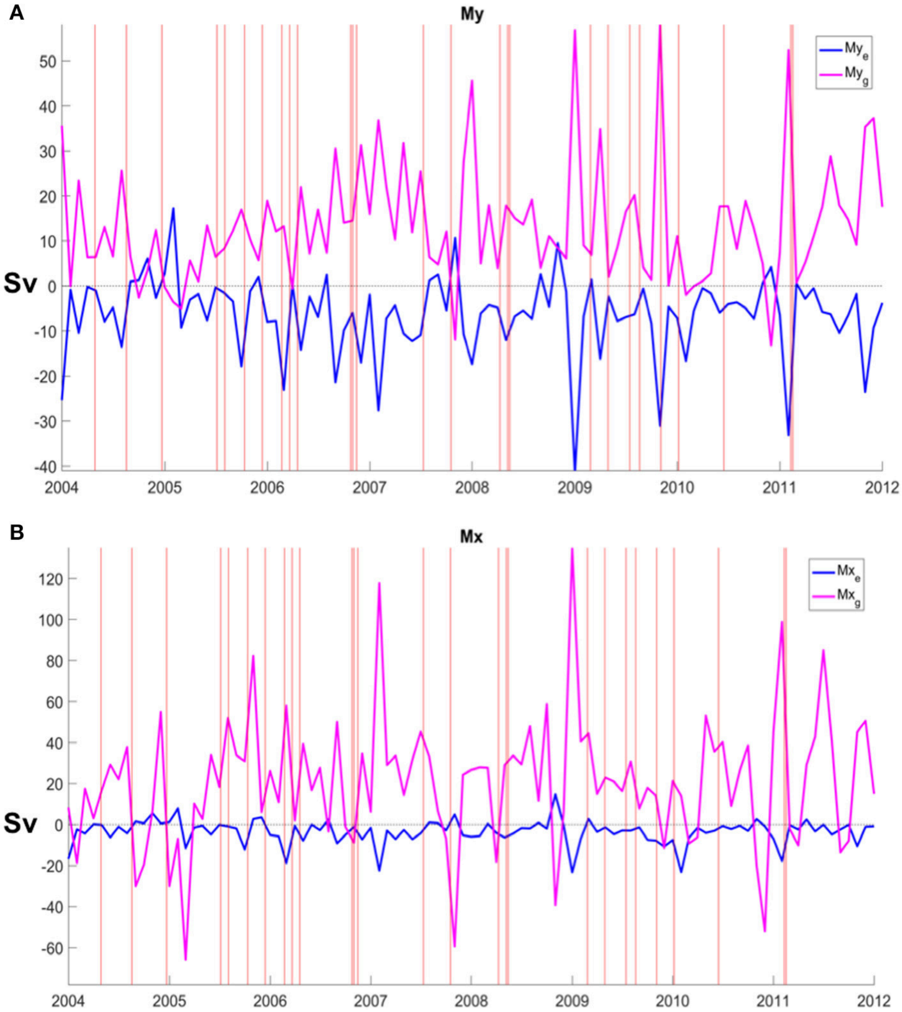

FIGURE 7 | Sverdrup volume transport components: (A) Meridional Transport (M_y); **(B)** Zonal Transport (M_x); Ekman (M_e) and Geostrophic (M_g) transports are represented separately for **(A,B)**. Vertical lines represent the instances of occurrence of incoming far-field eddies between 2004 and 2012.

the westward (negative) transport is almost exclusively Ekman induced. The geostrophic-induced transport is stronger in the zonal direction (Mx) than it is in the meridional (My). This suggests that incoming eddies and filaments that enter the archipelago sub-region from the north and/or from the west are likely to be advected by wind-induced transport (i.e., Ekman). Thus, we hypothesize that the Azores High Pressure system plays a major role in the formation of the oceanic convergence zone centered on the archipelago.

Recently, the self-induced Ekman pumping mechanisms in the interior of mesoscale ocean eddies were investigated (Gaube et al., 2015; Byrne et al., 2016). On average, eddy-induced Ekman pumping velocities approach 10 cm per day (Gaube et al., 2015). SST-induced Ekman pumping is often presented as secondary to the current-induced mechanisms. But in mid-latitudinal regions strongly affected by western boundary currents and with strong SST gradients (as is the case in the Azores), all mechanisms for eddy-induced Ekman pumping are of comparable magnitude (Gaube et al., 2015). Because the polarity of current-induced curl of the surface stress opposes that of the eddy, the associated Ekman pumping often attenuates the eddies (Gaube et al., 2015). Nevertheless, Byrne et al. (2016) proposed a thermodynamic pathway of energy compensation for this loss. Local variations in atmospheric temperatures might in turn generate local wind stress gradients that contribute to injecting kinetic energy back into these mesoscale eddies, acting as a net enhancement of the mesoscale field (Byrne et al., 2016). Future studies of the Azores region should not only consider the geostrophic circulation patterns but also the wind-induced transports as well as the eddy response to the local atmospheric phenomena (see also Small et al., 2008).

Analysis of the spatial distribution of SST anomalies (not shown) indicates that the region is warmer than the seasonal mean temperature (2–3°C) during summer and autumn; and colder during spring and winter (3–4°C). As previously documented by Bashmachnikov et al. (2004), the archipelago is also located in a frontal region affected by sub-tropical (warmer) waters (22–24°C) during summer and autumn, and temperate colder waters (17–18°C) during spring and winter. In fact, the tilting of the isotherm associated with this front might be a response to the eddy-induced circulation that affects the region. The same temperature ranges were also measured by Lafon et al. (2004). Analyzing the mean temperatures of each group of islands (boxes marked in **Figure 2**), each containing the same area, it is noticeable that the colder waters affect the EG (east group) during winter and spring (**Figure 8A**). During summer months the west group (WG) of islands have the warmest waters.

Volkov and Fu (2011) considered 20-years of satellite altimetry and reanalysis data (winds) to demonstrate that the primary contribution to the frontogenesis at the Azores Current is provided by the meridional Ekman-induced current convergence that always acts to tilt the near-surface isopycnals—thereby enhancing the front. In fact, this result also agrees with previous studies of subtropical frontal zones in the North Pacific (Kazmin and Rienecker, 1996; Qiu and Chen, 2010). Volkov and Fu (2011) have also discussed the possibility of the associated high EKE of the AC to be modulated by Ekman convergence. According to that study, the effects of the surface Ekman convergence at the front can be translated deeper, beyond the mixed layer, and influence the EKE generation. Adding to this discussion, our results suggest that it might be the westward propagating eddies, which in turn are highly affected by Ekman-induced transport (indirect effect), that promote the tilting of the Azores Front.

The mean chlorophyll concentration is highest during the spring months in the Central Group (CG) (**Figure 8B**). The least productive group during the spring bloom is the East Group (EG), suggesting that local nutrient / biological enrichment is highly dependent on the interactions of the islands with the incoming oceanographic features—i.e., meanders and filaments from the Gulf Stream. The East Group (EG) is also the least productive during winter. In order to better understand the spatial origin of the nutrient enrichment, and associated increase in phytoplankton growth around the Azores, the spatial means of chlorophyll concentration were calculated. **Figure 9** shows the seasonal maps of chlorophyll concentration derived from satellite data. The spring enrichment has its origins in the Gulf Stream (up north), however during winter the chlorophyll-rich surface waters reach the archipelago from the east. The mean eastern sea surface chlorophyll is approximately half ($\sim$0.3 mg m^{-3}) the mean chlorophyll concentration during the spring bloom ($\sim$0.6 mg m^{-3}). The Central island group shows the highest concentration of sea surface chlorophyll; thus we suggest the CG to be the center of the proposed confluence zone. These confluence zones are often presented as major atmospheric carbon sinks due to the amount of primary production that takes place there.

As expected, satellite-derived sea surface chlorophyll of the Azores follows an inverse pattern to that of SST; nutrient rich waters are often colder when they reach the surface compared with their surroundings. Therefore, the seasonal peaks of chlorophyll are coincident with the seasonal lows of SST, and the seasonal maximums of SST coincide with the seasonal lows of sea surface chlorophyll concentration. Typical of open-ocean oligotrophic (sub-tropical) regions (such as the Azores) where light is not a limiting factor, most nutrients are expected to surface via a dynamic process, such as an oceanic filament or an eddy, which acts to raise the nutricline to the euphotic zone.

There are quite a few examples of Gulf Stream vs. westward-propagating eddy enrichment scenarios. **Figure 10** shows maps of sea surface chlorophyll concentration for April 2009 and April 2010 (**Figures 10B,C**) as two cases where the enrichment reached the Azores from the northwest; whereas during March 2006 and April 2011 the enrichment reached the archipelago from the east. In contrast with the seasonal means, monthly sea surface chlorophyll means in the region can surpass 1 mg m^{-3}. Thus, we predict that in daily cloud free images, the local productivity will reach higher values.

The "island mass effect" (Doty and Oguri, 1956) or "island stirring" (Mann and Lazier, 1991) is the topographic disturbance of oceanic flow by an island, and its linked nutrient and biological impacts. This is certainly the case for other Macaronesian islands such as Madeira (e.g., Caldeira et al., 2002) and the Canaries (Hernandez-Leon, 1991; Aristegui et al., 1997). The island mass effect is often generated when the island has space to interact with the incoming flow and thereby generate its own wake and thus creating its own eddies. In an archipelago setting where individual islands are close to each other and separated by deep-water channels, the "individual island effect" (wake) is strongly constricted (Caldeira and Sangra, 2012), thus enhancing the multiple-island (archipelago) phenomena.

The current study supports the hypothesis that the group of islands (not individual islands), is responsible for the interaction with the incoming flow—thereby in the aggregate inducing the observed nutrient and/or biological enrichment. This ability of a group of seamounts (or islands) to retain properties of the incoming flow was coined by Wolanski (1994) as the "sticky water effect." This effect explains an increase in the retention capacity (i.e., anisotropic turbulence) of the recirculation of currents around and away from regions of high reef density (i.e., closely aggregated reefs or seamounts). At the archipelago scale, recent studies suggest mathematical interpretations for this increased retention by "chaotic advection" processes (Rypina et al., 2010).

Persistent and dynamical localized oceanographic phenomena can lead to the creation and/or modification of the water masses composition, therefore it is important to examine the water masses that comprise the region. As can be seen in **Figure 11**, the east group, being most exposed to westward-propagating flow, has a strong signal of high salinity waters—a.k.a. Mediterranean Intermediate Waters (MIW: T: 6–11.9°C; S: 35.3–36.5 PSU). However, the MIW was diluted in the central group and not present at all in climatological profiles extracted near the west group. The North Atlantic Deep Water (NADW: T: 3–4°C; S: 34.9–35.0 PSU) and the North Atlantic Central Surface Waters (NACSW: T: 4–20°C; S: 35–36.8 PSU) were present in all island groups. This east-west difference in water mass distribution, developing over a 1000 km ocean region, is also consistent with the Azores being a confluence /convergence zone between the incoming Gulf Stream tropical waters and the

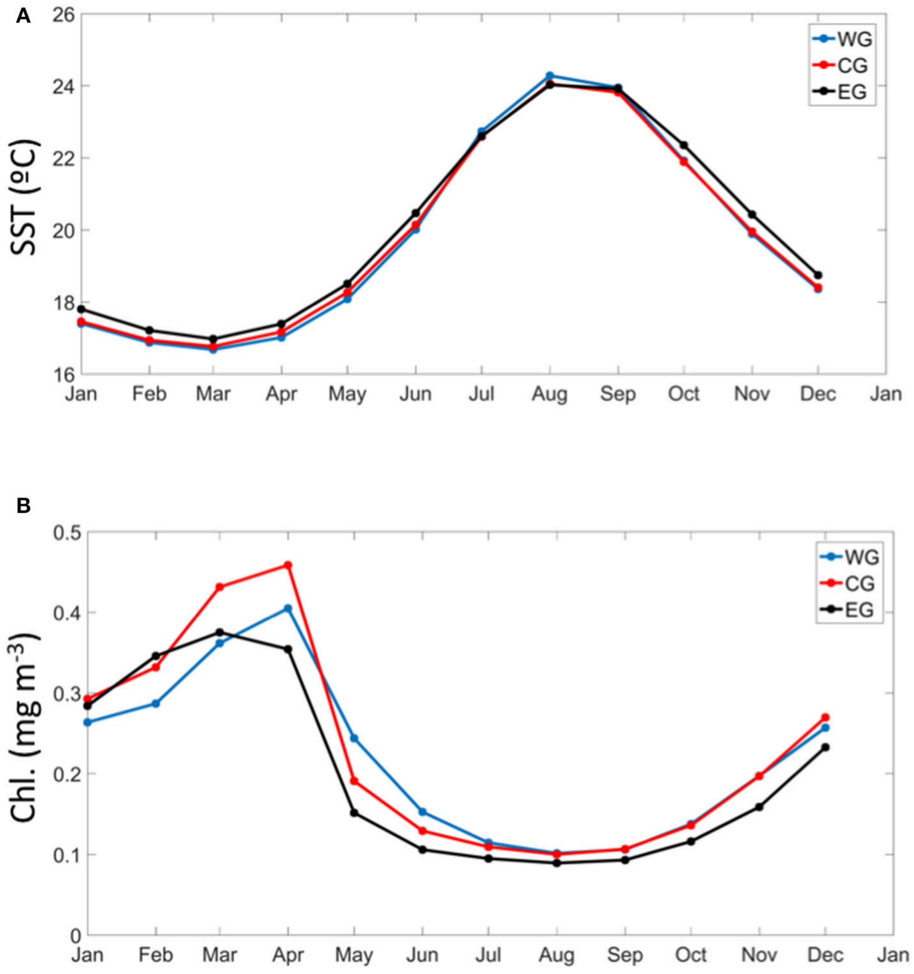

FIGURE 8 | Time-series of the (A) SST and **(B)** Sea Surface Chlorophyll for each island group: WG, West Group; CG, Central Group; EG, East Group.

westward-propagating eddies from the Azores Current, which transport MIW within.

Phosphate profiles extracted from climatology near the west and east groups also reveal some significant differences (**Figure 12**). In the Gulf Stream waters that often reach the West Group (WG), there is a two-layer, two-cline configuration: one nutricline below the surface (0–200 m) followed by a nutristad (200–350 m), and a second nutricline formed between 300 and 1000 m. This structure implies the presence of Subtropical Mode Water reaching the west group. In the profiles extracted in the vicinity of the East Group (EG) there is no two-layer configuration—i.e., no nutristad present in the profile. The maximum value of phosphate concentration is located at a slightly shallower depth (800 m). This E-W asymmetry can also help explain the differences in phytoplankton organisms observed by Silva et al. (2013), as well as suggest the incursion of sub-tropical warm waters (via filaments and/or eddies) from the Gulf Stream into the archipelago.

Subtropical Mode Water (STMW), is formed by convection each winter in an east-west band at the northern edge of the subtropical gyre, just south of the Gulf Stream (McCartney, 1982; Talley and Raymer, 1982). As pointed out by Palter et al. (2005), the presence of STMW inserts a sub-surface layer of nutrient-depleted water (nutristad) as observed in the west group profiles. As stated by Palter et al. (2005), in regions and years with a strong STMW signature, low-nitrate waters reside beneath the euphotic zone. During times when the characteristic STMW thermostad is lacking, the nutricline is no longer depressed and there exists a steep and nearly linear gradient between the base of the euphotic zone and the remineralized nutrients at depth.

CONCLUSIONS

Although the MAR has been the focus of many scientific studies, few concentrated their analysis and synthesis on the characterization of the oceanographic processes that affect the Azores Archipelago. To the best of our knowledge, this is one of the few discussions, together with Sala et al. (2015), on the dynamical oceanographic features that specifically affect the

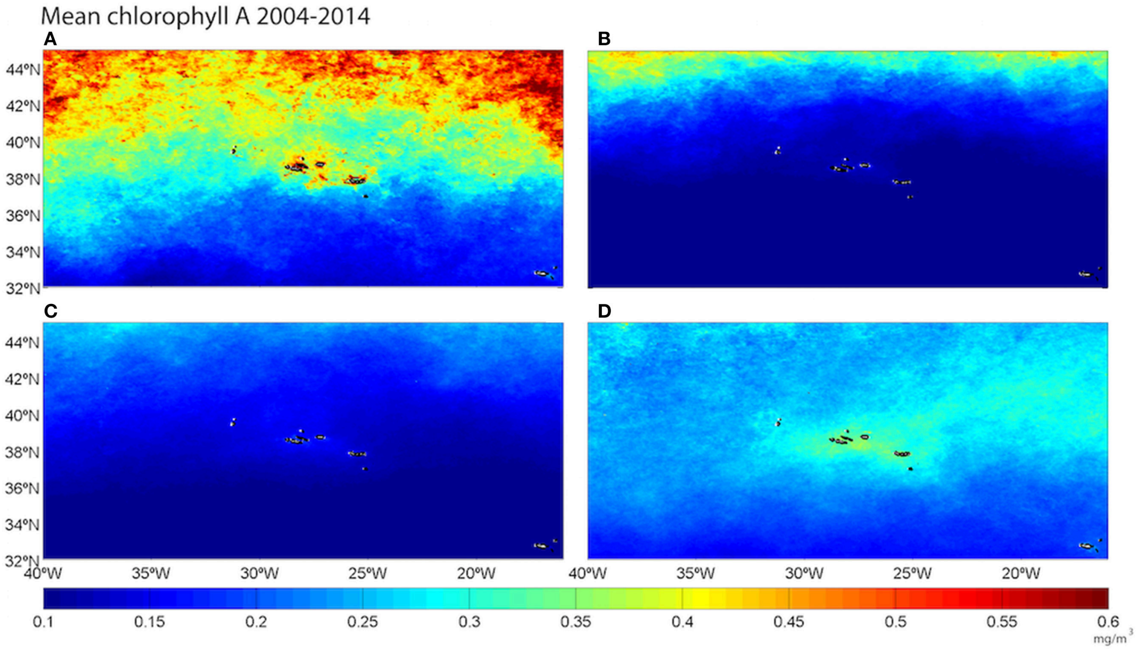

FIGURE 9 | Spatial distribution of the mean seasonal (2004–2014) sea chlorophyll concentration; (A) spring; **(B)** summer; **(C)** autumn; **(D)** winter.

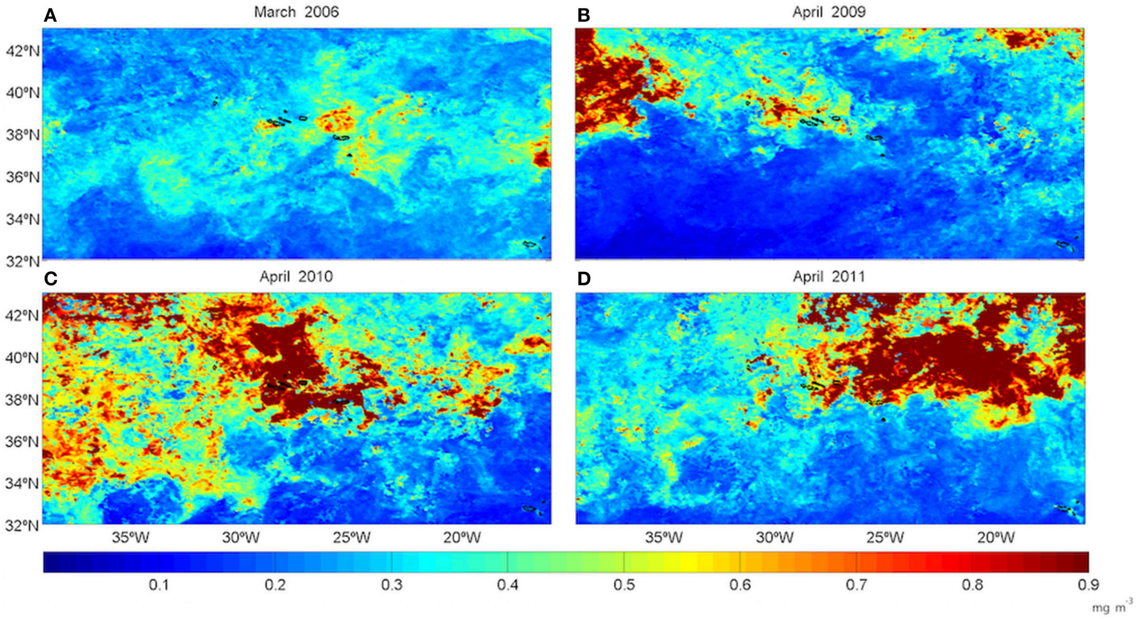

FIGURE 10 | Maps of sea surface chlorophyll concentration representing examples of westward and eastward penetration of productivity for monthly means: (A) March 2006; **(B)** April 2009; **(C)** April 2010; **(D)** April 2011.

Azores Archipelago. The most striking results from this study were that: (i) the west group of islands are affected mostly by the Gulf Stream (bifurcation) filaments, meanders and eddies; whereas (ii) the east group is affected by westward-propagating eddies, most likely the ones pinching off from the Azores current. This also helps explain the different phytoplankton communities observed in the northern vs. southern islands as reported by Silva et al. (2013); (iii) regional Ekman transport seems to be responsible for the confluence of these mesoscale phenomena in the Azores Archipelago; (iv) the differing physical nature of the dominant oceanographic processes that affect the west and the east groups are imprinted in their water mass

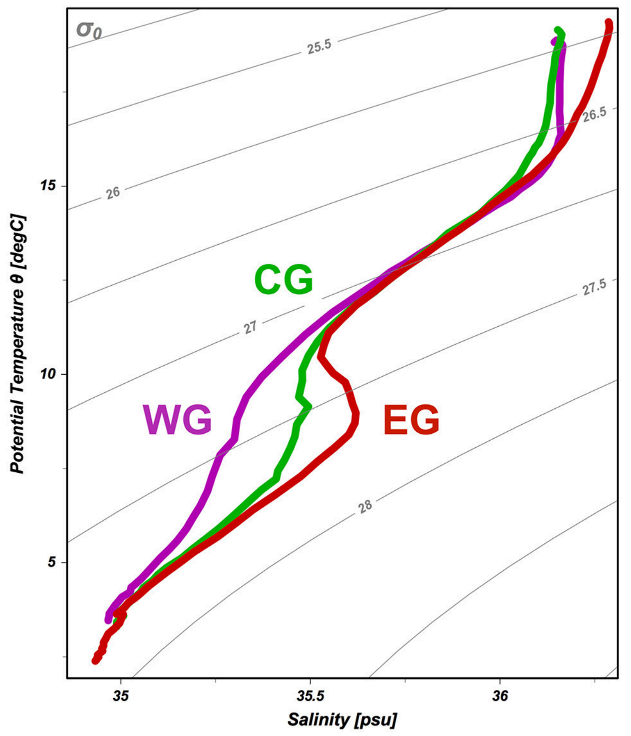

FIGURE 11 | Theta-Salinity diagram representing the main water masses present in each island group: WG, West Group; CG, Central Group; EG, East Group. Density (kg m^{-3}), sigma-t lines are also shown in the diagram for reference.

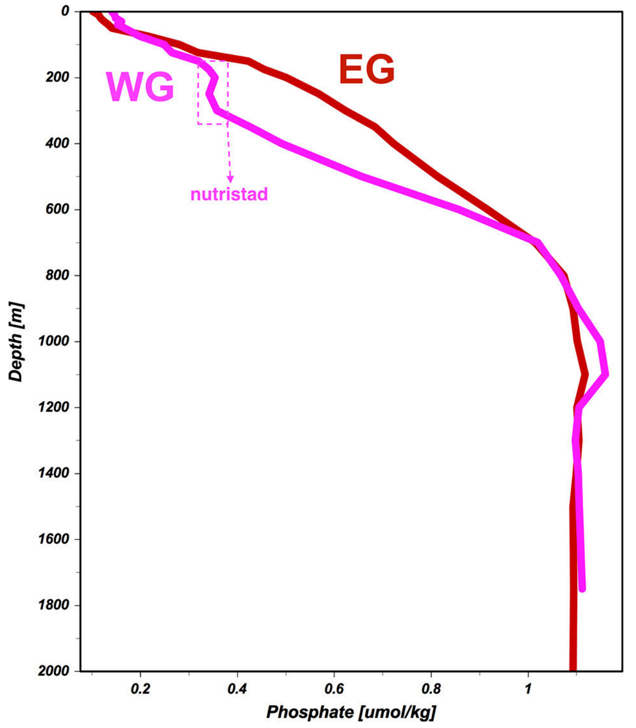

FIGURE 12 | Climatological profiles (0–2000 m) of phosphate concentration for the WG, West Group, and EG, East Group.

composition as well as in their nutrient (climatological) profiles. At the surface, a tilted frontal region denotes the asymmetry between the dominant processes that affect both ends—i.e., west and east island groups; (v) the biological enrichment is very seasonal and very dependent on the shallowing of the nutricline; it often reaches the islands from the north from the Gulf Stream, or from the east (Azores Current); far-field enrichment strongly surpasses the intensity of the observed local enrichment. Moreover, the intensity of northern domain enrichment seems to surpass that of the east, in agreement with the higher intensity of the north-west incoming features. The Central Group of islands has the largest oceanic imprint (in size and number of islands). Thus, it has higher capacity to stir the incoming flow, inducing a shallowing of the nutricline and/or "capturing" the biologically enriched incoming system of eddies and fronts.

Due to the convergence of oceanographic processes that manifest in the Azores Archipelago in combination with the highly energetic eddy field, we propose its designation as a confluence zone between the west and the east North Atlantic. Much remains to be studied and resolved. For instance, how can we unambiguously distinguish the dynamic characteristics of Gulf Stream eddies from westward-propagating eddies? Does the erosion of the MIW occur in the confluence region due to intense (local) vertical mixing induced by the mesoscale eddies that reach (and/or live) in the Azores Archipelago? Or do westward-propagating features carrying the MIW simply not reach the west group of islands?

The Azores Archipelagic region is of great interest to the scientific community because it plays an important role in the ocean circulation and biological enrichment of the Mid- and North Atlantic Regions. Yet the characterization and impacts of its oceanographic patterns has been under-studied. Hopefully future efforts will help clarify some of the hypotheses proposed herein.

AUTHOR CONTRIBUTIONS

Both authors contributed to the data analysis and RC assembled most of the writing. Both authors are aware of its full content and agree to submit it in its present form for scientific review.

ACKNOWLEDGMENTS

Special thanks to Dudley Chelton and Michael Schlax for making the eddy tracking data freely available. The altimeter products were produced by SSALTO/DUACS and distributed by AVISO with support from CNES (http://www.aviso.oceanobs.com/duacs/). The chlorophyll satellite data was provided by NOAA "CoastWatch" Program and NASA's Goddard Space Flight Center, "OceanColor Web." This study was partially supported by the Oceanic Observatory of Madeira (M1420-01-0145-FEDER-000001- Observatório Oceânico da Madeira-OOM). Comments from reviewers contributed to substantially improve the previous versions of the manuscript. Julie Pullen made important editorial comments, improving the (close to) final version of the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Marine Science

ORIGINAL RESEARCH
published: 07 March 2017
doi: 10.3389/fmars.2017.00056

Overview of the Ocean Climatology and Its Variability in the Azores Region of the North Atlantic Including Environmental Characteristics at the Seabed

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Specialty section:
This article was submitted to
Deep-Sea Environments and Ecology,
a section of the journal
Frontiers in Marine Science

Received: 22 January 2016
Accepted: 15 February 2017
Published: 07 March 2017

Citation:
Amorim P, Perán AD, Pham CK,
Juliano M, Cardigos F, Tempera F and
Morato T (2017) Overview of the
Ocean Climatology and Its Variability
in the Azores Region of the North
Atlantic Including Environmental
Characteristics at the Seabed.
Front. Mar. Sci. 4:56.
doi: 10.3389/fmars.2017.00056

Obtaining a comprehensive knowledge of the spatial and temporal variations of the environmental factors characterizing the Azores region is essential for conservation and management purposes. Although many studies are available for the region, there is a need for a general overview of the best available information. Here, we assembled a comprehensive collection of environmental data and briefly described the ocean climatology and its variability in the Azores. Data sources used in this study included remote sensing oceanographic data for 2003–2013 (sea surface temperature, chlorophyll-a concentration, particulate inorganic carbon, and particulate organic carbon), derived oceanographic data (primary productivity and North Atlantic oscillation index) for 2003–2013, and *in situ data* (temperature, salinity, oxygen, phosphate, nitrate and silicate) obtained from the World Ocean Atlas 2013. We have produced 78 geographic datasets of environmental data for the Azores region that were deposited at the World Data Center Pangaea and also made available at the SIGMAR Azores website. As with previous studies, our results confirmed a high spatial, seasonal and inter-annual variability of the marine environment in the Azores region, typical of mid-latitudes. For example, lower sea surface temperature was found in the northern part of the study area coinciding with higher values for chlorophyll-a concentration, net primary production (NPP), and particulate organic and inorganic carbon. Higher values for some of these parameters were also found on island slopes and some seamounts. Compiled data on the environmental conditions at near-seabed revealed some notable variations across the study area (e.g., oxygen and nutrients) and with depth (e.g., temperature, salinity, and oxygen). Knowledge of these patterns will help improve our understanding of the distribution of many deep-sea organisms such as fish, cold-water corals, and sponges, thereby supporting the implementation of marine spatial planning and other management measures. It should be noted that the assembled datasets suffer from a number of limitations related to the accuracy of remote sensing and global bathymetry data, or to the limited and unevenly distributed collection of environmental observations. Accordingly, an effective observing system for detecting oceanic change with adequate accuracy and precision is still required.

Keywords: Azores, environmental parameters, seabed conditions, sea surface temperature, chlorophyll-a

INTRODUCTION

Effective ecosystem management is often hampered by the paucity of information on the spatial distribution of marine species and habitats that can partly be filled by statistical modeling (Guisan and Zimmermann, 2000; Guisan et al., 2002; Guisan and Thuiller, 2005). For instance, species distribution models (SDMs) have proved useful for a broad variety of applications, such as assessing the potential impacts of climate change on species distribution (Thomas et al., 2004; Gritti et al., 2006; Wiens et al., 2009; Jones et al., 2013), designing marine protected areas (Sundblad et al., 2011) or predicting the potential distribution of invasive species (Tyberghein et al., 2012). Such models essentially rely on statistical correlations between existing data on species occurrence and environmental parameters to predict distribution across selected geographical areas. Therefore, the success of these statistical models depend heavily on the availability of ocean environmental data.

Several global and regional databases with relevant oceanographic data have been used to describe general climatological patterns. The most known is probably the World Ocean Atlas 2013 (WOA13; Boyer et al., 2013), which provides data on oxygen, nutrients, temperature, and salinity at different standard depths of the ocean. Additionally, remote sensing imagery is regularly compiled by several international organizations (e.g., NASA's Ocean Color Web), which provides satellite-based oceanographic data on chlorophyll-a concentration, and sea surface temperature among others, at different resolutions.

Contrary to ocean surface layers, where many environmental conditions are well-characterized, the application of SDMs in the deep sea has been hindered by the limited amount of high-resolution data on the environmental conditions near the seafloor (Vierod et al., 2014). However, global and regional scale studies have demonstrated the potential of large-scale oceanographic data (e.g., World Ocean Atlas; Boyer et al., 2013) to create grids representative of conditions at the seafloor, permitting the development of distribution models useful for management (Davies et al., 2008; Tittensor et al., 2009; Davies and Guinotte, 2011; Yesson et al., 2012, in press; Rengstorf et al., 2013; Guinotte and Davies, 2014; Anderson et al., 2016).

The Azores is an oceanic archipelago located in the middle of the North Atlantic Ocean, characterized by a large marine territory known to host a wide variety of open-ocean and deep-sea organisms. For example, the archipelago is recognized for its key role as a transitionary habitat for large open-ocean animals such as cetaceans, sharks, pelagic fish, or sea-turtles (Silva M. A. et al., 2013; Vandeperre et al., 2014; Prieto et al., in press; Tobeña et al., 2016) and to harbor valuable deep-sea resources and ecosystems such as deep-sea fish (Menezes et al., 2006) or cold-water coral aggregations (Braga-Henriques et al., 2013; Tempera et al., 2013; Pham et al., 2015). Therefore, obtaining a comprehensive knowledge of the spatial and temporal variations of the environmental factors in the open-ocean and deep-sea of the Azores region is essential for interpreting patterns of biodiversity distribution and for an improved management and conservation of the Azores marine biodiversity (see Abecasis et al., 2015) and resources as a whole.

Several studies have focused on specific aspects of the climatology of the North Atlantic. Lozier et al. (1995) described the climatology of the North Atlantic based on the mean pressure, temperature, salinity, and oxygen parameters collected in hydrographic stations between 1904 and 1990. Nutrient flow in the region was described in detailed by Pelegrí et al. (1996). Bashmachnikov et al. (2009) examined the presence of meddies (Mediterranean Water eddies) east of the Mid-Atlantic Ridge (MAR) through *in situ* data and remote sensing signature (altimetry data). Recently, Bashmachnikov et al. (2015) produced new climatological maps of temperature–salinity distribution for the northeastern Atlantic with a 25 m depth interval and a 30 km of horizontal resolution (MEDTRANS dataset). The variability of chlorophyll-a and primary production in the Eastern North Atlantic Subtropical Gyre was investigated by Teira et al. (2005).

Additionally, several studies focusing on the Azores region have been undertaken in recent years based on *in situ* and remote sensing data. Mesoscale and local sea surface temperature variability in the Azores region was studied by Lafon et al. (2004) based on Sea Surface satellite imagery (AVHRR and SeaWiFS) and *in situ* conductivity-temperature-depth (CTD) samples. Martins et al. (2009) investigated the inter-annual variability of near-surface phytoplankton biomass and sea surface temperature. Also the phytoplankton variability using chlorophyll-a as a proxy of biomass has been addressed by several studies in the Azores, mainly associated with seamounts (e.g., Mendonça et al., 2012; Santos et al., 2013) or in the vicinity of Azores islands (Silva A. et al., 2013).

Although many studies are available for the region, there is a need for an overview of the best broad-scale data available aiming at facilitating the development of marine biodiversity distribution models. Therefore, this study aims to assemble and make available a comprehensive collection of surface and at the seabed environmental data of the Azores, ready for use in several interdisciplinary studies. It contributes to improve the knowledge of the Azores and support an improved management and conservation of certain species and resources in the region.

MATERIALS AND METHODS

Study Area

The Azores archipelago is a group of nine volcanic islands located in the North Atlantic Ocean around the Mid-Atlantic Ridge with an Exclusive Economic Zone (EEZ) of ~1 million km^2 and a mean depth of about 3000 m. Areas shallower than 600 m cover <1% of the total EEZ (Perán et al., 2016). The seafloor surrounding the islands is characterized by very narrow shelves and steep slopes with an important rocky component and a very irregular topography. Seamounts or submarine elevations are common features in the Azores and may occupy 37% of the total area of the EEZ (Morato et al., 2008, 2013). For the purpose of this study we have considered the Economic Exclusive Zone around the Azores along with the adjoining area of extended continental shelf claimed by Portugal, ranging between 28° – 40°N and 17° – 41°W (**Figure 1**).

The archipelago is situated in the inter-gyre region of the eastern North Atlantic between 34° and 50°N (Maillard, 1986). The region is characterized by complex ocean circulation patterns resulting from the interaction of the North Atlantic Current (in the North) and the Azores Current (in the south) with many unstable eddies and meanders (Santos et al., 1995; Alves and de Verdière, 1999; Johnson and Stevens, 2000; Bashmachnikov et al., 2009, 2015). Several water masses are present in this region: the North Atlantic Central Water until about 700 m depth; the Northern Sub-Polar Water, the Antarctic Intermediate Water, and the Mediterranean Outflow Water at intermediate depths; and the North Atlantic Deep Water below 2,000 m depth (Santos et al., 1995; Mann and Lazier, 1996; Johnson and Stevens, 2000). The eastward-flowing Azores current separates the colder Eastern North Atlantic Central waters from the warmer and more saline Subtropical waters (Martins et al., 2008) and it is considered as the northern limit of the North Atlantic Subtropical Gyre (Juliano and Alves, 2007).

In general, the Azores region experiences large scale spatial and seasonal variation of oceanographic conditions (Lafon et al., 2004). Sea surface temperature (SST) range from an average of 15°C in the winter to a maximum of 27°C in the summer (Martins et al., 2007). A deep mixed layer is present at ~150 m depth during the winter, while a seasonal thermocline usually develops between 40 and 100 m depth in the summer (Santos et al., 1995). *In situ* data indicated that maximum chlorophyll-a concentrations correspond to periods of lower SST, usually occurring during winter and spring (Santos et al., 2013). In contrast, minimum chlorophyll-a concentrations have been observed during the summer, when SST is typically higher (Santos et al., 2013). Although these are the general patterns, high inter-annual variability has been observed in this region (Martins et al., 2009).

Several data sources and types were used to compile the climatology characteristics of the Azores region (**Table 1**). Surface environmental conditions were determined with remotely-sensed data (including productivity), while conditions at the seabed were derived from the World Ocean Atlas 2013 (Boyer et al., 2013).

Sea Surface Environmental Data

Monthly data products of Ocean Color (http://oceancolor.gsfc.nasa.gov/) were obtained through the MODIS sensor and compiled for the study area from 2003 to 2013 (NASA/OEL/OBPG, 2014). These included SST derived from daytime long-wave (11–12 μm) thermal radiation, as well as near-surface data on chlorophyll-a concentration, PIC, and particulate organic carbon (**Table 1**). Data was obtained at 4-km resolution in both latitude and longitude. High-resolution satellite imagery is a powerful tool to resolve patterns in space and time. However, sensor penetration is restricted to the near-surface layer of the ocean and could therefore produce biased estimates when applied to volumes.

A measure of primary production was obtained from the ocean net primary productivity derived from MODIS data (http://www.science.oregonstate.edu/ocean.productivity). This parameter is based on the standard algorithm for the Vertically Generalized Production Model (VGPM; Behrenfeld and Falkowski, 1997). This model is based on the chlorophyll-a concentration and it estimates the NPP using a temperature-dependent description of chlorophyll-specific photosynthetic efficiency. We used monthly data with global grid size of 1/12° (≈ 9 km) in both latitude and longitude for the period 2003–2013.

Spatially-explicit remote sensing data (SST, chlorophyll-*a* concentration, PIC, and particulate organic carbon) and derived oceanographic data (primary production and NAO index) were obtained for each month for the period 2003–2013, resulting in 132 geospatial datasets (a.k.a., GIS layers) for each environmental parameter. For each parameter, we then computed the minimum, maximum, range, mean, and standard deviation of each monthly-imagery for the whole period to obtain overall statistics for each month. Monthly and inter-annual variability was also assessed for all parameters. Finally, monthly anomalies were calculated for each parameter based on the difference between each monthly value and the overall mean value obtained for each month. The same approach was applied to inter-annual anomalies; the difference between each year mean value and the overall mean value obtained for all years. Pearson correlation coefficients were calculated between monthly values of all the environmental parameters to test for possible covariation (Dalgaard, 2002).

At Seabed Environmental Data

Several environmental parameters distributed from surface waters to deep layers of the ocean were obtained for our study area from the World Ocean Atlas 2013 (Boyer et al., 2013). These parameters included temperature (Locarnini et al., 2013), salinity (Zweng et al., 2013), apparent oxygen utilization, dissolved oxygen, percent oxygen saturation (Garcia et al., 2014a), phosphate, nitrate, and silicate (Garcia et al., 2014b; **Table 1**). Apparent oxygen utilization represents one estimate of the dissolved oxygen utilized due to biochemical processes relative to a preformed value. Oxygen saturation was estimated as the ratio of measured dissolved oxygen and the maximum

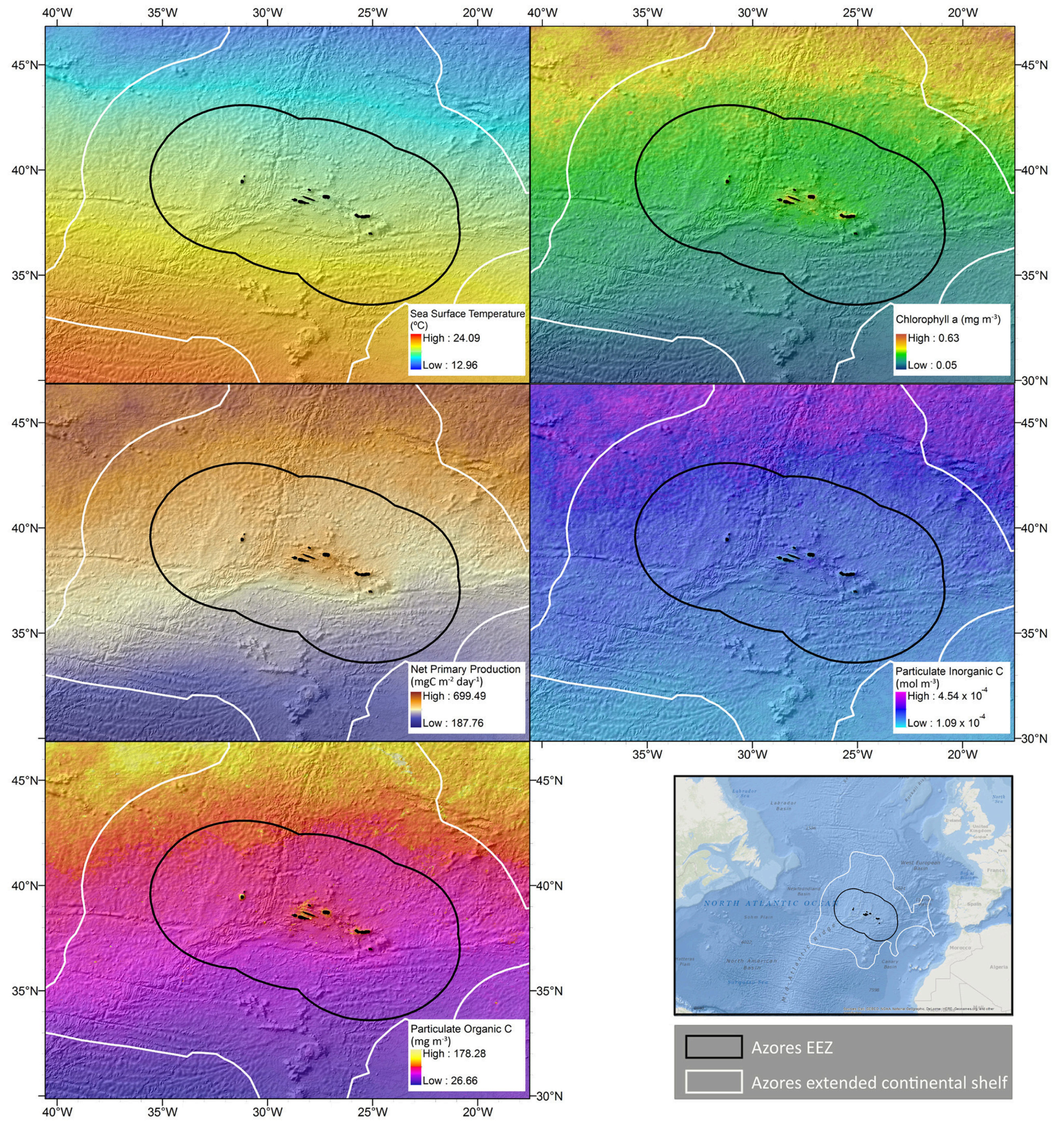

FIGURE 1 | Overall mean of selected near surface oceanographic parameters in the Azores region obtained between 2003 and 2013 through remote sensing data. Black line represents the Portuguese Economic Exclusive Zone around the Azores and white line represents the claimed extended continental shelf. Color scale is shown as a liner stretch between minimum and maximum observed values.

amount of oxygen that will dissolve in water with the same physical and chemical properties under stable equilibrium (Garcia et al., 2014a). Apparent oxygen utilization (mL L^{-1}) and oxygen saturation (%) are derived parameters from dissolved oxygen (mL L^{-1}) measurement only when *in situ* temperature and salinity were also measured at the same geographic location, time, and depth. Thus, the total number of observations available for calculating apparent oxygen utilization and oxygen saturation is slightly smaller in number than the available number of dissolved oxygen observations (Supplementary Figure 1).

Spatial data on the overall mean at each depth strata (50 m depth strata down to 2,000 m depth and 100 m depth strata

TABLE 1 | List of the oceanographic parameters compiled and data sources used to describe the ocean climatology and its variability in the Azores region, North Atlantic.

Source	Environmental data	Method	Units	No. datasets/observations	Spatial resolution
Ocean color (NASA/OEL/OBPG, 2014)	Chlorophyll-a concentration	MODIS-AQUA sensor	mg m^{-3}	132 GIS datasets	4 km
	Particulate Inorganic Carbon	MODIS-AQUA sensor	mol m^{-3}	132 GIS datasets	4 km
	Particulate Organic Carbon	MODIS-AQUA sensor	mg m^{-3}	132 GIS datasets	4 km
	Sea Surface Temperature	MODIS-AQUA sensor	°C	132 GIS datasets	4 km
Ocean productivity (Behrenfeld and Falkowski, 1997)	Ocean Net Primary Productivity	Derived[a]	mgC m^{-2} day^{-1}	132 GIS datasets	9 km
NAO indices (Climate Prediction Center (CPC) Internet Team, 2012)	NAO index	Derived[b]	–	132 data points	–
World Ocean Atlas (Boyer et al., 2013)	Temperature	From *in situ*	°C	1 GIS dataset based on 11,105 data points	0.25°
	Salinity	From *in situ*	PSU	1 GIS dataset based on 1,137 data points	0.25°
	Dissolved Oxygen	From *in situ*	mL L^{-1}	1 GIS dataset based on 720 data points	1°
	Percent Oxygen Saturation	From *in situ*	%	1 GIS dataset based on 665 data points	1°
	Apparent Oxygen Utilization	From *in situ*	mL L^{-1}	1 GIS dataset based on 661 data points	1°
	Silicate	From *in situ*	μmol L^{-1}	1 GIS dataset based on 469 data points	1°
	Phosphate	From *in situ*	μmol L^{-1}	1 GIS dataset based on 565 data points	1°
	Nitrate	From *in situ*	μmol L^{-1}	1 GIS dataset based on 501 data points	1°

[a] *From MODIS data (http://www.science.oregonstate.edu/ocean.productivity).*

[b] *From the Climate Prediction Center (NCEP/NOAA http://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml).*

for depths of more than 2,000 m) and available periods were extracted from WOA13 for each environmental parameter. Data was available at a spatial resolutions of 0.25° of latitude and longitude for temperature and salinity, and at a spatial resolution of 1° for all other parameters (Boyer et al., 2013). For temperature and salinity, the analyses described below (see Section At Seabed Environmental Data) were based on the average of 6 decadal climatological means (calculated from 1955 to 2012). For oxygen, phosphate, silicate, and nitrate, the climatological mean used all available data regardless of time period (from the early 1900s' to the present). The resulting datasets were used to compute the distribution of environmental conditions at seafloor depth for each parameter. The spatial distribution of the number of observations are shown as Supplementary Figure 1.

In order to create continuous datasets of seafloor conditions over the entire extent of our study area, we interpolated the World Ocean Atlas 2013 (Boyer et al., 2013) data using a resolution refinement method to create climatological grids with increased spatial resolution. This method was shown to be adequate to provide environmental oceanographic data to feed predictive habitat modeling (Davies and Guinotte, 2011). Bathymetric data from "The Global Bathymetry and Elevation Data at 30 Arc Seconds Resolution" SRTM30_PLUS (Becker et al., 2009) was used to resample the WOA13 gridded data for producing continuous 30-arc second (~1 km^2) grids. The resolution refinement process was initiated by extracting each parameter from every depth level into a single shapefile. We then interpolated each parameter using the inverse distance weighting algorithm at a resolution of 0.1°. Subsequently, each raster was resampled in order to obtain the same spatial extent and cell size (1 km^2) as the SRTM30_PLUS bathymetry. We then overlapped each bathymetry area corresponding to the different depth levels with each resampled raster that corresponded to the same depth level. Additionally, we computed the mean and standard deviation at the seabed per depth strata across the entire study area to construct general profiles for all these parameters at different seabed depths from shallow water to 6,500 m depth.

NAO Index

We obtained monthly North Atlantic Oscillation (NAO) index from the Climate Prediction Center (NCEP/NOAA http://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml) for the period 2003–2013 (Climate Prediction Center (CPC) Internet Team, 2012). The NAO index is a climatic pattern in the North Atlantic Ocean resulting from differences on the surface sea-level atmospheric pressure between the Subtropical (Azores) High and the Subpolar (Icelandic) Low. Its value fluctuates between phases of strong and weak differences and is associated with strong effects on oceanic conditions, namely temperature and salinity, current system, and wave heights (ICES, 2014). The positive phase of the NAO reflects below-normal geopotential heights and sea-level atmospheric pressure across the high latitudes of the North Atlantic. Opposite patterns of geopotential heights and sea-level atmospheric pressure anomalies are typically observed during negative NAO phases. Monthly and inter-annual variability of the NAO was assessed.

RESULTS

We have produced 78 geographic datasets of environmental data for the Azores region from remote sensing and *in situ* data (see Supplementary Table 1 for a complete list of environmental geospatial datasets available for download). These datasets, with a resolution between 1 and 9 km, were deposited at Pangaea, Data Publisher for Earth and Environmental Science (https://doi.org/10.1594/PANGAEA.872601) and also made available for download on the SIGMAR Azores website (http://sigmar.azores.gov.pt).

The summary statistics obtained for each environmental parameter (remotely-sensed data) in the study area between 2003 and 2013 are shown in **Table 2**. SST as measured by Ocean Color varied between 15.55 and 23.20°C while the concentration of chlorophyll-a varied between 0.09 and 0.43 mg m^{-3}, which is characteristic of oligotrophic oceanic regions. The NAO index also showed a wide amplitude, varying between −2.5 and 2.5 during the study period (**Table 2**).

Spatial Variability

The overall mean values for the five main environmental parameters as measured by Ocean Color sensor from January 2003 to December 2013 are shown in **Figure 1**, while the temporal-spatial variability is shown as the range of its values in **Figure 2**. As expected, zonal (i.e., latitudinal) trends observed in the values for environmental parameters were much greater than meridional (i.e., longitudinal) trends. Lower mean values of SST were found in the northern part of the study area coinciding with higher values for chlorophyll-a concentration, NPP, and organic and inorganic carbon (**Figure 1**). Additionally, higher chlorophyll-a concentration, NPP, and particulate organic carbon were observed to be associated to the slopes surrounding the islands. Particulate organic carbon was also higher on some seamounts and large banks.

Areas showing higher degree of variability varied between environmental parameters (**Figure 2**). Areas with higher variability of SST were observed on the western part of the study area at mid-latitudes. Chlorophyll-a and NPP showed higher variability in the southern part of the study area while PIC and POC showed higher variability at higher latitudes. An area between the central and the eastern group of islands displayed distinct patterns of variability when compared to neighboring zones (**Figure 2**). This patch showed a markedly low range of chlorophyll-a and NPP whilst variability of POC was considerably higher than adjacent areas.

Seasonal Variability

Monthly mean values for each environmental parameter in the study area between 2003 and 2013 are shown in **Figure 3**. SST as measured by Ocean Color varied seasonally with a well-known and defined pattern in this region with lower SST during winter months and higher SST during summer. March presented the lowest mean SST (16.1 ± 0.3°C) and August was the warmest month (22.7 ± 0.4°C). A different pattern was detected for near surface chlorophyll-a concentration and particulate organic carbon with higher values during spring and lower during summer. Highest concentrations of chlorophyll-a and POC were obtained in May (0.31 ± 0.06 mg m^{-3}) and April (73.8 ± 6.4 mg m^{-3}), respectively, while lowest concentrations were detected in September (0.12 ± 0.02 and 42.1 ± 2.9 mg m^{-3} for chlorophyll-a and POC, respectively). PIC and NPP also showed a well-defined seasonal pattern with higher values during spring and lower observed in autumn or winter. NPP showed the highest concentrations in May (704 ± 64 mgC m^{-2} day^{-1}) and the lowest in December (307 ± 15 mgC m^{-2} day^{-1}). On the other hand, the NAO index showed positive and negative phases in all seasons with no clear patterns (**Figure 3**).

Inter-Annual Variability

Throughout the study period, 2011 seemed to be the most unusual year, displaying the highest NAO index, resulting in the lowest temperature observed and highest variability on chlorophyll-a and PIC concentrations (**Figure 4**). Nevertheless, mean annual SST remained somehow stable over the study period with no pronounced pattern, ranging from a 18.6 ± 2.6°C in 2011 and 19.11 ± 2.5°C in 2008 (**Figure 4**). The concentration of chlorophyll-a varied between a minimum of 0.183 ± 0.060 mg m^{-3} in 2005 and a maximum of 0.217 ± 0.074 mg m^{-3} in 2003 and 0.216 ± 0.097 mg m^{-3} in 2011. There was a slight decrease in the concentration of chlorophyll-a between 2003 and 2007 and a small increase thereafter (**Figure 4**). Our anomaly analyses (**Figure 5**) indicated that between 2005 and the first half of 2009, SST was in general higher and chlorophyll-a lower than the overall mean (positive and negative anomalies, respectively). In contrast, the second half of 2009 until 2011 were characterized by negative SST and positive chlorophyll-a anomalies (**Figure 5**).

PIC concentration ranged from a minimum of $1.94 \cdot 10^{-4} \pm 0.55 \cdot 10^{-4}$ mol m^{-3} in 2005 to a maximum of $2.32 \cdot 10^{-4} \pm 1.11 \cdot 10^{-4}$ mol m^{-3} in 2011 (**Figure 4**). POC concentration ranged from a minimum of 55.12 ± 10.29 mg m^{-3} in 2006 and 2007 to a maximum of 60.09 ± 11.29 mg m^{-3} in 2003 (**Figure 4**). PIC and POC anomalies showed unclear trends and patterns (**Figure 5**). In general PIC anomalies were positive in 2003-2004 and 2009-2013 and mostly negative in 2005-2008. POC anomalies, were mostly negative in 2004 and 2009 and thereafter alternated between positive and negative phases (**Figure 5**). NPP concentration ranged from 442.43 ± 130.56 mg m^{-3} in 2007 to a maximum of 482.04 ± 175.63 mg m^{-3} in 2011 (**Figure 4**) showing unclear anomaly patterns (**Figure 5**). Annual geographic datasets for these environmental parameters were also deposited at Pangaea and on the SIGMAR Azores website.

NAO index calculated for the whole studied period indicated that 2008, 2010, and 2012 presented the "higher" negative anomalies (**Figure 4**). Contrastingly, 2004, 2011, and 2013 presented the higher positive anomalies. Actually, NAO index for 2010 was the most negative (−1.153), being much lower than the overall mean for the entire period (−0.153). In contrast, 2011 was the year showing the highest mean NAO index (0.294). Annual geographic datasets for these environmental parameters were at Pangaea and on the SIGMAR Azores website and are presented in Supplementary Figures 2–6.

Relationship between Oceanographic Parameters

Pearson correlation coefficients calculated for all environmental parameters showed significant correlations for most parameters with the exception of the NAO index (**Table 3**). Comparison of

TABLE 2 | Summary statistics for the environment parameters obtained by remote sensing data in the Azores region for the period 2003 and 2013.

	SST (°C)	Chl-a (mg m^{-3})	PIC (mol m^{-3})	POC (mg m^{-3})	NPP (mgC m^{-2} day^{-1})	NAO index
Mean	18.87	0.20	$2.1 \cdot 10^{-4}$	57.75	464.3	−0.153
Min	15.55	0.09	$1.3 \cdot 10^{-4}$	37.43	284.2	−2.530
Max	23.20	0.43	$4.9 \cdot 10^{-4}$	86.61	812.7	2.520
STD	2.42	0.07	$0.8 \cdot 10^{-4}$	11.19	142.2	1.034
Range	7.65	0.34	$3.6 \cdot 10^{-4}$	49.18	528.5	5.050

Statistics presented here are overall temporal and spatial means and were calculated using the monthly mean images. SST, Sea Surface Temperature; Chl-a, Concentration of chlorophyll-a; PIC, Particulate Inorganic Carbon; POC, Particulate Organic Carbon; NPP, Net Primary Production; NAO, North Atlantic Oscillation Index.

monthly mean SST and POC revealed an out-of-phase seasonal response, with periods of higher temperatures associated with lower concentrations of POC, showing a significant negative correlation ($r = -0.82$, $p < 0.01$, $n = 132$; **Table 3**). Although less strong, this negative correlation is also observed between SST and chlorophyll-a concentration ($r = -0.68$, $p < 0.01$, $n = 132$; **Table 3**), which explain the high positive correlation between chlorophyll-a and POC concentrations ($r = 0.96$, $p < 0.01$, $n = 132$; **Table 3**). PIC is also positively correlated with the concentration of chlorophyll-a, although the peak seems to occur 1 month later than the peak of chlorophyll-a (**Figure 5**). Additionally, PIC and NPP parameters presents a positive correlation ($r = 0.84$, $p < 0.01$, $n = 132$; **Table 3**), emphasizing similar pattern of variability observed in the maps of these two environmental parameters. These results indicated that an increase of PIC leads to an increase of NPP. The NAO index did not show significant relationships with the other environment parameters analyzed in this study.

Oceanographic Conditions on the Seabed

Spatial Variability

Environmental conditions at the seabed showed large variability across the study area. There was no clear spatial pattern in the temperature and salinity conditions along the seabed found throughout the study area. These two parameters appeared to be tightly linked to water depth (**Figure 6**), being higher at shallower depths around the islands, banks, and seamounts and above the MAR, and dropping sharply at abyssal depths.

Although, a clear relationship was also evident between depth and the oxygen (dissolved oxygen, apparent oxygen utilization, and oxygen saturation) and nutrient-related parameters (nitrates, phosphates, and silicates), we identified some distinctive spatial patterns that appeared to be independent of water depth (**Figure 6**). Both dissolved oxygen and oxygen saturation values were higher to the west of the MAR and around the islands, whereas the eastern section of the study area presented generally lower values. Apparent oxygen utilization presented the opposite pattern, being lower at the western side of the MAR and higher on the eastern section of the study area. Additionally, the north-western tip of the area was characterized by a lower apparent oxygen utilization. The spatial pattern of nutrient concentrations on the seabed also showed an eastern-western (zonal) gradient with lower concentrations on the western side of the MAR and around the islands, and higher concentrations on the eastern section (**Figure 6**).

Depth Variability

Environmental conditions at the seabed revealed some notable variations with water depth. Mean values of temperature and salinity at different depths of the seabed sharply decreased from 17.38 ± 1.17°C (mean, SD) and 36.18 ± 0.25 PSU at 50 m depth to 3.72 ± 0.15°C and 34.98 ± 0.04 PSU at 2,000 m depth, respectively (**Figure 7**). No significant variation was detected at greater depths, reaching a mean of 2.47 ± 0.06°C and 34.89 ± 0.01 at 5,000 meters depth. For both parameters, the greatest variability was identified between the very shallow seabed down to 500 m depth.

Dissolved oxygen and oxygen saturation on the seabed displayed a similar behavior with increasing depth; decreasing severely until 750 meters depth, reaching a minimum of 4.28 ± 0.13 mL L^{-1} and 67.37 ± 1.96%, respectively. However, this was followed by a net increase of both parameters (**Figure 7**) with maximum values attained at 2,000 m depth (6.07 ± 0.16 mL L^{-1} and 82.91 ± 0.82%, respectively). Thereafter, neither parameters presented significant variation, reaching values of 5.66 ± 0.12 mL L^{-1} and 74.60 ± 1.40% at 5,000 m depth, respectively. However, patterns maybe masked due to the high level of variability observed between 2,000 and 5,000 m depth.

Apparent oxygen utilization on the seabed presented an opposite pattern, increasing markedly until 750 m depth, reaching a maximum of 2.08 ± 0.13 mL L^{-1}, followed by a net decrease to a mean concentration of 1.25 ± 0.13 mL L^{-1} at 2,000 m depth (**Figure 7**). At greater depths, apparent oxygen utilization displayed a small increase to a concentration of 1.93 ± 0.11 mL L^{-1} at 5,000 m depth.

Nutrient concentrations (silicates, nitrates, and phosphates) on the seafloor displayed a continuous increase with depth (**Figure 7**). Nitrates and phosphates displayed the same behavior despite their inherent differences in magnitude. Both nutrients increased from a surface concentration of 0.44 ± 0.16 and 0.16 ± 0.02 μmol L^{-1}, up to a maximum concentration of 19.02 ± 0.93 and 1.17 ± 0.07 μmol L^{-1} at 1,000 m depth. In deeper waters both nutrients displayed a small increase in concentration with a higher level of variability compared to the upper layers. The pattern of increase in the concentration of silicate with increasing depth was slightly different. Silicate displayed a continuous increase in concentration from shallow waters to 5,000 m depth, where it reached a maximum average concentration of 46.36 ± 3.50 μmol L^{-1}.

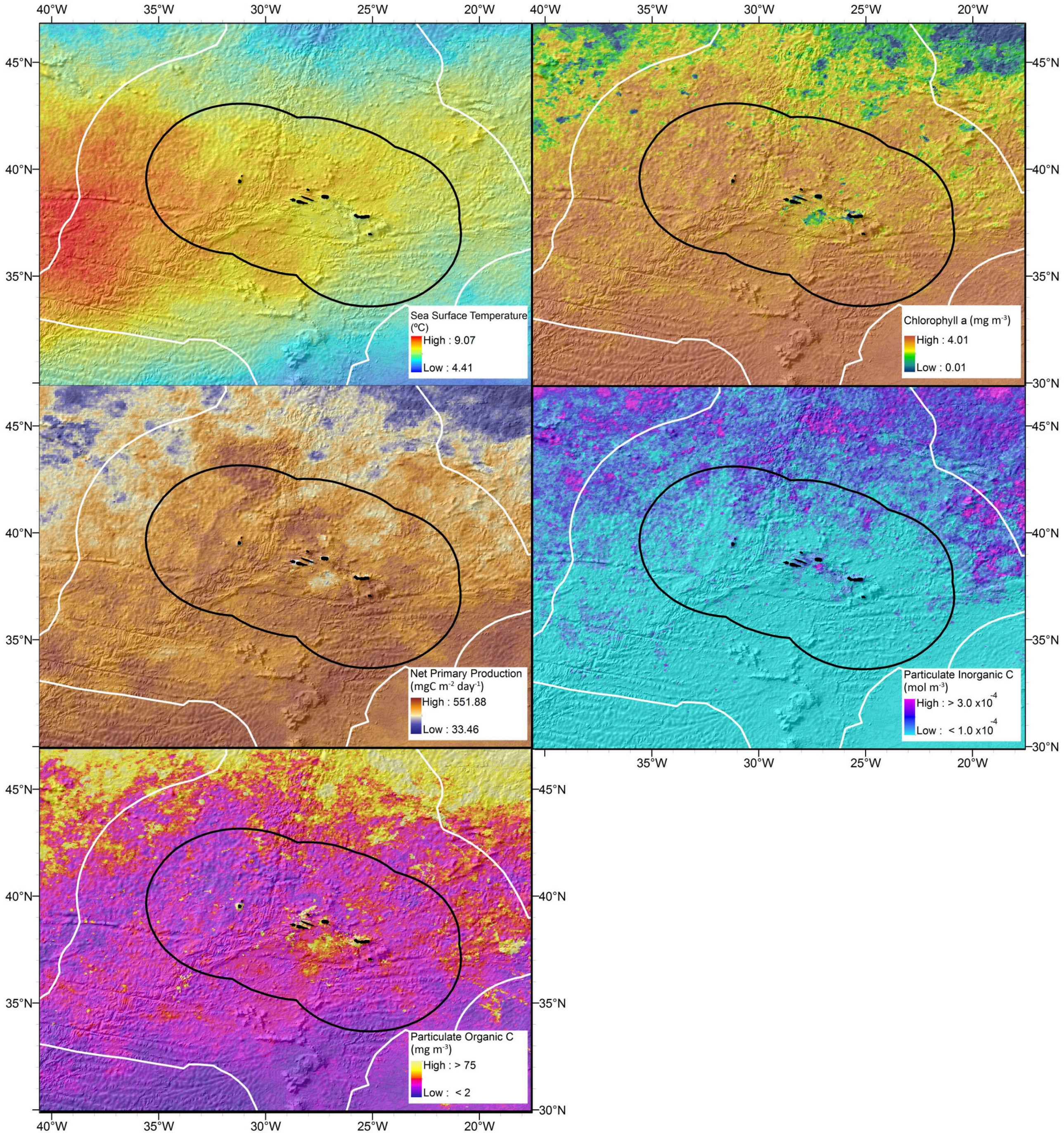

FIGURE 2 | Range of values observed for selected near surface oceanographic parameters in the Azores region obtained between 2003 and 2013 through remote sensing data. Black line represents the Portuguese current Economic Exclusive Zone around the Azores and white line represents the claimed extended continental shelf. Color scale is shown as a liner stretch between minimum and maximum observed values.

DISCUSSION

This paper highlights some general environmental characteristics of the Azores region and delivers some useful information required for marine spatial management. It does not pretend to provide an exhaustive analysis of the oceanography dynamics occurring in the area but rather assembling a comprehensive collection of environmental data for the Azores region, including data from high-resolution satellite imagery for several parameters: SST, near-surface concentration of chlorophyll-a,

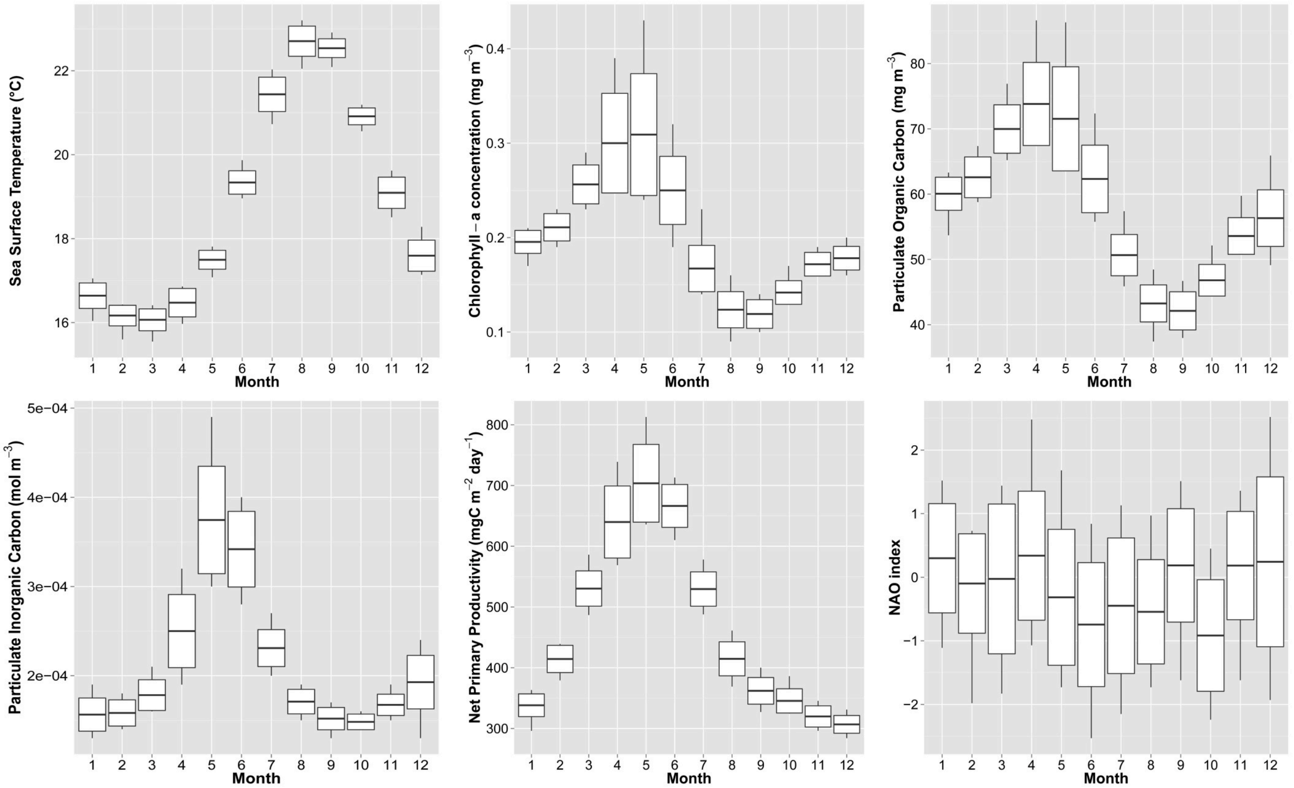

FIGURE 3 | Boxplots of monthly values of the mean, standard deviation and range of the oceanographic parameters in the Azores region between 2003 and 2013, calculated using the means of yearly values for each month. NAO is the North Atlantic Oscillation Index.

particulate organic and inorganic carbon, and ocean net primary production. This information is now available for many different purposes, including to support spatial management and decision-making. The climatological geographic datasets highlighted in this paper will also serve as a foundation for improving our knowledge on the distribution of marine fauna inhabiting the Azores region and help understanding the environmental factors driving some observed variation.

The Azores represent an important habitat for a wide range of migrating marine fauna ranging from seabirds (Monteiro et al., 1996), cetaceans (Silva A. et al., 2013), elasmobranchs (Vandeperre et al., 2014), or tuna (Pham et al., 2013) whose migrations are tightly linked to environmental factors (Amorim et al., 2009; Afonso et al., 2014; Prieto et al., in press; Tobeña et al., 2016; Druon et al., 2017). All these studies found SST and primary productivity or chlorophyll-a concentrations as the main environmental factors explaining the spatial distribution of large migratory species. Additionally, geomorphologic characteristics and features such as bathymetric slope or distance to seamounts (Amorim et al., 2009; Afonso et al., 2014) have also been referred as important drivers of the distribution of large pelagic animals, highlighting the usefulness of the comprehensive review of the geomorphology of the Azores region (Perán et al., 2016).

Environmental conditions at the seabed revealed some notable variations across the study area and with water depth. It should be noticed that although not calculated in detail, temporal variability at depths shallower than a few 100's of meters would be also highly pronounced. The temperature and salinity conditions along the seabed appeared to be tightly linked to water depth being higher at shallower depths around the islands, banks and seamounts and above the MAR, and dropping sharply at abyssal depths. There was also an apparent non-linear relationship between depth and oxygen measurements (dissolved oxygen, apparent oxygen utilization, and oxygen saturation) and apparent increase with depth of the nitrates, phosphates, and silicates. Other distinctive spatial patterns were identified that were independent of water depth. Notably, dissolved oxygen and oxygen saturation were higher to the west of the MAR and around the islands, whereas the eastern section of the study area presented generally lower values. Nutrient concentrations on the seabed also showed an eastern-western gradient with lower concentrations on the western side of the MAR and around the islands, and higher concentrations on the eastern section. These longitudinal patterns appear to coincide with the presence of a topographic discontinuity created by the MAR but could also reflect an oceanographic transition zone between water masses. This has important implications for understanding trans-Atlantic deep-sea biogeography and connectivity patterns but will also help improving our understanding of the distribution of important habitat-forming organisms, such as cold-water corals

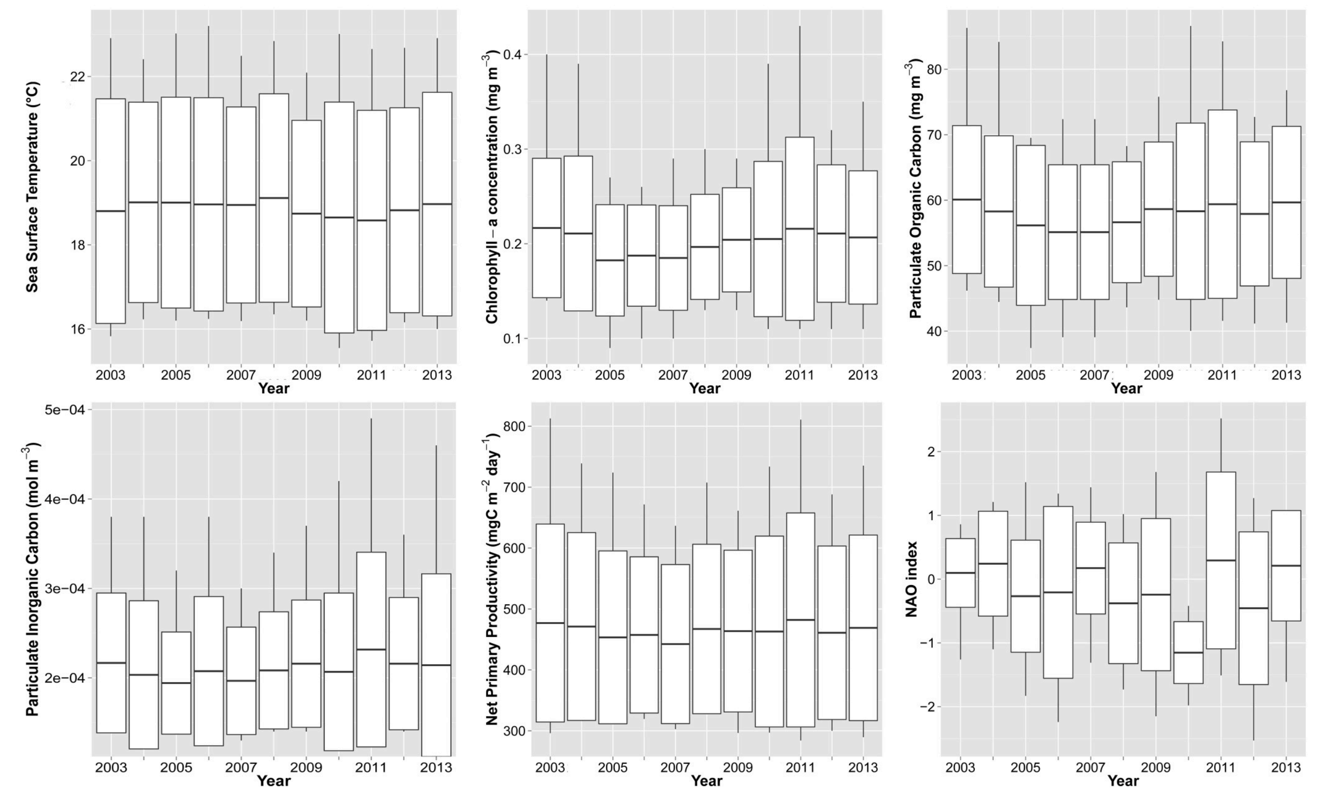

FIGURE 4 | Boxplots of yearly values of the mean, standard deviation and range of the oceanographic parameters in the Azores region between 2003 and 2013, calculated using the means of monthly values for each year. NAO, North Atlantic Oscillation Index.

and sponges, for which very little is known (Braga-Henriques et al., 2013).

Our study also contributed toward a comprehensive knowledge of the spatial and temporal near-surface variability of the environmental parameters characterizing the Azores. Similarly to previous studies, our results confirmed high spatial, seasonal and inter-annual variability of the marine environment in the Azores region, typical of mid-latitudes (Bashmachnikov et al., 2004; Lafon et al., 2004; Martins et al., 2009; Mendonca et al., 2010; Santos et al., 2013). In this study, SST as measured by Ocean Color varied between 15.55 and 23.20°C while chlorophyll-a concentration varied between 0.09 and 0.43 (mg m^{-3}). These results are corroborated by *in situ* measurements on the Condor seamount (Azores; Martins et al., 2011; Santos et al., 2013). Also, the previously described summer minimum chlorophyll-a concentrations was also observed when SST is higher (Santos et al., 1995; Martins et al., 2011; Santos et al., 2013).

The North Atlantic is considered as one of the most productive marine regions on the planet (DeYoung et al., 2004). However, the Azores region is located in oligotrophic waters with areas on the northern sector being more productive than those on the south. Most of the annual production in the North Atlantic, including the Azores region as confirmed by our analysis, occurs during spring (Schiebel et al., 2011; Abell et al., 2013). The surface POC concentrations obtained in the Azores were generally in the range obtained for other areas (Allison et al., 2010). Although these are the general patterns, high inter-annual variability has been observed in this region (Martins et al., 2009) but our analyses did not identify a clear trend. Nevertheless, the period between 2004 and 2008 was characterized by warmer waters than the long-term mean (2003–2013) but was less productive than the mean.

Habitat suitability models based on reliable environmental data is the most cost-effective and timely solution for determining the location of vulnerable marine ecosystems in the Azores. Actually, such models are recognized to be fundamental when designing management plans for protecting vulnerable marine ecosystems from anthropogenic impacts such as fishing (Ardron et al., 2014). Furthermore, oxygen levels, temperature, aragonite and calcite concentrations at the seabed have been important parameter for explaining the distribution of black corals (Yesson et al., in press) and other cold-water coral species (e.g., Davies and Guinotte, 2011; Yesson et al., 2012; Bostock et al., 2015). Our compilation of the environmental conditions at the seabed will therefore, facilitate future effort to predict the potential habitat of those key structuring fauna or explain potential biogeographic patterns in the region.

Although the compilation produced here is of utmost interest for several proposes, the dataset suffers from a number of

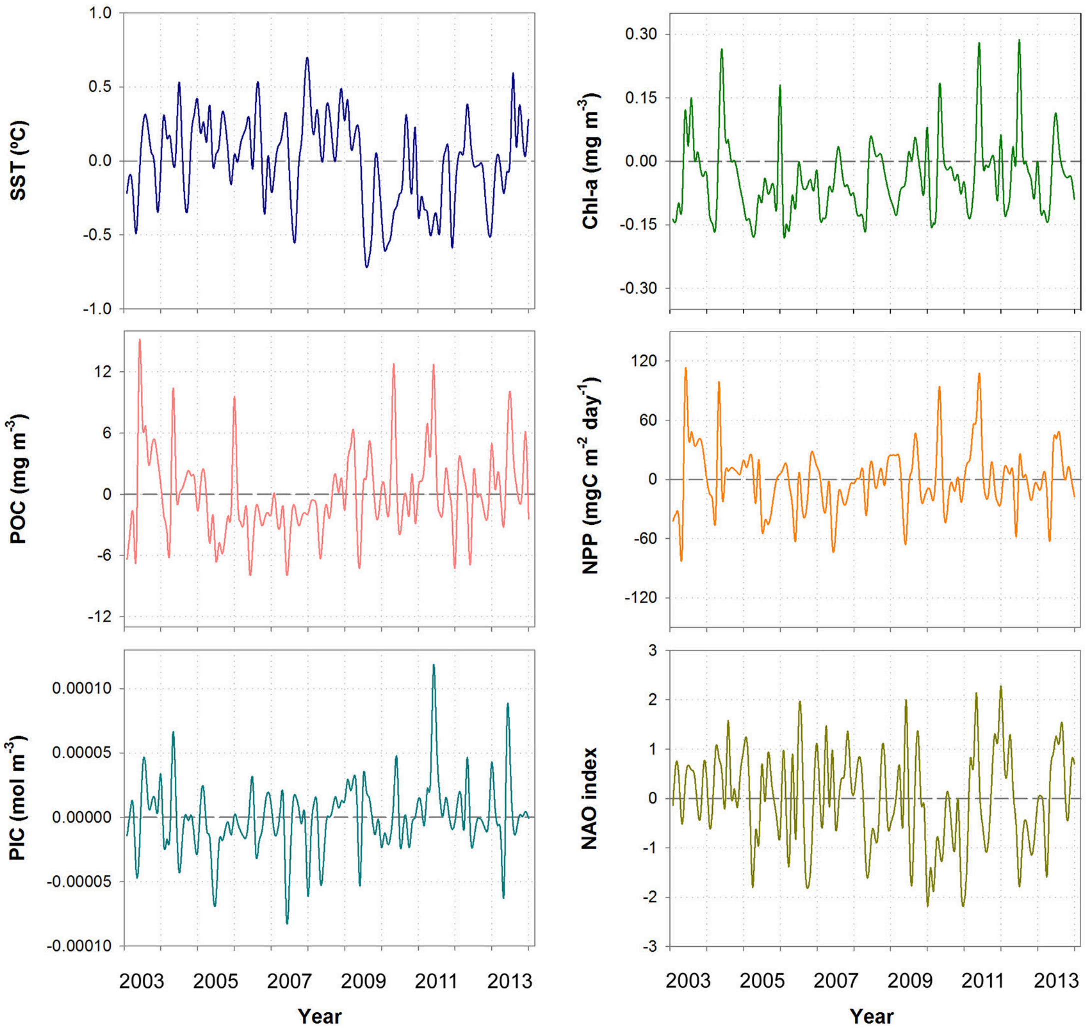

FIGURE 5 | Monthly anomalies calculated for each environmental parameter in the Azores region between 2003 and 2013. SST, Sea Surface Temperature; Chl-a, chlorophyll-a concentration; POC, Particulate Organic Carbon; NPP, Net Primary Production; PIC, Particulate Inorganic Carbon; NAO, North Atlantic Oscillation Index.

TABLE 3 | Pearson correlation coefficients calculated between all near-surface environmental parameters.

	SST	Chl-a	PIC	POC	NPP	NAO index
SST	–	−0.68*	−0.15	−0.82*	−0.22	−0.18
Chl-a		–	0.69*	0.96*	0.79*	0.09
PIC			–	0.54*	0.84*	−0.07
POC				–	0.67*	0.14
NPP					–	−0.08
NAO						–

*SST, Sea Surface Temperature; Chl-a, Concentration of chlorophyll-a; PIC, Particulate Inorganic Carbon; POC, Particulate Organic Carbon; NPP, Net Primary Production; NAO, North Atlantic Oscillation Index. *Indicates significant correlations ($p < 0.01$).*

shortcomings and has the potential to be significantly improved in the future. For example, accuracy issues associated with remote sensing or global bathymetry data increase the level of uncertainty of the outputs (Mendonca et al., 2010; Moore et al., 2015; Anderson et al., 2016). Additionally, the reduced and poorly-distributed historical environmental observations required a considerable amount of interpolation to describe the environmental conditions at the seabed (Supplementary Figure 1), leading to potentially large spatial and temporal errors, mainly for the deep ocean (Wunsch, 2016). Parra et al. (in press) developed predictive distribution models for deep-sea fish in the Azores and suggested that the global nature of datasets of the environmental conditions at the seabed may not reflect the actual fine-scale variation, making difficult to specify which environmental factors are primarily responsible for the observed patterns. It has therefore been suggested that such datasets require a large amount of validation and that an effective observing system for detecting oceanic change with adequate accuracy and precision is still required (Wunsch, 2016).

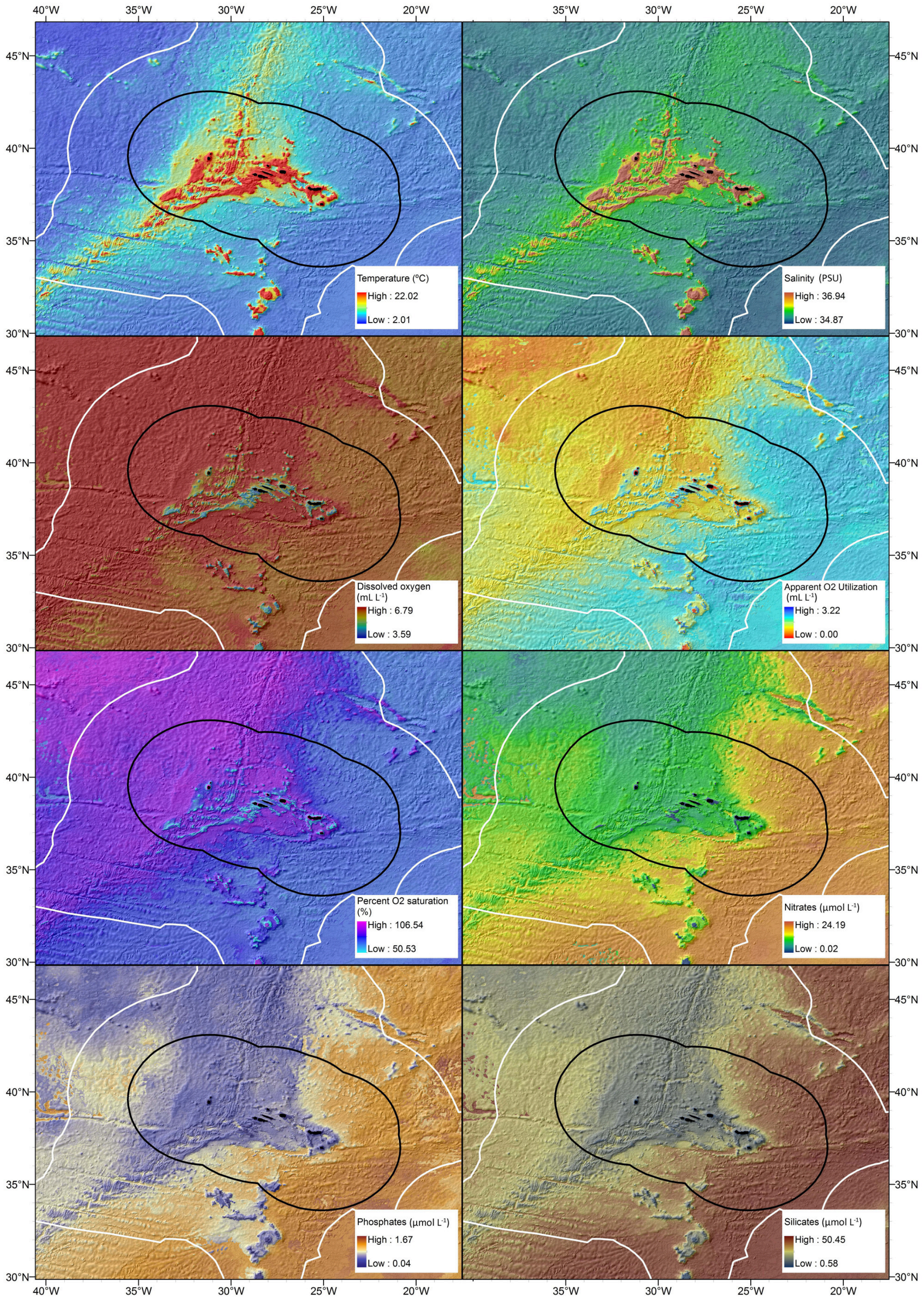

FIGURE 6 | Mean values of different environmental parameters estimated for the seabed in the Azores region by bathymetry-based resolution refinement methodology. For temperature and salinity, the average of 6 decadal means (calculated from 1955 to 2012) are shown while for oxygen, phosphate,

(Continued)

FIGURE 6 | Continued
silicate, and nitrate, the climatological mean was computed with all available data regardless of time period (from the early 1900s' to the present). Black line represents the Portuguese current Economic Exclusive Zone around the Azores and white line represents the claimed extended continental shelf. Color scale is shown as a linear stretch between minimum and maximum observed values.

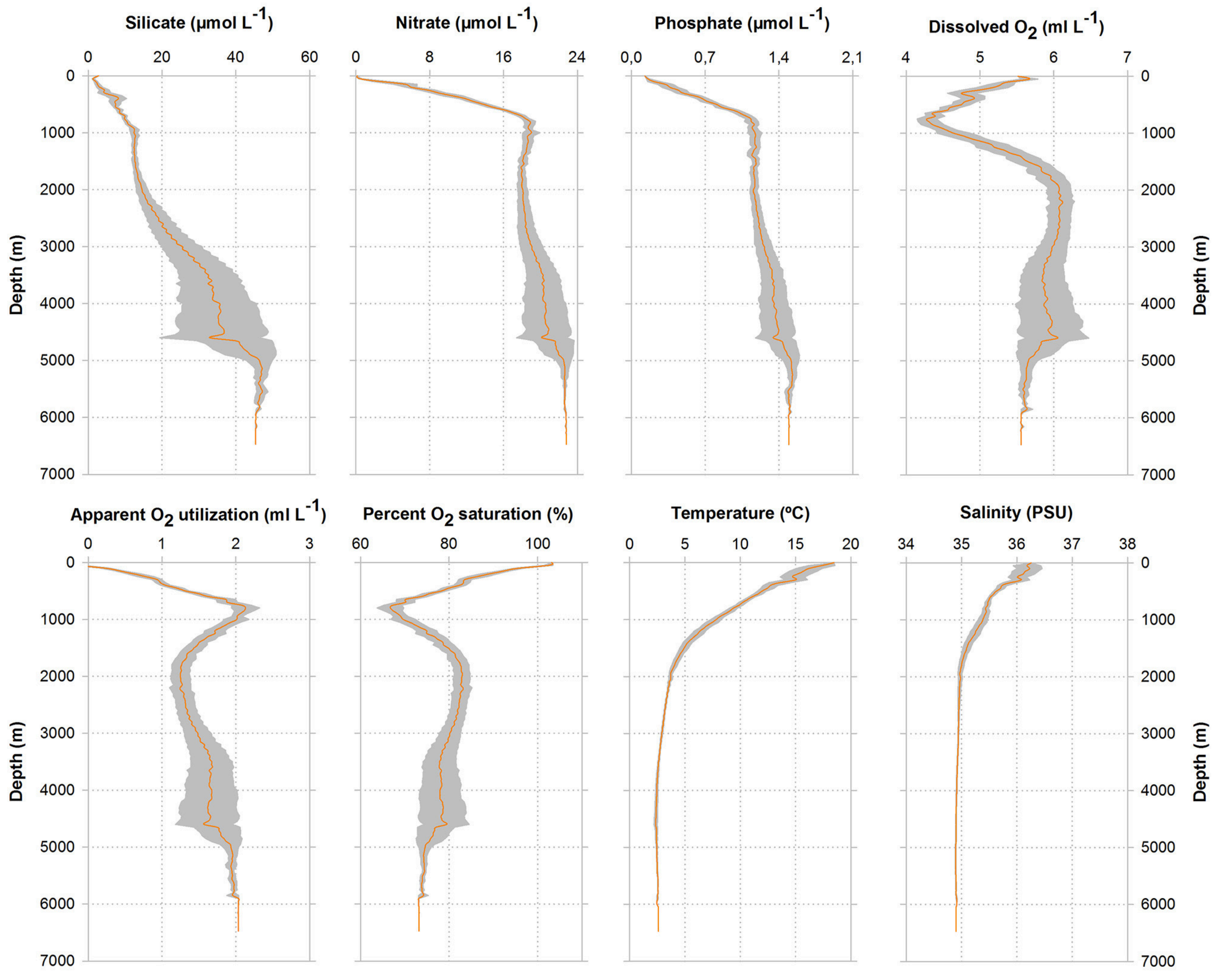

FIGURE 7 | Depth profiles and associated standard deviation (shaded area) of different environmental parameters in the Azores region. Standard deviation represents spatial variability of values observed at each depth of the seafloor.

Over the last two decades there have been significant advances in high-resolution remote sensing providing high resolution near-surface spatial and temporal data (Blondeau-Patissier et al., 2014; Finkl and Makowski, 2014). These new technologies will provide powerful tools for sampling marine ecosystems at finer spatial and temporal scales and produce better estimations that would never be possible with field work. However, they require a systematic *in situ* validation of the estimated data and lack capability of sampling the whole three-dimensional complexity of the oceans. Therefore, expanding fixed-point *in situ* seafloor observatories, moored oceanographic arrays, and drifting profilers are of paramount importance to measure essential ocean variables (Cristini et al., 2016).

AUTHOR CONTRIBUTIONS

TM, CP, FC, and FT designed the study. PA, AP collected and processed most of the data through GIS software. TM, CP, PA, MJ, and AP preformed most of the analyses. PA, AP, CP, FC, FT, MJ, and TM wrote the paper.

FUNDING

This research received funding from Fundo Regional da Ciência, Tecnologia (FRCT), through the research project 2020-M2.1.2/I/026/2011 (Pro-Convergência), and the European

Union Seventh Framework Programme (FP7/2007-2013) under the MIDAS project, grant agreement 603418. The authors also acknowledge funds provided by the Fundação para a Ciência e a Tecnologia (FCT) through the strategic project (FCT/UID/MAR/04292/2013) granted to MARE. TM is supported by Program Investigador FCT (IF/01194/2013) and IFCT Exploratory Project (IF/01194/2013/CP1199/CT0002) from the Fundação para a Ciência e Tecnologia (POPH and QREN), PA is currently supported by the Fundação para a Ciência e a Tecnologia (FCT) under a PhD fellowship (SFRH/DB/103504/2014), AP was partially supported by the Estagiar-L program from the Government of the Azores, CP was supported by the MIDAS project grant agreement 603418, and FC was supported by IMAR and the European Marine Observation and Data Network through contract IMAR/EMODnet Biology/001-2014. FT has been supported by a CORALFISH contract and a post-doctoral grant (ref. SFRH/BPD/79801/2011) from the Foundation for Science and Technology (Portugal). Data analyses were supported by projects CORALFISH (FP7ENV/2007/1/213144) and MeshAtlantic (AA-10/1218525/BF).

ACKNOWLEDGMENTS

We thank Chris Yesson for his collaboration with the extraction of a series of oceanographic and biogeochemical parameters and with implementing resolution refinement methodologies. We acknowledge data provided by NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2017.00056/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Marine Science

ORIGINAL RESEARCH
published: 16 March 2017
doi: 10.3389/fmars.2017.00075

Congruent Molecular and Morphological Diversity of Macaronesian Limpets: Insights into eco-evolutionary Forces and Tools for Conservation

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Combined analysis of genetic and morphological variation can provide synergistic insights into eco-evolutionary forces shaping biodiversity, as well as tools for conservation and management. Macaronesian limpets are undergoing severe declines due to overexploitation which calls for an evaluation of the evolutionary significance and taxonomic status of populations. This study details the analysis of genetic (mtDNA sequencing) and morphological (geometric analysis of shell shape) variation among Macaronesian populations of *Patella aspera*, *P. rustica,* and *P. candei*. In the case of *P. aspera* and *P. rustica*, this also included analysis of mainland conspecifics. mtDNA revealed distinct phylogeographic patterns for the three species. For both *P. aspera* and *P. rustica* Macaronesian and continental samples were reciprocally monophyletic, with shallower, and distinct, phylogeographic structure within both clades. For *P. candei*, the Macaronesian endemic, three reciprocally monophyletic groups corresponding to (i) the Azores, (ii) Madeira and (iii) Selvagens and Canary Islands were resolved. The different patterns for each species are compatible with independent processes of colonization and demographic processes. Morphological differentiation matched the major phylogeographic groupings (i.e., Macaronesian v Continent for *P. aspera* and *P. rustica*; Azores/Madeira/Selvagens and Canary Islands for *P. candei*) compatible with such variation being shaped by genetic drift associated with distinct demographic histories of lineages as well as historical/recurrent selection pressures. The genetic/morphological congruence supports the formal recognition of at least three described *P. candei* subspecies. Moreover, the data prompt recommendation of the separate management of limpets from each archipelago. At present management efforts are hampered by illegal harvesting of limpets. From an applied viewpoint, this study confirms that morphology retains useful information on genetic status and thus represents a potentially cheap method applicable to limpet conservation.

Keywords: Gastropods, phylogeography, evolution, conservation, phenotype, biodiversity

OPEN ACCESS

Edited by:
Tony J. Pitcher,
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Specialty section:
This article was submitted to
Deep-Sea Environments and Ecology,
a section of the journal
Frontiers in Marine Science

Received: *30 December 2016*
Accepted: *02 March 2017*
Published: *16 March 2017*

Citation:
Carreira GP, Shaw PW, Gonçalves JM and McKeown NJ (2017) Congruent Molecular and Morphological Diversity of Macaronesian Limpets: Insights into eco-evolutionary Forces and Tools for Conservation. Front. Mar. Sci. 4:75.
doi: 10.3389/fmars.2017.00075

INTRODUCTION

Patterns of variation in morphological and genetic diversity for a species reflect to varying degrees, historical and recurrent evolutionary processes, and can provide insights into the interplay between neutral and adaptive forces. Such information is fundamental to understand eco-evolutionary processes (Slatkin, 1987) and can be useful for the conservation of intraspecific biodiversity in the case of vulnerable or highly exploited species (Hilborn et al., 2003; Mariani et al., 2012). While advances in molecular biology are providing increased resolution of biocomplexity among marine taxa, there remains a major demand to obtain reliable and informative biological information for a plethora of populations/species at low operational costs for management and conservation purposes (Frankham, 2010). As such, comparative studies of morphological and genetic divergence can still have an important contribution to biodiversity conservation (Strange et al., 2008; Mariani et al., 2012).

The biogeographic region of Macaronesia is comprised of the four ocean archipelagos of the Azores, Madeira, Selvagens and Canaries (the archipelago of Cabo Verde is also sometimes included into this definition). These islands are all the result of volcanic activity and have never been connected to continents, thus their biota are believed to have resulted from colonization and *in situ* evolution. Across that region, Patellid limpets represent an important socioeconomic resource and have likely been exploited since the islands were first colonized (Hawkins et al., 2000), which, in the case of Canaries, goes back to around the middle of the 1st millennium B.C.E with recognized effects on the abundance of *P. candei*, at least in one island of the archipelago (Gonzalez-Lorenzo et al., 2015) (the human colonization of the Azores and Madeira goes back to the 15th century). The high levels of exploitation have contributed to severe declines in limpet abundance with many populations considered to be overexploited (Martins et al., 2008). The reductions in limpet abundance is also reported to be altering ecosystem services of the coastal areas, as it has been linked to the increase in turf-forming algae (Martins et al., 2010).

Three species of *Patella* are recognized on the Macaronesian islands: *Patella aspera*, *P. rustica*, and *P. candei* (Christiaens, 1973; Hawkins et al., 1990; Ridgway et al., 1998; Koufopanou et al., 1999). *P. aspera* is the widest distributed *Patella* species. It inhabits the lower intertidal and sub-tidal down to 6 m deep and is distributed across most of Europe, Mediterranean, North Africa, as well as the Azores, Madeira, Selvagens, and Canaries. Continental populations have been referred to as *P. ulissyponensis*, while Macaronesian populations have been referred to as *P. aspera* (Hawkins et al., 2000; Weber and Hawkins, 2005), sometimes also called *P. u. aspera* (Ferraz et al., 2001). *P. rustica* occurs throughout Europe, up to northern Iberia, including the Mediterranean and North West African Atlantic coasts south to Mauritania. *P. rustica* inhabiting the Macaronesian Islands are sometimes referred to as *P. piperata* (Christiaens, 1968; Côrte-Real et al., 1996b). This species is absent from the Azores and is believed to have undergone a recent range expansion across the western coast of Iberia due to climate change (Lima et al., 2006). *P. candei* is endemic to the Macaronesian Islands, where it inhabits the intertidal fringe, usually less than 3 m depth. This species overlaps in its habitat with other species, according to the archipelago. In Madeira and Canaries, two species share partially the same habitat with *P. candei: P. rustica* (upper intertidal) and *P. aspera* (low intertidal and subtidal). In the Azores, however, only *P. aspera* partially shares the same habitat with *P. candei*, in the low intertidal and upper subtidal, as *P. rustica* is absent from that archipelago.

Phylogeographic patterns among Macaronesian limpets are well established (Sá-Pinto et al., 2008) and reveal ancestral splits and contemporary restricted gene flow from mainland forms (for *P. aspera* and *P. rustica*), as well as further restricted gene flow among archipelagos (for all three species). In contrast, informative quantitative morphological data are lacking, largely due to difficulties in identifying appropriate and informative landmarks on shells (e.g., Cabral and Jorge, 2007). Where morphology reflects genetic patterns, preliminary morphological surveys can motivate and inform future studies into factors shaping gene flow. Furthermore, in such cases phenotypic traits can be used as valid criteria to establish management units (Garnier et al., 2005). Additionally, morphological differentiation can reveal cryptic patterns of incipient genetic divergence (e.g., that may not be detected at assayed genetic markers that have not attained migration-drift equilibrium or sufficient statistical power (Nice and Shapiro, 1999). Generation of robust morphological data is particularly relevant to the taxonomy of *P. candei* for which early morphological patterns prompted the description of four geographically distinct subspecies (*P. c. gomesi* in Azores; *P. c. ordinaria* in Madeira, *P. c. candei* in Selvagens, and *P. c. crenata* in Canaries (Christiaens, 1973). However, subsequent studies have disagreed with various aspects of this taxonomy and it remains controversial (Côrte-Real et al., 1996a,b; Weber and Hawkins, 2002; Sá-Pinto et al., 2008).

This study details the analysis of genetic (mtDNA sequencing) and morphological variation among Macaronesian populations of *P. aspera*, *P. rustica* and *P. candei*. In the case of *P. aspera* and *P. rustica*, this also included analysis of mainland conspecifics. Morphological variation was assessed using the first, to our knowledge, implementation of a geometric approach for limpets and particular attention was paid to the morphological diagnosability of members of different lineages. This information is then used to discuss (i) the factors shaping biodiversity and (ii) the potential utility of such an inexpensive morphological approach as a management tool. The patterns are also interpreted in the context of *P. candei* taxonomy.

MATERIALS AND METHODS

Specimens of *P. aspera*, *P. rustica*, and *P. candei* were collected from across their distribution ranges across the Azores, Madeira, Selvagens and Canaries. For *P. rustica* and *P aspera,* representative continental samples were also collected and examined (**Table 1**). Samples were collected randomly by hand, throughout the intertidal rocky shore, during low tide periods. Tissues were preserved in ethanol (96%) and shells cataloged for

TABLE 1 | Number of specimens examined for the three *Patella* species, localities of collection and data (COI and cytochrome b, or CYTB) and shell shape (2-D conformations, composed of 27 landmarks).

Species	Geographical distribution	Area/Archipelago	Locality/Island	COI	CYTB	COI-CYTB	Morphology
Patella candei	Azores	Azores	Corvo	25	27	15	43
	Madeira		Flores	8	19	4	26
	Selvagens		Graciosa	11	8	4	20
	Canary Islands		So Jorge	13	11	4	58
			Terceira	13	16	5	38
			Faial	12	16	2	55
			Pico	17	19	4	206
			So Miguel	10	16	4	89
			Santa Maria	10	12	–	57
			Formigas Islets	14	18	9	§
		Madeira	Madeira	14	17	10	126
			Porto Santo	21	16	3	38
			Deserta	19	17	10	98
		Selvagens	Selvagem Grande	20	20	6	§
		Canary Islands	Gran Canária	22	19	13	34
			Lanzarote - Punta Pechiguera	13	23	–	35
			Lanzarote - El Cochino, Tymanfaya	14	14	10	21
			La Graciosa	5	14	3	41
P. rustica	Madeira,	Madeira	Deserta	3	3	3	4
	Selvagens,		Porto Santo	10	14	4	21
	Canary Islands,	Canary Islands	Gran Canária	14	10	8	18
	North west Africa,		Lanzarote	10	19	6	16
	Atlantic SW Europe,		La Graciosa	12	8	6	14
	West Mediterranean,	North west Africa	Mauritania	1	3	3	4
	Aegean Sea.	Atlantic SW Europe,	Algarve	16	16	15	15
		West Mediterranean	Ceuta	14	23	13	44
			Tuscany	5	13	4	18
		Aegean Sea	Greece	19	13	10	30
P. aspera	Azores,	Azores	Corvo	16	9	8	43
	Madeira,		Flores	2	2	2	§
	Selvagens,		São Jorge	26	13	12	§
	Canary Islands,		Faial	13	13	10	15
	Atlantic Europe,		Terceira	8	5	2	29
	West Mediterranean,		Pico	25	18	13	20
	Aegean Sea.		São Miguel	19	9	5	28
		Madeira	Madeira	12	4	1	59
			Porto Santo	14	11	5	17
			Deserta	4	4	4	2
		Selvagens	Selvagem Grande	11	5	4	4
		Canary Islands	Gran Canária	13	18	4	37
			La Graciosa	1	3	–	2
			Lanzarote	14	2	1	15
		Atlantic Europe	Algarve	10	21	6	13
			Costa da Caparica	12	17	9	42
			Figueira da Foz	15	12	12	13
			Devon, Great Britain	1*	–	–	–
		West Mediterranean	Ceuta	5	3	3	§
			Tuscany	7	10	5	4
		Aegean Sea	Greece	11	13	5	19
	Total			611	606	289	1564

**Tissue sample obtained from a voucher deposited in the Natural History Museum of London, UK; § locations for which the shells were not included for analysis, due to the fact that these were highly eroded shells.*

further morphometric analysis. In the case of shells, only non-broken and not severely eroded specimens were considered for morphometric study.

Genetic Analysis

Where possible sequences were obtained for each individual for the cytochrome oxidase I gene (~650 bp fragment PCR amplified using universal primers LCO1490 and HCO2198, Folmer et al., 1994) and cytochrome B gene (~350 bp PCR amplified using degenerate primers UCYTB151F and UCYTB270R, Merritt et al., 1998). PCR products were cleaned using ExoSap and sequenced in both directions on an Applied Biosystems sequencer using Big Dye technology. Sequences were trimmed and edited manually in CHROMAS (http://www.technelysium.com.au) and the alignments were analyzed with the programs ESEE (Cabot and Beckenbach, 1989), BioEdit 7.0.9.0 (Hall, 1999), DnaSP 4.50.3 (Rozas et al., 2003), MEGA 4.0.2 (Tamura et al., 2007), and DAMBE 5.0.52 (copyright© Xuhua Xia, http://dambe.bio.uottawa.ca/Include/software.aspx). Neighbor joining P-uncorrected phylogenies were inferred by using PAUP∗ Neighbor joining P-uncorrected trees obtained in MEGA. The selection of the best DNA substitution model was performed for the concatenated datasets through MrMODELTEST 2.3 (Nylander, 2004), jointly with PAUP∗ 10b (Swofford, 2003). Maximum likelihood (ML) phylogenies for the COI-CYTB composite (concatenated sequence between COI and cytochrome b) haplotypes were inferred with the routine implemented in PhyML, as described by Guindon and Gascuel (2003). ML phylogenies were assessed by bootstrapping, with 2,000 pseudo replicates (Felsenstein, 1985). The ML trees were mid-point rooted, visualized and edited using FigTree 1.2.2 (Andrew Rambaut, 2006–2009, http://tree.bio.ed.ac.uk/). Genetic variation was described using indices of haplotype and nucleotide diversity (Nei and Tajima, 1981; Nei, 1987; h and $\prod$, respectively), extracted through DnaSP.

Morphological Analysis

Each shell was photographed with a digital camera (Nikon CoolPix 775, with lens Nikkor 5.8–7.4 mm, I:2.8–4.9) fixed to a tripod. Each shell was superimposed to a fan composed of a system of axes equally distant in 15°, and centered to a frame of size 110 × 70 mm (**Figure 1**). Each shell was orientated with the anterior end to the left and two additional lines were used on the right side, distant to the horizontal line in ±22°. TPS data files were prepared with tpsUtils (Rohlf, 2006a) and the digitalization of each specimen was made with tpsDig (Rohlf, 2006b). This system allowed the collection of 27 landmarks in each shell (one located on the shell apex, and the remaining landmarks located throughout the shell border). The pictures were individually scaled and a dataset composed of shape conformations obtained, consisting of two-dimensional (x,y) coordinates of the 27 landmarks that were collected from each specimen (**Figure 1**).

The individual conformations were aligned with the generalized Procrustes superimposition method, as implemented in tpsRelW (Rohlf, 2006c). In order to relax the assumption of homology among landmarks, the border points were allowed to slide as semi-landmarks along the shell border, according to a pre-established sliders file, prepared for each dataset with tpsUtils. A matrix of shape descriptors generated on tpsRelw (Rohlf, 2006c), known as the weight matrix, was extracted with tpsRelw. This matrix is composed of the partial warps (PW) and the two uniform (affine) shape components. First, a relative warp analysis (RWA) was performed. For this analysis, and to avoid the noise provided by the typical (and possibly random) reticulated nature of the shell border in limpets, we set α parameter of the RWA to 1, which drives the analysis to focus primarily on the overall information on shape, when performing a RWA. The matrix of relative warps (RW) was analyzed by plotting means and 95% confidence intervals for each group previously defined as a molecular lineage.

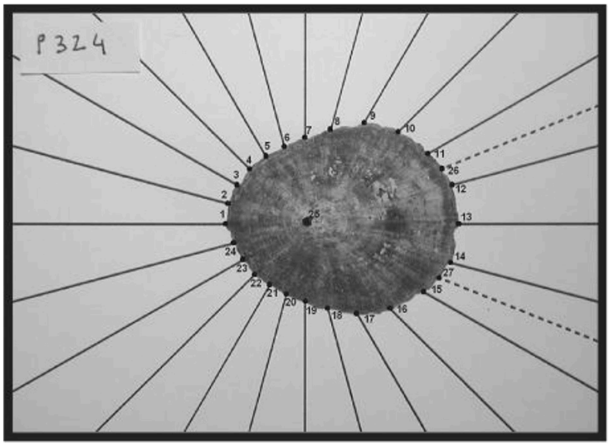

FIGURE 1 | Scheme for shape data collection on limpet shells considering 27 landmarks. In this case, a specimen of *P. candei* collected on Pico Island (Azores).

One-way analyses of variance (ANOVA) between groups (mitochondrial lineages) were performed and Bonferroni pairwise tests were computed in order to statistically assess shape differences between pairwise groups, as described by the first three RW components. A visual representation of the shape variation described by RW was obtained by plotting thin-plate-spline deformation grids associated with extreme values of RW for each group, which consist of a graphical illustration of the bending energy matrix, as described by each RW component.

Descriminant Analysis and Assessment of Molecular Lineage/Morphological Congruence

The weight matrixes were imported to the STATISTICA®—data analysis software system, version 6.0 (http://statistica.software.informer.com/6.0/, Inc. 2001), and a generalized discriminant analysis performed by defining the groups according to the mitochondrial lineages. In addition, cross-validation procedures were performed by previously keeping 25% (*P. candei*) or 33% (*P. rustica* and *P. aspera*) (taken randomly from the specimen groups included in each clade) as a training sample.

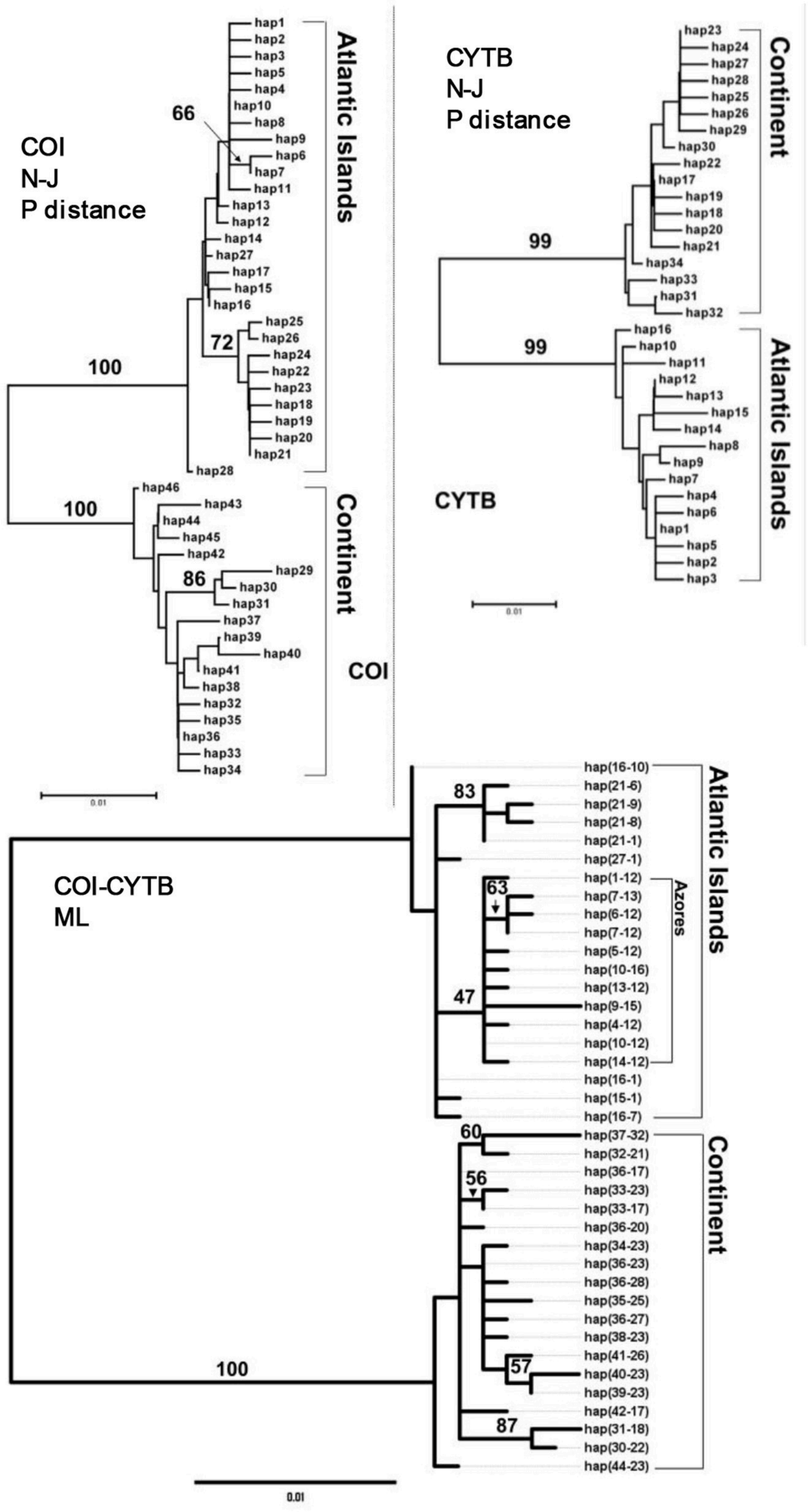

FIGURE 2 | Neighbor joining P-uncorrected phylograms for COI and CYTB haplotypes, and ML tree among concatenated haplotypes in *P. aspera*. Values located next to the branches indicate percentage of bootstrap replicates that supported each branch (2,000 bootstrap replicates).

In order to visually inspect the shape variability associated with the inferred discriminant model, multivariate regression analyses were computed of the weight matrix (set as dependent variable matrix) on the coefficient of variate matrix (CV, set as the matrix of independent variables). The fit of these regression analyses were assessed through the significance of the multivariate Goodall F, based on a re-sampling procedure (5,000 permutations). These analyses were performed on tpsRegr (Rohlf, 2006d), which also allowed the visualization of the correspondent deformation grids, under a thin-plate-spline model, based on the bending energy matrix. The congruence between molecular lineage/morphology was assessed

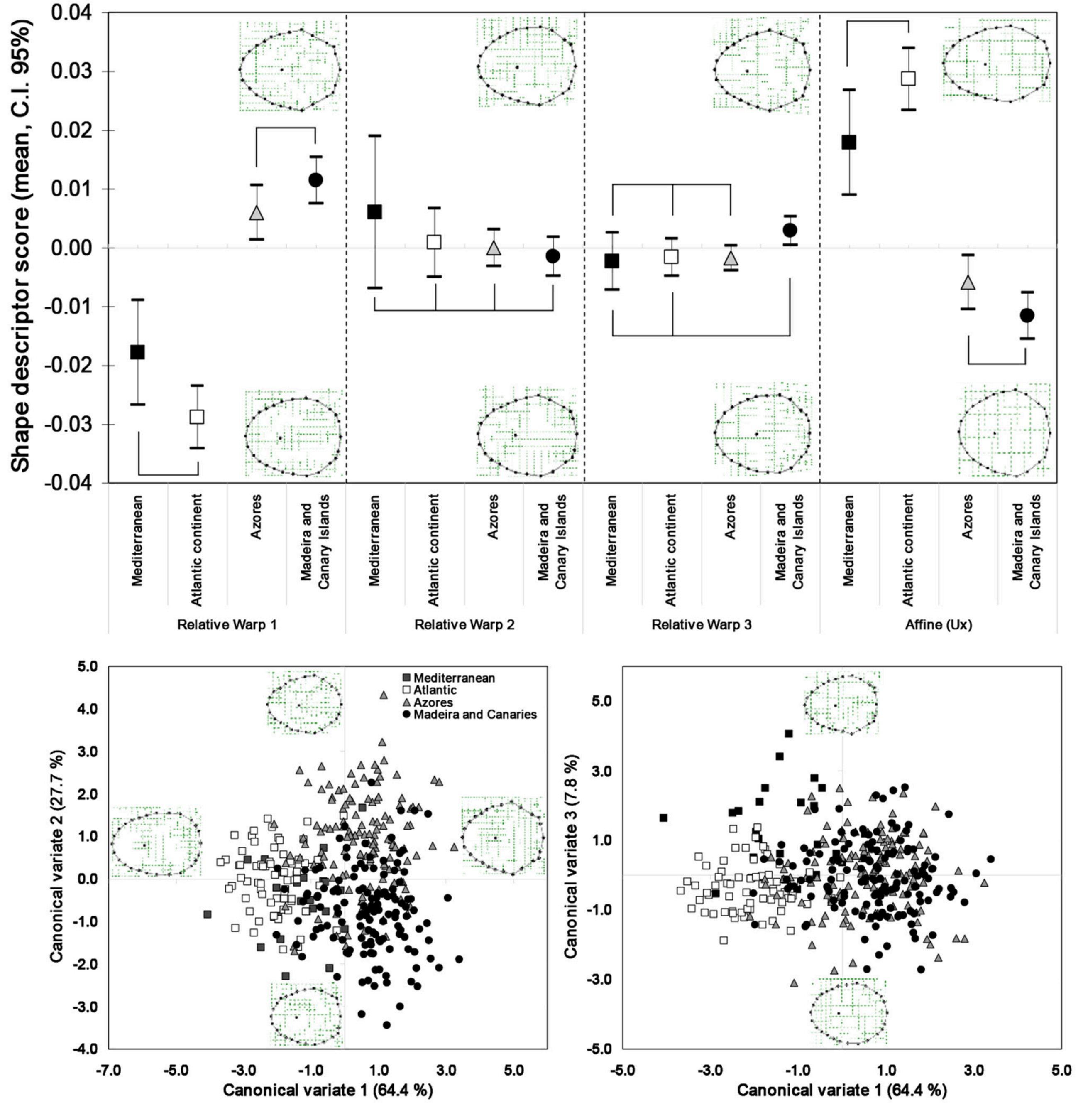

FIGURE 3 | Mean and 95% confidence interval of the relative warp scores and first uniform (affine) shape component, for individuals from the four identified P. aspera mitochondrial lineages. The linking lines indicate non-significant differences, according to the pairwise Bonferroni post-hoc multiple comparison ($p > 0.05$). Scatter plots of the canonical variates (roots 1, 2, and 3) obtained by discriminant analysis of the shape descriptors (weight matrix) of *P. aspera*, and considering the four mitochondrial lineage groups. Goodall $F = 30.1909$, df = 150, 17,900, $P = 0.0000$.

by evaluating the degree of molecular disjunction between clades and the statistical grouping both for RW and for discriminant analysis (cross-validation).

RESULTS

Patella Aspera

In 240 individuals of *P. aspera* that were screened for COI, 46 haplotypes were detected (h = 0.82 ± 0.020), and 34 haplotypes were detected in 175 individuals that were screened for cytochrome b (h = 0.82 ± 0.020). The concatenated dataset was composed of 39 different haplotypes. The nucleotide diversity of COI for the complete alignment was 0.02165 ± 0.00124. The nucleotide diversity of the complete cytochrome b alignment was 0.03350 ± 0.00128.

Both the neighbor joining p-uncorrected phylograms and the ML inferred phylogeny revealed two reciprocally monophyletic groups, one composed of the haplotypes sampled across the Macaronesian islands and the second containing haplotypes sampled across the Atlantic and Mediterranean continental coasts (**Figure 2**). Within both clades there was further phylogeographic structuring. Among the Macaronesian samples, the Azores shared no haplotypes with the other archipelagoes, while there was also no haplotype sharing between the Atlantic and Mediterranean samples. Canaries and Madeira shared haplotypes for both COI and cytochrome b.

Patterns of shell shape variation showed concordance with the inferred phylogeographic patterns: the main divergence in terms of shell shape was found between the two main mitochondrial phylogenetic lineages (Macaronesia/continent), particularly demonstrated for the RW1 and the uniform (affine) shape descriptors (**Figure 3**). The ANOVA clearly split the insular from the Atlantic and Mediterranean continental populations, in terms of polygonality of the shells (ANOVA, RW1, F = 48.26248, df = 358, P = 0.000013) as well as the lateral vs. longitudinal compression (ANOVA, Ux, F = 48.46422, df = 358, P = 0.000012). The RW1 characterized the polygonality, typical of the Macaronesian shells, by the eccentricity of the landmarks 9, 13, 17, 26, and 27, as well as a more posteriorly positioned apex. The continental shells, on the other hand, presented a smoother and less angular shell shape. The affine shape descriptors showed the continental shells as laterally compressed, in opposition to the Macaronesian shells, which were wider and longitudinally compressed. This differentiation was evident in the high percentage of correct assignment of individuals to either the Macaronesian (83.3%) or continental (80.0%) groups (overall 84.4% correct assignment to regional group) (**Figure 4**, **Table 2**). Lower shell shape differentiation was reported among the lineages within the Macaronesian and continental groups. A gradient of shape was obtained (**Figure 4**) ranging from the continental shells, characterized by only slight polygonal and laterally compressed shell shapes, to the Macaronesian shells, characterized by highly polygonal and laterally wider/longitudinally compressed shell shapes.

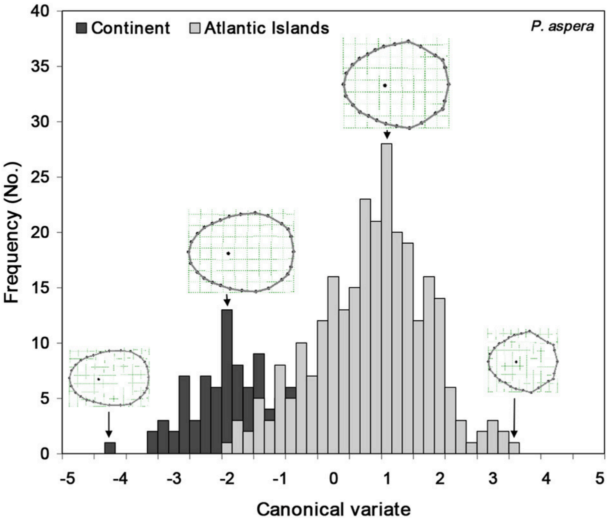

FIGURE 4 | Canonical variates obtained from discriminant analysis, when analyzing the two main clades of P. aspera: Atlantic Islands (composed of the two reciprocally monophyletic groups of Madeira and Canary Islands); and Continent (comprising the sample localities sampled across the Atlantic European, Atlantic African, Mediterranean African and Mediterranean European coasts). A cline on the shell apex position is visible, from more anterior (Atlantic Islands) to more central (Continent). Goodall F = 62.7807, df = 50, 18,000, P = 0.0000.

P. rustica

In 110 specimens of *P. rustica* that were screened for COI, 41 haplotypes were found (h = 0.94 ± 0.011), and 30 cytochrome b haplotypes were found in 115 specimens (h = 0.83 ± 0.024). 39 contiguous haplotypes were identified. Inferred phylogenies revealed a hierarchically clustering into four monophyletic phylogeographic groups (**Figure 5**). The major phylogenetic split separated the Macaronesian and continental lineages. Within both clades reciprocally monophyletic units composed of (i) the Madeira and Canary islands and (ii) Aegean Sea and Atlantic/west Mediterranean were also resolved.

Shell shape variation for *P. rustica* also aligned with the phylogeographic patterns in clearly separating the Macaronesian and continental samples, whilst also reporting a lower level of diagnosability of members of the sub-clades (i.e., Madeira, Canary Islands, Atlantic/west Mediterranean, Aegean Sea). The RW1 (which explained 48.15% of the variation in shell shape) separated Macacronesian and continental shells as well as shells from the Canary Islands and Madeira, (**Figure 6**). The main character that was responsible for this observed pattern was the relative location of the shell apex, which was more anterior among Madeira individuals, and to a lesser degree in Canary Island individuals. The shells from the Atlantic and Mediterranean showed a more relatively centered apex location. This pattern was also apparent in RW3 (19.10% of shell shape variability). The shells from Madeira were also significantly more laterally compressed, when compared to the other three lineages, which did not significantly differ ($P > 0.05$) by presenting average values of the uniform (affine) shape component.

TABLE 2 | Cross-validation reassignments, based on the GDA of the weight matrixes, composed of the non-uniform (PW) and uniform (affine) shape descriptors for each species.

P. aspera - Correct cross-validation (train sample = 33%), Canonical $R = 0.77343$, Eigen-value = 1.487927, Wilk's lambda = 0.186704, $\chi 2 = 359.1412$, df = 150, $P = 0.00000$.

Lineage	Mediterranean	Atlantic	Azores	Madeira and Canary Islands	Total (%)	Main disjunction (%)
Mediterranean	2	3	1	1	29	84
Atlantic	9	10	2	2	43	
Azores	1	6	25	13	56	80
Madeira and Canary Islands	3	4	13	25	56	
Total	15	23	41	41	52	

P. rustica - Correct cross-validation (train sample = 33%), Canonical $R = 0.869988$, Eigen-value = 3.113166, Wilk's lambda = 0.068103, $\chi 2 = 255.2398$, df = 150, $P = 0.00000$.

Lineage	Atlantic and west Mediterranean	Eastern Mediterranean	Madeira	Canary Islands	Total (%)	Main disjunction (%)
Atlantic and west Mediterranean	16	5	3	3	59	84
Eastern Mediterranean	5	5	0	0	50	
Madeira	0	1	4	3	50	83
Canary Islands	0	3	6	7	43	
Total	21	14	13	13		

***P. candei* -** Correct cross-validation (train sample = 25%), Canonical $R = 0.8603$; Eigen-value = 2.8483; Wilk's lambda = 0.1481; $\chi 2 = 1286.3080$; dF = 100; $P = 0.00000$.

Lineage	Azores	Madeira	Canary Islands	–	Total(%)	–
Azores	132	0	3	–	98	–
Madeira	4	55	6	–	85	–
Canary Islands	5	3	25	–	76	–
Total	141	58	34	–	91	–

The four lineages were also separated significantly (Canonical $R = 0.862436$, Eigen-value = 2.903149, Wilk's lambda = 0.109511, $\chi^2 = 345.0298$, df = 150, $P < 0.00001$) based on the discriminant model inferred by GDA, although a pattern of partial overlap was found (**Figure 6**). The first canonical root (73%) clearly separated Macaronesian and continental shells, based on the more anterior position of the apex. The second canonical root, on the other hand, separated shells from the two island populations, with the ones from the Madeira archipelago presenting a more anterior apex and being slightly laterally compressed. The third canonical root (9%), although showing some overlap, tended to separate shells based on the anterior border, which was anteriorly pointed in Aegean Sea shells compared to the Atlantic and Western Mediterranean. Polygonality was not apparent on *P. rustica* shells.

The shape overlap found in both the RWA and GDA was reflected in the results of the cross-validation assignment tests wherein high levels of assignment success were obtained between the Macaronesian and continental samples but assignment success was lower when classification was to the four mtDNA clades i.e., Madeira/ Canary islands/Atlantic/Mediterranean) (**Table 2**). The GDA, when performed by assuming these two main mitochondrial lineages as discriminant groups, was significant (Goodall $F = 127.8290$, df = 50, 9100, $P < 0.0001$) and showed a clear separation (**Figure 7**) based on the canonical root. The thin-plate-spline regression of the weight matrix on the canonical root confirmed the apex position as the main character separating these two lineages: Macaronesian specimens presented significantly anterior apex locations when compared to the continental populations.

P. candei

In 261 individuals of *P. candei* that were screened for COI (628 bp), 81 haplotypes were detected ($h = 0.93 \pm 0.010$). For cytochrome b (308 bp) 40 haplotypes were detected in 306 screened individuals of *P. candei* ($h = 0.73 \pm 0.022$).The nucleotide diversity (π) in the Azores was 0.00548 ± 0.00051 for this species and for cytochrome b was $\pi = 0.04822 \pm 0.00373$. The concatenated dataset was composed of 58 composite haplotypes. Phylogenetic analysis revealed a strong partitioning of three phylogeographic groups corresponding to (i) the Azores, (ii) Madeira and (iii) Selvagens and Canary Islands (**Figure 8**).

The complete disjunction that was detected among the three geographically-based mitochondrial lineages of *P. candei* was also

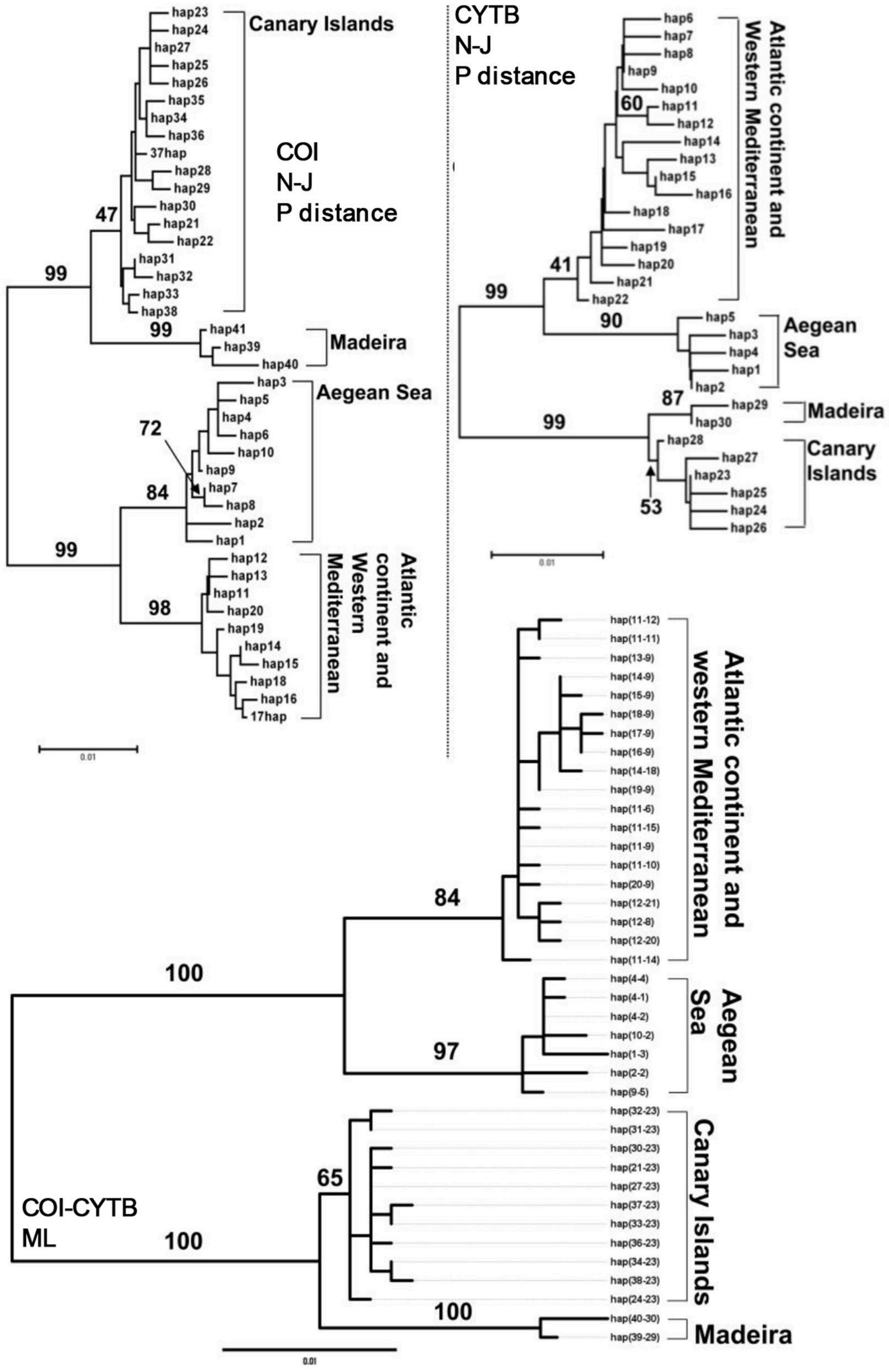

FIGURE 5 | Neighbor joining P-uncorrected phylograms for COI and CYTB haplotypes, and ML tree among concatenated haplotypes in *P. rustica.* Values located next to the branches indicate percentage of bootstrap replicates that supported each branch (2,000 bootstrap replicates).

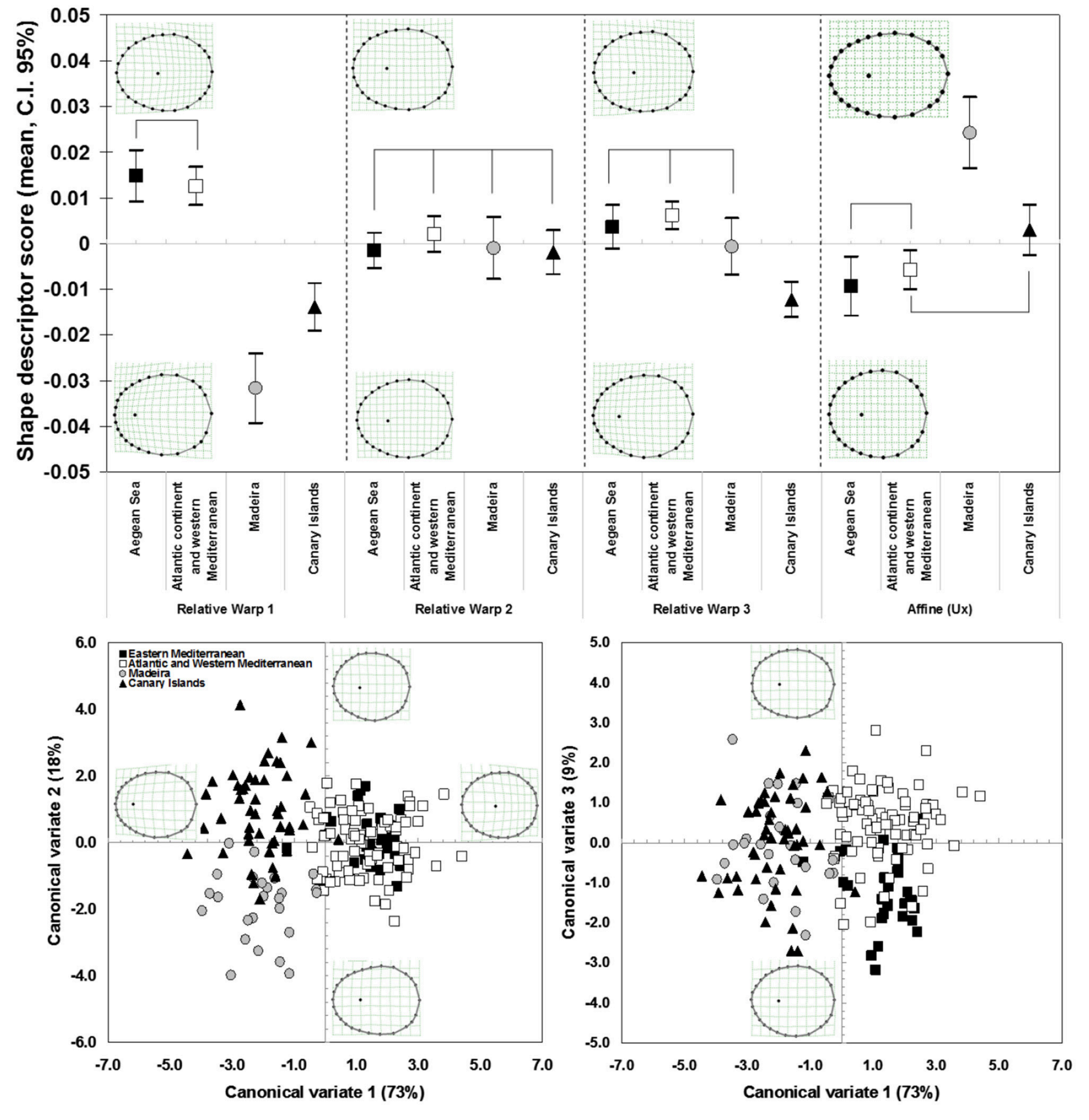

FIGURE 6 | ***Above*: Mean and 95% confidence interval of the relative warp scores and first uniform (affine) shape component, for each *P. rustica* mitochondrial lineage.** The linking lines indicate non-significant differences, according to the pairwise Bonferroni *pos-hoc* multiple comparison ($p > 0.05$). Deformation grids were based on the matrix of bending energy, under the model of thin-plate spline, and correspond to the most extreme axe RW scores. *Below*: Scatter plots of the canonical variates (roots 1, 2, and 3) obtained by discriminant analysis. Deformation grids obtained by regression ($F = 52.4915$, df = 150, 9,000, $P = 0.0000$).

resolved in the shell shape (**Figure 9**). The relative warp analysis completely separated the three lineages, based on the polygonal degree (RW1, $F = 24.783$, DF = 931, $P = 0.0000$), on the eccentricity of the apex position (RW3, $F = 29.420$, DF = 931, $P = 0.0000$), and on the shell lateral compression (Ux, $F = 21.818$, DF = 931, $P = 0.0000$). Only RW2 displayed non-significant differences among the three mitochondrial lineages (ANOVA, $F = 2.874$, DF = 931, $P = 0.0570$) (**Figure 9**).

This morphometric analysis revealed that the lineages inhabiting the Madeira and Canary archipelagos are typified

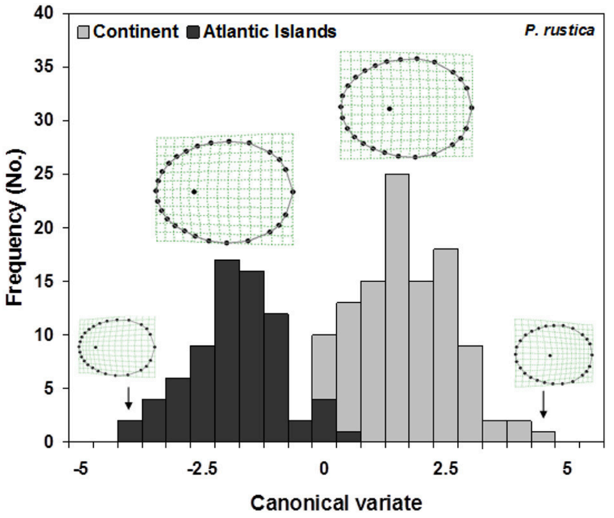

FIGURE 7 | Plot of the canonical variates obtained with discriminant analysis, when analyzing the two main clades of *P. rustica*: Atlantic Islands (composed of the two reciprocally monophyletic groups of Madeira and Canary Islands); and Continent (comprising the sample localities sampled across the Atlantic European, Atlantic African, Mediterranean African, and Mediterranean European coasts). A cline on the shell apex position is visible, from more anterior (Atlantic Islands) to more centrally located (Continent). Goodall $F = 127.8290$, df = 50, 9100, $P = 0.0000$.

by clear polygonal shell shapes, and that a relatively anterior positioned apex characterizes individuals in the lineage inhabiting the Azores. The affine shape descriptor showed a gradient of lateral compression, from Canary Islands (more rounded and longitudinally compressed) to the Azores where the shells tended to be more laterally compressed.

The discriminant analysis performed among molecular lineages was significant (Canonical $R = 0.8572$, Eigen-value $= 2.7714$, Wilk's lambda $= 0.1520$, $\chi^2 = 1707.667$, DF $= 100$, $P < 0.0001$), and the canonical variate roots separated the three lineages based on the following shape characters (**Figure 9**): the first canonical root (which described 78.8% of the shape variation) primarily separated the Azores from Madeira, based on the degree of polygonality. Shells from Madeira presented highly polygonal shells, characterized by the eccentricity of the landmarks 2, 9, 17, 23, 26, and 27. A number of landmarks showed concentric displacements, such as landmarks 1, 3, and 8. The shells from the Azores lineage, on the other hand, showed a more oval general shape. The shells from the Canary Islands were positioned intermediate between the other two lineages, and were positively separated based on the second canonical root (which accounted for 21.2% of the shape variation), characterized by a posteriorly positioned apex and a more reticulated shell border. Landmark 13 was typically positioned eccentrically.

The cross-validation percentage of correct shell-shape reassignment of specimens to their true phylogenetic lineage was high (**Table 2**), especially for Azores individuals for which only 3 specimens (2% of the training sample) were misclassified as belonging to the Canary Islands clade.

DISCUSSION

Macaronesian limpets are undergoing severe declines due to overexploitation which calls for an evaluation of the evolutionary significance and taxonomic status of populations. This study reports considerable evolutionary divergence of the Macaronesian limpets, revealed through highly concordant patterns of genetic and morphological variation. mtDNA revealed distinct phylogeographic patterns for the three species compatible with historical and contemporary gene flow restrictions previously reported by Sá-Pinto et al. (2008). Specifically, for both *P. aspera* and *P. rustica* Macaronesian and continental samples were reciprocally monophyletic, with lower levels of phylogeographic structure occurring within both clades. For *P. candei*, the Macaronesian endemic, three reciprocally monophyletic groups corresponding to (i) the Azores, (ii) Madeira and (iii) Selvagens, and Canary Islands were resolved. The different patterns found among these species are compatible with independent processes of colonization and demographic processes for the three species.

Geometric morphometric analysis detected significant morphological differentiation that matched major phylogeographic groupings (i.e., Macaronesian v Continent for *P. aspera* and *P. rustica*; Azores/Madeira/Selvagens and Canary Islands for *P. candei*). While plasticity is described for limpets (Hawkins et al., 1990) and widely reported for molluscs (Trussell, 2000) such concordant genetic and morphological differentiation is often taken as indicating the roles of genetic drift and/or natural selection. While a greater understanding of the relative roles of selection and plasticity could be obtained through comparison of Q_{ST} and F_{ST} values (but see Whitlock, 2008) this requires a common garden approach. We suggest that the results strongly indicate that morphological variation has in some way been shaped by genetic drift associated with distinct demographic histories of lineages as well as historical/recurrent selection pressures.

The development of geometric morphometric techniques has considerably advanced morphological studies (Davis et al., 2016) and in comparison to traditional distance-based methods permits a more detailed description of phenotypic variation. For both *P. aspera* and *P. rustica*, Macaronesian and continental populations were observed to be highly genetically diverged and reciprocally monophyletic. These major genetic breaks coincided with the largest components of morphological divergence. For *P. aspera* the continental shells were characterized as being less polygonal and more laterally compressed than their Macaronesian counterparts which showed a trend to become more polygonal and reticulated, presenting a lateral expansion. For *P. rustica* the relative apex position appeared to be the main character difference between continental and Macaronesian shells. Among the Archipelagos both species reported differing levels of genetic distinctiveness. For *P. aspera* there were clear haplotype frequency differences among sites, but not reciprocal

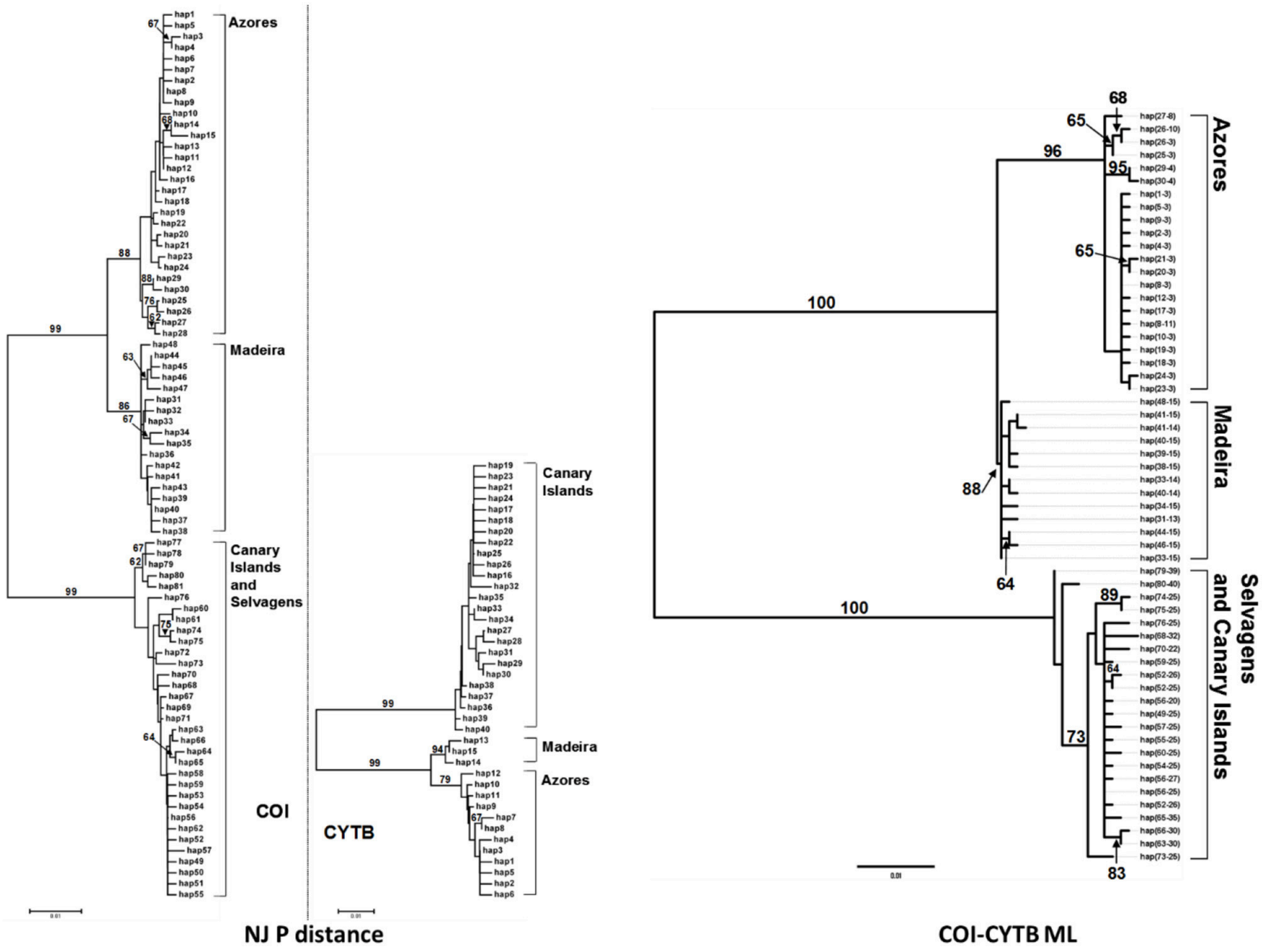

FIGURE 8 | Neighbor joining P-uncorrected phylograms for COI and CYTB haplotypes, and ML tree among concatenated haplotypes in *P. candei*. Values located next to the branches indicate percentage of bootstrap replicates that supported each branch (2,000 bootstrap replicates).

monophyly, whereas for *P. rustica* there was a congruent complete lineage sorting between Madeira and Canary islands. These differing depths of divergence were reflected in the observed morphological differentiation. For *P. aspera* individuals could not be morphologically discriminated across islands, whereas for *P. rustica* morphological differentiation between Madeira and Canaries was significant, though lower than that reported in comparisons with continental conspecifics, which also reflects the hierarchical patterns resolved by mtDNA.

Despite the general correspondence between genetic and morphological data, *P. rustica* revealed an interesting incongruence. Whereas morphological differentiation was detected between the genetically distinct archipelagos no morphological differentiation was detected between Aegean Sea and the Western Mediterranean /Atlantic lineages despite the comparably high genetic divergence. While it must be stressed that only one sampling location from the Aegean Sea has been included in this study, such a morphological similarity could reflect stasis due to stabilizing selection. Additionally, this result could reflect the accelerated evolution of Macaronesian limpet diversity due to historical demographics and selection factors.

P. candei exhibited the highest levels of clade divergence, with three reciprocally monophyletic groups. Sá-Pinto et al. (2008) interpreted such divergence as indicating single colonization events, and subsequent genetic isolation for each archipelago. Such isolation, along with post colonization adaptation, would be expected to drive phenotypic divergence and this pattern was supported by morphometrics which reported the three lineages to exhibit a greater level of morphological differentiation, than observed for the other species. The shells carried by limpets inhabiting Madeira are characteristically polygonal, when compared with the shells of the limpets that inhabit the Azores. The shells from the Canary Islands, on the other hand, present a typical reticulated border and with its shell apex centrally located, when compared with the other two lineages of *P. candei*. These results confirm the high morphological differentiation described (see for example Christiaens, 1973) between the three subspecies *P. c. gomesi* (Azores), *P. c. ordinaria* (Madeira) and *P. c. crenata*

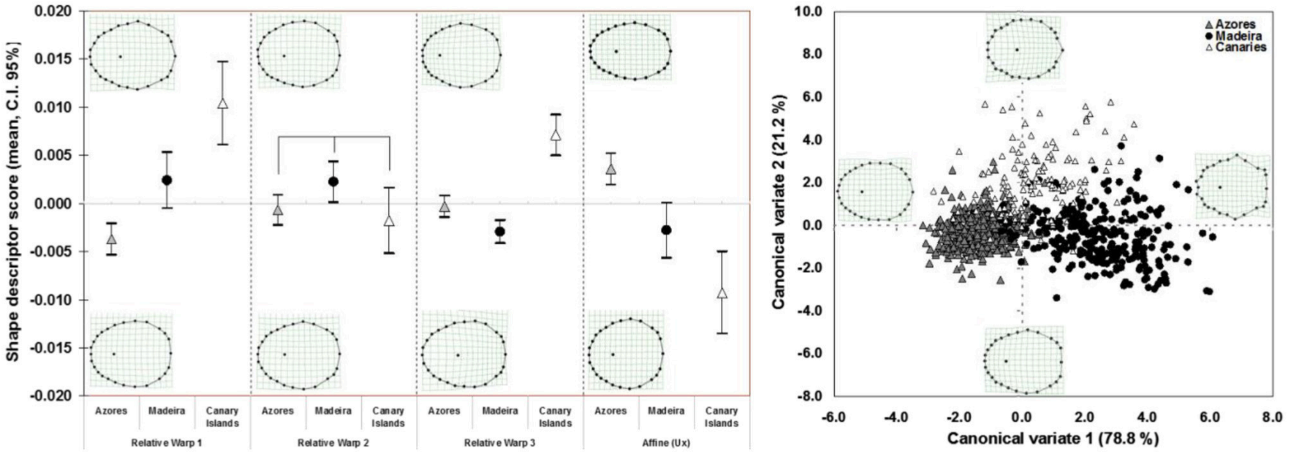

FIGURE 9 | Relative warp scores and first uniform (affine) shape component (left), for each *P. candei* mitochondrial lineage. The linking lines indicate non-significant differences, according to the pairwise Bonferroni *pos-hoc* multiple comparison ($P > 0.05$). Deformation grids were based on the matrix of bending energy, under the model of thin-plate spline, and correspond to the most extreme axe RW scores. The grids for the affine component were obtained by setting $\alpha = 0$, when performing the relative warp analysis. Scatter plot of the canonical variates (roots) obtained by discriminant analysis of the shape descriptors (weight matrix) of *P. candei* (right), and considering the mitochondrial lineage groups. Deformation grids obtained through multivariate regression. Goodall $F = 67.2600$, DF = 100, 46550, $P < 0.0001$.

(Canary Islands) *of P. candei*. Specimens from *P. c. candei* (Selvagens) were not included in the analysis here, given their eroded status, however, subsequent studies suggest this eroded phenotype may have a genetic component (Carreira, 2010). While mtDNA has failed to differentiate *P. candei* from Canaries and Selvagens, this eroded phenotype may reflect reproductive isolation and incipient divergence that may be detectable with more powerful genetic markers such as microsatellites.

Islands are regarded as excellent model systems to investigate the relative roles of historical contingency and ecological determinism in shaping biodiversity (Emerson, 1985). Cunha et al. (2008) reported replicated biogeographic patterns between large and small coned venomous snails in Cabo Verde wherein ecological determinism, specifically recurrent gene flow restrictions and adaptation, had overcome the effects of different evolutionary histories. In this study, the most pronounced phylogeographic and morphological diversity among archipelagos was reported for *P. candei*, with lower levels of genetic/morphological divergence reported for the other species. While the distinct phylogeographic structures support unique colonization histories for the three species (Sá-Pinto et al., 2008), as *P. candei* are the oldest of the three species on Macaronesia, it may be that the differing patterns among the species in Macaronesia reflect different temporal stages of divergence by post-colonization determinism toward a replicated, albeit general, model of among archipelago diversification. As such the Macaronesian limpets represent an excellent model system for studying the stages of evolutionary divergence.

A fundamental aim of conservation is to identify and prioritize evolutionary significant components of biodiversity. Comparative genetic and morphometric analysis here highlight the unique genetic and morphological characteristics of the Macaronesian limpets, and implicate underpinning roles for historical contingency and contemporary determinism in the evolution of this biodiversity. The subtlety of evolutionary processes can complicate conservation efforts focused at the sub-species rank (Crandall et al., 2000), however the genetic and morphological divergence support the formal recognition of at least three described *P. candei* subspecies. For all three species the genetic divergence among archipelagos must be considered a conservative reflection of contemporary isolation, and it is recommended that each archipelago be managed separately as such isolation increases the vulnerability of populations, which in the case of *P. candei* represents a real extinction risk. At present management efforts are severely hampered by illegal harvesting of limpets. From an applied viewpoint, this study confirms that morphology retains useful information on genetic status and thus represents a potentially cheap method applicable to limpet forensics.

DATA ACCESSIBILITY

All sequences have been deposited on GenBank (accession numbers: KY674542-KY674813).

AUTHOR CONTRIBUTIONS

All the four authors met the four criteria of authorship, namely: Substantial contributions to the conception or design of the work (GC, PS, and JG); or the acquisition (GC), analysis (GC and NM), or interpretation of data for the work (GC and NM); Drafting the work or revising it critically for important intellectual content (All); Final approval of the version to be published (All); Agreement to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved (All).

ACKNOWLEDGMENTS

This study was conducted at Royal Holloway, University of London and at the Departamento de Oceanografia e Pescas, da Universidade dos Açores. This study benefited from the scholarship SFRH/BD/6897/2001, through the Portuguese Foundation for Science and Technology and the following grants: OGAMP (Interreg IIIB-MAC/4.2/A2), MARMAC (Interreg 03/MAC/4.2/A1) and BANGEN PCT/MAC/1/C070—Banco genético marinho da Macaronésia. All the samples were collected according to the law enforced on each locality at the time of collection. In Canary Islands, samples were collected during the survey campaigns of the project "Canarias por una costa viva," in collaboration with the team of the University of Las Palmas (Gran Canaria). Finally, the open access publication was supported by Portuguese "Fundação para a Ciência e a Tecnologia (FCT)" through the strategic project (FCT/UID/MAR/04292/2013) granted to MARE.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 25 April 2017
doi: 10.3389/fmars.2017.00109

Underwater Ambient Noise in a Baleen Whale Migratory Habitat Off the Azores

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Assessment of underwater noise is of particular interest given the increase in noise-generating human activities and the potential negative effects on marine mammals which depend on sound for many vital processes. The Azores archipelago is an important migratory and feeding habitat for blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*) and sei whales (*Balaenoptera borealis*) en route to summering grounds in northern Atlantic waters. High levels of low frequency noise in this area could displace whales or interfere with foraging behavior, impacting energy intake during a critical stage of their annual cycle. In this study, bottom-mounted Ecological Acoustic Recorders were deployed at three Azorean seamounts (Condor, Açores, and Gigante) to measure temporal variations in background noise levels and ship noise in the 18–1,000 Hz frequency band, used by baleen whales to emit and receive sounds. Monthly average noise levels ranged from 90.3 dB re 1 μPa (Açores seamount) to 103.1 dB re 1 μPa (Condor seamount) and local ship noise was present up to 13% of the recording time in Condor. At this location, average contribution of local boat noise to background noise levels is almost 10 dB higher than wind contribution, which might temporally affect detection ranges for baleen whale calls and difficult communication at long ranges. Given the low time percentatge with noise levels above 120 dB re 1 μPa found here (3.3% at Condor), we woud expect limited behavioral responses to ships from baleen whales. Sound pressure levels measured in the Azores are lower than those reported for the Mediterranean basin and the Strait of Gibraltar. However, the currently unknown effects of baleen whale vocalization masking and the increasing presence of boats at the monitored sites underline the need for continuous monitoring to understand any long-term impacts on whales.

Keywords: underwater noise, ship noise, baleen whales, MSFD, open ocean environment

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Specialty section:
This article was submitted to
Deep-Sea Environments and Ecology,
a section of the journal
Frontiers in Marine Science

Received: *07 June 2016*
Accepted: *04 April 2017*
Published: *25 April 2017*

Citation:
Romagosa M, Cascão I,
Merchant ND, Lammers MO,
Giacomello E, Marques TA and
Silva MA (2017) Underwater Ambient
Noise in a Baleen Whale Migratory
Habitat Off the Azores.
Front. Mar. Sci. 4:109.
doi: 10.3389/fmars.2017.00109

INTRODUCTION

Marine acoustic pollution has become an issue of special concern over recent decades. Measurements from the North Atlantic show that average noise at 50 Hz has increased about 5.5 dB per decade from 1950 to 1970 (Ross, 2005) and about 2.8 dB from 1966 to 2013 (Širović et al., 2016). A similar trend has been found in the North Pacific with noise increasing at an average rate of 2.5–3 dB per decade at 30–50 Hz since the 1960s (Andrew et al., 2002; McDonald et al., 2006; Chapman and Price, 2011). This rise has been mainly due to shipping and together with seismic surveys has become one the principal sources of ambient noise below ∼1 kHz. (Wenz, 1962; Andrew et al., 2002; McDonald et al., 2006; Hildebrand, 2009; Klinck et al., 2012; Nieukirk et al., 2012). Shipping noise contribution can be at very low frequencies below 200 Hz (Ross, 1976), when is given by the summation of many distant large ships scattered throughout an ocean basin. When a ship passes nearby, however, it increases temporarily and substantially noise levels at that location at much greater frequencies since propagation removes the high frequency portion of the spectrum (Wenz, 1962; Hildebrand, 2009).

Baleen whales emit sounds with fundamental frequencies below 1 kHz (Richardson et al., 1995) which overlap with peak power in ship noise (Wenz, 1962; Hildebrand, 2009). The production and reception of baleen whale vocalizations have been associated to vital biological processes such as feeding, mating, group cohesion and social interaction (e.g., Payne and Webb, 1971; Dudzinski et al., 2002) which make these animals especially vulnerable to this source. Noise in the environment can limit the range for successful detection of signals through masking, thus significantly affecting the acoustic communication in large whales (Samaran et al., 2010; Ponce et al., 2012; Hatch et al., 2012; Erbe et al., 2015). Blue whales (*Balaenoptera musculus*) have shown increased source levels of their D calls (<100 Hz) as well as increased multiple callers when ships are nearby (McKenna, 2011; Melcón et al., 2012) and North Atlantic right whales (*Eubalaena glacialis*) call louder with increasing background noise levels (Parks et al., 2010). Following the mounting evidence of noise impact on marine mammals, the U.S. National Research Council (NRC) established the 120 dB re 1 μPa as the noise level above which marine mammals might be adversely affected by sound (NRC, 2005). Vessel avoidance behavior has been documented for some species of baleen whales at received sound pressure levels (SPLs) of 92.8–148.6 dB re 1 μPa, but especially above 120 dB re 1 μPa (Richardson et al., 1995; Richardson and Würsig, 1997; Southall et al., 2007). In addition, in the presence of shipping noise, North Atlantic right whales have been shown to exhibit increased stress levels (Rolland et al., 2012) and humpback whales (*Megaptera novaengliae*) changed their foraging activity (Blair et al., 2016).

In the long term, behavioral disturbance and physiological stress caused by noise could lead to population-level effects. Changes in vocal behavior in response to noise during feeding, socializing (Di Ioro and Clark, 2010) and breeding (Miller et al., 2000) may have energetic costs, and potential avoidance of noisy foraging/breeding/resting areas (Castellote et al., 2012) could reduce energy intake and disrupt behavior at key life stages. These effects could have a negative impact at a population level by affecting growth, survival and reproductive success of individual animals. However, determining a causal link between noise exposure through effects on individual vital rates to population consequences is extremely difficult and further studies are needed and models developed to answer these questions.

Although research on noise levels and the impacts on marine life have been increasing over recent years (Williams et al., 2015), most studies have focused on whales' feeding grounds and coastal continental areas (Parks et al., 2010; Dunlop, 2016) with fewer studies on open ocean waters (Dziak et al., 2015; Bittencourt et al., 2016). In the central Atlantic area, only one measurement has been made north of the Azores archipelago (Castellote et al., 2012) and only one study has been published documenting airgun seismic noise in mid-Atlantic waters (Nieukirk et al., 2012).

The region around the Azores is a migratory habitat for several species of baleen whales. Blue and fin (*B. physalus*) whales interrupt their journeys to northern latitudes to feed in the archipelago every spring and early summer (Silva et al., 2013, 2014). Sei whales (*B. borealis*) travel through the archipelago in spring on their way up to the Labrador Sea but they do not seem to forage routinely in the area (Prieto et al., 2014). Moreover, preliminary acoustic data suggest the presence of fin whale (Silva et al., 2011) and blue whale (unpublished data) calls also during the winter. This finding is in accordance with a study documenting winter calling by fin and blue whales around the mid-Atlantic ridge, south of the Azores (Nieukirk et al., 2012). Therefore, the region around the Azores may be an important habitat for these species in the central North Atlantic and noise pollution should be carefully monitored to inform effective management of human activities in these waters.

This work investigates low-frequency underwater noise levels at an important baleen whale habitat in the North Atlantic, the Azores archipelago by: (a) investigating the spatial and temporal variability within the 18–1,000 Hz frequency band (calling range of most baleen whales), (b) determining the contribution of local ship and wind driven noise (c) describing noise levels above 120 dB re 1 μPa, reported to cause behavioral responses to baleen whales (NRC, 2005) and (d) discuss potential effects of these results on baleen whales in the Azores. In addition, we investigated variability of noise levels in one-third octave bands centered at 63 and 125 Hz, which have been specifically proposed by EU Marine Strategy Framework Directive (MSFD) as a measure of noise from distant shipping (2008/56/EC, European Commission 2008).

MATERIALS AND METHODS

Deployment Locations

The three deployment locations are seamounts and were chosen for their distinct importance for baleen whales and their differences in anthropogenic usage. Condor seamount, located 17 km southwest of Faial Island, became a scientific observatory in 2008 when local authorities, researchers, fisherman and other stakeholders agreed on designating it as a protected area for scientific research. Since 2010, demersal fisheries are banned, tuna and big game fishing are permitted upon prior authorisation and scientific and recreational activities (such as shark diving) are allowed (Giacomello et al., 2013; Ressurreição and Giacomello, 2013). Açores seamount, located 40 km southwest off Faial Island, is frequented by small commercial fishing and recreational activities, although to a much lesser extent than Condor

(**Figure 1**). Gigante seamount, located 100 km west-northwest of Faial Island along the Mid-Atlantic Ridge, is used by commercial fisheries and lies close to major marine traffic lanes.

The areas around Condor and Açores seamounts are frequently used by blue and fin whales for foraging (Silva et al., 2013, 2014) and by sei whales for migrating (Prieto et al., 2014). Gigante seamount is close to a transit area for the three species, and occasional feeding may also occur there. Other species of baleen whales may also occasionally occur in these areas (Silva et al., 2014).

Acoustic Data

Bottom-mounted Ecological Acoustic Recorders (EARs; Lammers et al., 2008) were deployed at the three seamounts at an approximate depth of 190 m. The EAR consists of a sensor Technology SQ26-01 hydrophone with a response sensitivity of −193.14/−194.17 dB re 1 V/μPa (varying between deployments) for Condor and Açores and −193.64/−193.14 dB for Gigante and a flat frequency response (±1.5 dB) from 18 Hz to 28 kHz. A Burr-Brown ADS8344 A/D converter was used with a zero-to-peak voltage of 1.25. A total system gain of 47.5 dB re 1 μPa was used during all recordings resulting in a noise floor of 89 dB re 1 μPa (18–1,000 Hz), 65.5 dB re 1 μPa (63 Hz octave band) and 66.7 dB re 1 μPa (125 Hz octave band). Dynamic range of the instrument was of 57 dB re 1 μPa reaching saturation at 146 dB re 1 μPa.

EARs recorded from March 2008 to October 2012 at Condor, from November 2011 to October 2012 at Açores and from April 2008 to February 2011 at Gigante with several gaps due to equipment failure or maintenance duties. Sampling rates and duty cycles were constrained by battery life and disk space limitations, given programmed deployment durations (**Table 1**).

Noise Measurements

Recordings with sample rates of 50 kHz were re-sampled to 2 kHz using Adobe Audition 3.0 software (Adobe Systems Incorporated, CA, USA) to standardize all acoustic data from 18 to 1,000 Hz, which is the bandwidth dominated by anthropogenic noise (Wenz, 1962) and overlaps the vocalizing range of balaenopterids. Self-system tonal noise within the frequency band of interest was identified only in recordings with sampling rates of 2,000 Hz which correspond to deployments at Condor and Açores from 2011 and 2012. 1-Hz Spectrogram Power Density (SPD) plots were made for each month to precisely identify which frequency bins were affected so they could be removed before computing broadband SPLs. Given that all self-system noise identified was highly tonal, removing these few frequency bins is likely to have a negligible effect on averaged broadband SPLs and on the characterization of shipping noise, which spreads across a wide range of frequencies. Moreover, self-system noise removed was found in frequencies well above the one-third octave bands analyzed in this study (63 and 125 Hz). From the SPD plots we can say that data were not clipped since there is no flat line of data points at high noise levels clustered at the limit value of 146 dB where the system saturates (see **Figure 4** from results section).

Each month of recordings was grouped and concatenated to form a single file to be analyzed with Matlab code written by Merchant et al. (2015). The time-series of every signal was divided into m 1-s segments of consecutive samples overlapping in time (50% overlap). Each segment was then multiplied by a Hann window and transformed to the frequency domain via the Discrete Fourier Transform (DFT). Spectra were then averaged to a 90-s resolution via the standard Welch method (Welch, 1976). The power spectrum (P) was then computed from the DFT, which for the m^{th} segment, of signal X at frequency f and for N number of samples in each segment is given by:

$$P^{(m)}\ (f) = \left|\frac{X^m(f)}{N}\right|^2$$

For each deployment, calibration data from the EAR, including the hydrophone sensitivity (M_h), system gain (G) and the zero-to-peak voltage of the analog-to-digital converter (V_{ADC}), were used to calculate a correction factor (S(f)) computed by:

$$S\left(f\right) = M_h + G\left(f\right) + 20log_{10}\left(\frac{1}{V_{ADC}}\right) + 20log_{10}\left(2^{N_{bit}-1}\right)$$

where N_{bit} is the bit-depth of the digital signal (16 bits). S(f) was then used to obtain SPLs in the bandwidth from 18 to 1,000 Hz by:

$$SPL_{(m)} = 10log_{10}\left(\frac{1}{P_{ref}^2}\sum_{f'=f_{low}}^{f'=f_{high}}\frac{P^{(m)}(f')}{B}\right) - S$$

where p_{ref} is the reference pressure of 1 μPa for underwater measurements, f_{low} and f_{high} are the lower and upper bounds of the frequency range under consideration and B is the noise power bandwidth of the window function, which corrects for the energy added through spectral leakage.

Noise Data Analysis

The effect of different duty cycles on the calculation of monthly average background noise levels was investigated by concatenating a full month of data (May 2008 from Condor), treating it as a continuous recording, and then subsampling it according to the different duty cycles used in this study (**Table 1**). To test for statistical differences in SPLs between different duty cycles, a first order autoregressive model was fitted to the SPL time series of mean SPL per sample for each duty cycle. Then, based on the estimated parameters and corresponding standard errors, 95% confidence intervals for each duty cycle mean SPLs were derived, assuming a Gaussian distribution for the parameter estimates. Number of samples (N) was the number of files resulting from the different duty cycles applied.

To investigate differences in noise levels between locations, only Condor's data from 2011 and 2012 were analyzed to compare with time series of similar length from Açores and Gigante. For every location, the arithmetic mean (AM) over the

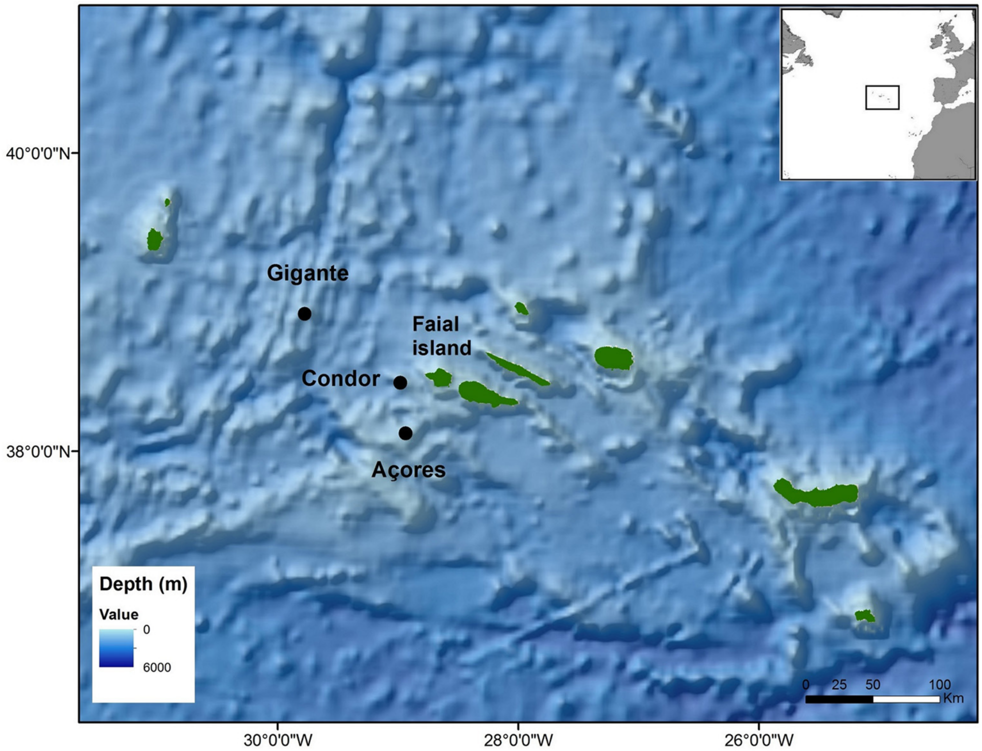

FIGURE 1 | Ecological Acoustic Recorders (EARs) deployment locations in the Azores archipelago (black dots).

TABLE 1 | Summary of acoustic data used in this work including recording dates, deployment depth, sampling rate, duty cycle, and total recording time.

Location	Dates of recording	Depth (m)	Sampling rate (Hz)	Minutes on/off	Total recording time (hours)
Condor	March 2008–May 2008	189	50,000	0.5/10	88.6
	Aug 2008–Dec 2008	190	50,000	1.5/15	326.5
	July 2009–Oct 2009	190	50,000	1.5/15	295.2
	Apr 2010–Feb 2011	190	50,000	1.5/15	746.2
	Nov 2011–Feb 2012	195	2,000	60/138	1,361
	June 2012–Oct 2012	195	2,000	60/210	948
Total					3,765.5
Açores	Nov 2011–March 2012	190	2,000	60/210	830
	May 2012–Oct 2012	190	2,000	60/210	1,262
Total					2,092
Gigante	Apr 2008–May 2008	175	50,000	0.5/10	70.8
	Aug 2008–Nov 2008	190	50,000	1.5/15	279.6
	July 2010–Aug 2010	190	50,000	1.5/15	135.6
	Oct 2010–Feb 2011	190	50,000	1.5/15	343
Total					829

period considered was calculated. For N samples p^2_{rms}, AM is given by:

$$AM = 10log_{10}\left(\frac{\frac{1}{N}\sum_{i=1}^{N} p^2_{rms,\,i}}{p^2_{ref}}\right)$$

where $p^2_{rms,i}$ is the ith value of the mean squared pressure given by:

$$p^2_{rms} = \sum_{f'=f_{low}}^{f'=f_{high}} \frac{P^{(m)}(f')}{B}$$

To test for statistical differences in SPLs between locations, a first order autoregressive model was fitted to the SPL time series of each location (containing daily averaged SPLs). Then, based on the estimated parameters and corresponding standard errors, confidence intervals (95%CI) for each location mean SPLs were derived, assuming a Gaussian distribution for the parameter estimates. Number of samples (N) was the number of days.

Variability in noise levels for every location was analyzed using the coefficient of variation (CV), which allows comparison between datasets with different means.

Within each location, temporal variability of noise levels was explored by calculating hourly and monthly averaged, median and 5th, 75th, and 95th percentiles SPLs for the frequency band of 18–1,000 Hz. Also, hourly and monthly averaged one-third octave bands centered in 63 and 125 Hz were calculated to specifically measure the contribution of distant ship noise to ambient noise as suggested by the MSFD (2008/56/EC, European Commission 2008).

Seasons were defined according to the location (North-East Atlantic) as follows: Spring: March–May, Summer: June–August, Autumn: September–November and Winter: December–February.

To allow for comparisons, average SPLs were calculated for the three noisiest months in Condor (July-September, 2010), Açores (May-July, 2011) and Gigante (May–September, 2008) in the frequency band of 10–585 Hz to be compared to SPLs found in the Mediterranean by Castellote et al. (2012). Also, median levels in the frequency band of 10–25,000 Hz were measured in Condor (July-September, 2010) to compare it with levels found in another oceanic archipelago by Bittencourt et al. (2016).

Ship Noise Analysis

In the absence of an operative antenna in the area for receiving information from Automatic Information System (AIS) installed in ships during the recording period, a methodology was used to study the contribution of local ship noise to general background noise levels. Using the broadband (18–1,000 Hz) noise background levels for every recording, an Adaptive Threshold Level (ATL; Merchant et al., 2012b) was obtained to identify local intermittent ship noise. The ATL was calculated by computing the minimum SPL in a certain period of time (W) and summing a tolerance above this minimum, a threshold ceiling (C) in dB re 1 μPa:

$$ATL\,(t) = \min[SPL\,(t)]_{t-\frac{w}{2}}^{t+\frac{W}{2}} + C$$

Due to differences in background noise levels and duty cycles in this study compared with Merchant et al. (2012b), two different periods of time (W) (1 and 7 hours of recordings) and 4 different threshold ceilings (C) (from 4, 6, 8, and to 12 dB) were tested. Firstly, an appropriate time period, W, was selected by visually inspecting plots of SPL values and thresholds and selecting the one that best discriminated wind-wave driven noise from intermittent noise. Once W had been specified, results from the ATL applying different values of C were compared to visually confirmed boats in the spectrogram for one chosen month per location (July 2012 for Condor, May 2012 for Açores and July 2010 for Gigante). Those parameters that resulted in the best compromise between visually confirmed boats detected by the ATL (true positives) and detections by the ATL not corresponding to boats (false positives) were selected.

Once W and C were set, ATL was calculated for every month and location. Time with levels above the threshold was summed and divided by the total recording time to obtain the Percentage of Time with noise levels Above the Threshold Level (PT-ATL). The PT-ATL was then used to investigate spatial variations in boat presence using a Kruskal-Wallis ANOVA and a *post-hoc* Dunn test for multiple comparisons.

To test the efficiency of the methodology at detecting the presence of vessels, a comparison was made between monthly PT-ATLs and the number of days per month with boat presence in Condor. Data on boat presence were obtained from logbooks that contained information on the number of boats and type of activity conducted at the Condor seamount area per day from 2008 to 2012. The type of boats' activities recorded were: recreational activities, such as big-game fishing and shark diving, with data logged by the operators themselves; scientific research, based on information provided by scientists conducting research at Condor; and tuna fishing, based on data recorded by onboard observers under the Azorean Fisheries Observer Programme (POPA).

Contribution of Wind-Wave and Vessel-Driven Noise

An analysis of wind-wave driven noise and intermittent ship noise was implemented to compare the relative contribution of natural and anthropogenic sources to background noise levels in this region. Windiest months were selected for the three locations and daily averaged SPLs and wind speeds calculated. Days with maximum and minimum SPLs coincided with maximum and minimum wind speeds. For every month, averaged SPLs were calculated from 10 min sound files free of ship noise (visually inspected spectrograms) selected from 2 days, one with maximum and one with minimum wind speed. Similarly, for all months and for all locations, average SPLs were calculated for periods of time above the threshold and compared to those with minimum wind conditions. Differences between quietest average and noisiest average were then calculated for the wind and for the ship contribution. Daily averaged wind speeds (km/s) were obtained from Weather Underground historical data (www.wunderground.com) for each location.

Noise Levels above 120 dB re 1 μPa

Since baleen whales have been shown to avoid vessels at noise levels above 120 dB re 1 μPa (Richardson et al., 1995; Richardson and Würsig, 1997; Southall et al., 2007), percentage of time with SPL above this level was also calculated for every month of study. To do so, broadband average SPL for every month and location were used to calculate the amount of time with noise levels above 120 dB re 1 μPa and divide that by total recording time.

RESULTS

Ship Noise Analysis

The only anthropogenic noise source found in the recordings was ship noise, which had the maximum energy above 100 Hz for boats with higher noise levels, or in the bandwidth of 10–100 Hz for boats with lower noise levels.

The ATL only detected local boat noise that increased noise levels significantly and intermittently (**Figure 2**). The most adequate time period (W) to calculate minimum SPLs was 1 h of recordings for both duty cycles as this discriminated well between wind-driven and intermittent noise. The best compromise considering a minimum of 90% of visually confirmed boats in the spectrogram detected by the ATL, and a maximum of 5% of false positives was obtained using a threshold ceiling $C = 4$ dB for duty cycle of 3,600 s every 12,600 s, and $C = 8$ dB for the 90 and 30 s duty cycle (**Table 2**). False positives were mainly caused by loud biological sounds consisting of low frequency clicks produced by delphinids and sperm whales.

Logbook data from Condor was compared to the acoustic recordings resulting in 19 months of simultaneous data. There was a weak correlation ($R^2 = 0.354$, $p < 0.05$, $n = 19$) between boat presence from logbooks and PT-ATL from 2008 to 2012, mainly because the high peak in PT-ATL in June was not matched by a higher presence of boats (**Figure 3**). Removing June 2012 from the analysis resulted in a stronger correlation ($R^2 = 0.582$, $p < 0.001$, $n = 18$). Recordings from this month were visually inspected and boat noise detected by the ATL was confirmed to be mainly present during daylight hours.

Spatial Variability in Ambient Noise Levels and Peak-Generating Vessels

The different duty cycles used in this study did not significantly affect the average monthly SPLs. Differences between the assumed "continuous" recording (AM = 91.8, 95%CI = 91.78–91.82) and the different duty cycles were very small (1.5/15: AM = 91.9, 95%CI = 91.72–92.02; 0.5/10: AM = 91.6, 95%CI = 91.45–91.62; 60/138: AM = 91.4, 95%CI = 91.40–91.47; 60/210: AM = 91, 95%CI = 90.99–91.08), as were differences between duty cycles. Therefore, comparison of noise levels between deployments and locations with different duty cycles should remain valid.

The arithmetic mean of SPLs was calculated for the 18–1,000 Hz band for Condor, Açores and Gigante over 9, 11, and 14 months, respectively. Açores had the lowest value (92.9 dB re 1 μPa), followed by Gigante (95.9 dB re 1 μPa), with higher mean SPL in Condor (97.6 dB re 1 μPa). Higher variability was found

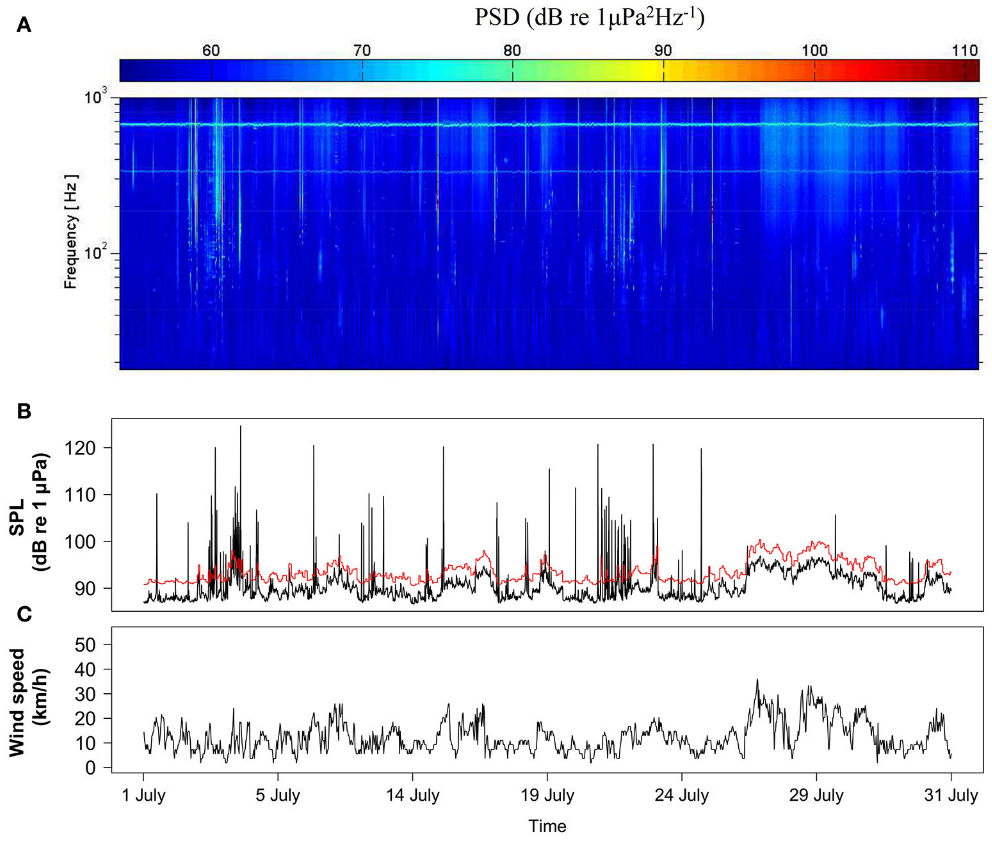

FIGURE 2 | Example of a time-series analysis of intermittent noise for July 2012 at Condor seamount. (A) Spectrogram composed of Power Spectral Densities (PSDs) with 1-s time segments; **(B)** Broadband (18–1,000 Hz) SPLs measurements and threshold (red line) for boat detection and; **(C)** 30-min interval wind speed measured in Castelo Branco, Faial Island.

TABLE 2 | Percentages of True Positives (TP), False Positives (FP), and False Negatives (FN) resulting from the comparison between boat detections applying the ATL function with different threshold ceilings (C) and visually confirmed boats in the spectrogram.

Threshold ceilings (dB)	CONDOR			AÇORES			GIGANTE		
	TP	**FP**	**FN**	**TP**	**FP**	**FN**	**TP**	**FP**	**FN**
4	98.3	11.1	1.6	91.3	4.6	8.7	97.2	8.7	2.8
6	95.9	8.5	4.1	82.6	3.4	17.4	95.3	5.6	4.7
8	90.9	4.5	9.1	69.6	2.3	30.4	90.6	4	9.4
10	81	2.8	19	56.5	2.2	43.5	72.6	4.5	27.4
12	74.4	3.1	25.6	45.6	0	54.4	58.5	4.5	41.5

Results are for July 2012 in Condor, May 2012 in Açores, and July 2010 in Gigante.

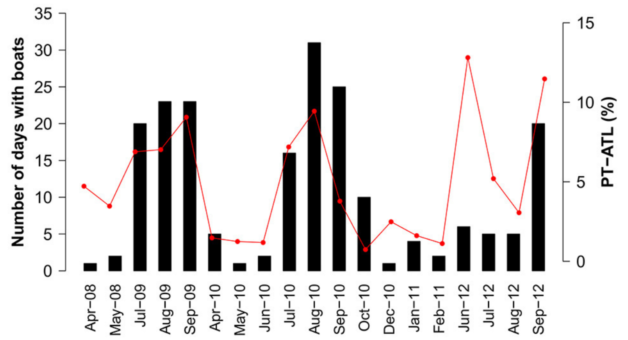

FIGURE 3 | Number of days with boats registered in logbooks (bars) and PT-ATL from the acoustic data (red line).

TABLE 3 | Arithmetic mean (AM) (±*SD*) and median SPL at broadband levels (18–1,000 Hz) and one-third octave bands 63 and 125 Hz, and total PT-ATL for Condor, Açores and Gigante calculated over 9, 11, and 14 months, respectively.

Location	Broadband noise levels (1–1,000 Hz)		63 Hz	125 Hz	PT-ATL (%)
	AM ± *SD*	**Median**	**AM ± SD**	**AM ± *SD***	**Total**
Condor	97.6±8.5	93.1	72.4 ± 5.6	79.5 ± 10.2	4.5
Açores	92.9 ± 6.6	90.1	70.2 ± 9.2	74.6 ± 9.8	1.9
Gigante	95.9 ± 8.2	91.6	73.6 ± 12.8	76.0 ± 11	6.0

in Condor (CV = 0.098) followed by Gigante (CV = 0.085) and Açores (CV = 0.071). Median values of noise levels were higher for Condor and Gigante (93.1dB re 1 µPa and 91.6 dB re 1 µPa, respectively) and lower for Açores (90.1 dB re 1 µPa). Averaged noise levels for the 63 and 125 Hz one-third octave bands were also lower in Açores (70.2 dB re 1 µPa and 74.6 dB re 1 µPa, respectively), while the highest levels at the 63 Hz band were found in Gigante (73.6 dB re 1 µPa) and for the 125 Hz band in Condor (79.5 dB re 1 µPa; **Table 3**). There was no overlap in the 95%CI of SPL within the 18–1,000 Hz, the 63 Hz and the 125 Hz one-third octave bands for Condor, Açores and Gigante, suggesting differences in average ambient noise levels between the three locations were highly significant (see Supplementary Table 1 for details on 95%CI values).

Differences in average noise levels for the 63 and 125 Hz one-third octave bands are supported by the spectral characteristics of sound for every location. Looking at the noisiest months, we can see that Gigante showed higher levels of noise from ships <100 Hz (**Figure 4C**) while Condor and Açores had higher ship noise levels >100 Hz (**Figures 4A,B**).

PT-ATL averaged across the same months showed that Gigante had the highest percentage of boat noise followed by Condor and Açores (**Table 3**). However, Condor showed a much higher variability (CV = 0.97) than Açores (CV = 0.4) and Gigante (CV = 0.3). PT-ATLs differed between locations (Kruskal-Wallis H = 13.806, *df* = 2, $p < 0.01$) but only differences between Gigante and Açores ($p < 0.001$) and Gigante and Condor ($p < 0.05$) were statistically significant.

Temporal Variability in Ambient Noise Levels and Peak-Generating Vessels

In Condor seamount, percentage of time with boats peaked during the summer months (June–August) extending to September in some years (**Figure 5D**). This is well illustrated by increased broadband and 125 Hz octave band noise levels at these periods (**Figures 5A,C**). Açores seamount also showed higher PTL-ATL during summer months, especially in June, with another peak seen in November (**Figure 6D**). These peaks are well reflected in the higher average broadband and 63 and 125 Hz octave band noise levels (**Figures 6A,C**). In Gigante, values of PTL-ATL tended to be greater in summer months or in September, although differences to other seasons were not as obvious as in Condor and Açores (**Figure 6D**). In this case, temporal patterns in broadband and one-third octave bands SPLs did not match those of boat time (**Figures 6A,C,D**).

Note that fluctuations in the 75th percentile noise levels are still highly affected by wind-driven noise in all locations (**Figures 5B**, **6B**) and only the 95th percentile is affected by the presence of boats in accordance to the low PT-ATL found in all areas (**Figures 5D**, **6D**). Average levels (AM) are more affected by brief and high amplitude events such as ships and might not represent the real average of noise data which has a highly skewed distribution. However, average levels are a robust metric that can be used to assess shipping noise if presented in combination with other metrics that identify loud events, such as the PT-ATL used here (Merchant et al., 2012a).

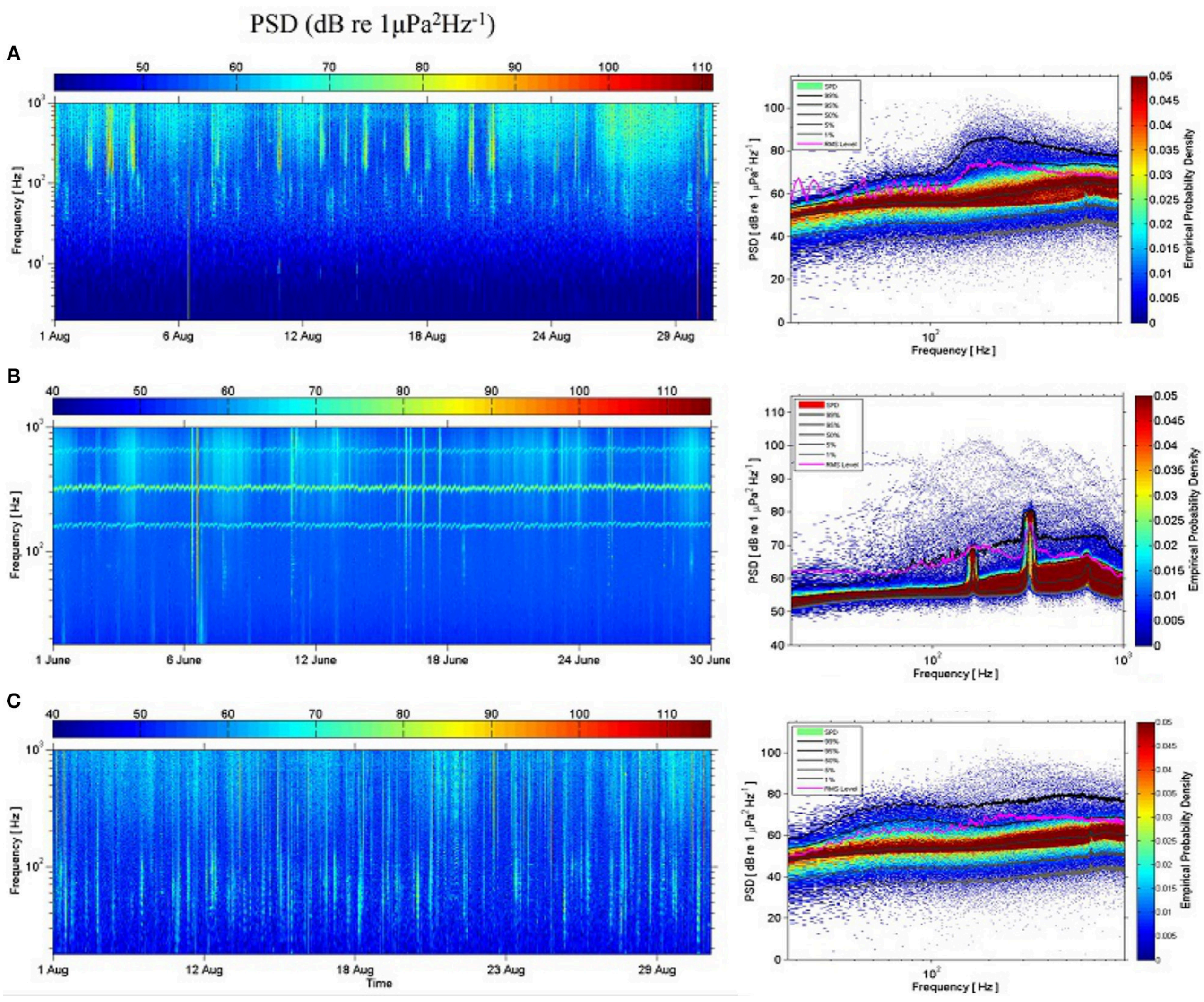

FIGURE 4 | Spectrograms composed of PSDs with 1-s time segments (left) and spectral probability densities (SPDs), percentiles and root-mean-square (RMS) level (right) of 1 month of recordings for (A) Condor; **(B)** Açores; and **(C)** Gigante.

Annual trends in PT-ATL values for Condor averaged within seasons showed a decrease of boats from 2008 to 2010 in spring (**Figure 7A**), an increase between 2008 and 2010 in the summer (**Figure 7B**), a decrease from 2008 to 2011 and a subsequent increase in 2011 and 2012 in autumn (**Figure 7C**) and little variation over time in winter (**Figure 7D**).

Contribution of Wind-Wave and Vessel-Driven Noise

A strong correlation was found between daily averaged noise levels and wind speed for the windiest months (November) in Condor ($R^2 = 0.8$, $p < 0.001$, $n = 30$) and Açores ($R^2 = 0.6$, $p < 0.001$, $n = 30$) and a weak correlation for Gigante ($R^2 = 0.3$, $p < 0.001$, $n = 30$). Average contribution of wind noise to background noise levels was of 10.8 ± 3 dB in Condor ($n = 25$), 7.7 ± 2.5 dB in Açores ($n = 8$) and 11.7 ± 3.4 dB in Gigante ($n = 11$).

Months with higher boat presence (August 2010 for Condor, June 2012 for Açores and August 2008 for Gigante) showed no or only a weak correlation between daily SPLs and wind speeds (Condor: $R^2 = 0.11$, $p = 0.003$, $n = 31$; Açores: $R^2 = -0.03$, $p = 0.9$, $n = 30$; Gigante: $R^2 = 0.06$, $p = 0.1$, $n = 26$). In average, SPLs for intermittent noise increased background noise levels in 19.3 ± 3.6 dB in Condor ($n = 32$), 16.2 ± 3 dB in Açores ($n = 11$) and 18.3 ± 3 dB in Gigante ($n = 14$) with a maximum value of 29.1 dB for Condor in July of 2010.

Noise Levels above 120 dB re 1 μPa

Percentage of time with noise levels >120 dB re 1 μPa was higher in Condor with a maximum of 3.3% in July of 2010. In 13 out of 32 months sampled, noise levels were always <120 dB and for the remaining months, time with boats varied from 0.007 to 0.4%, with greater percentages in summer and autumn. In Açores, noise levels >120 dB were recorded only in the noisiest months, May

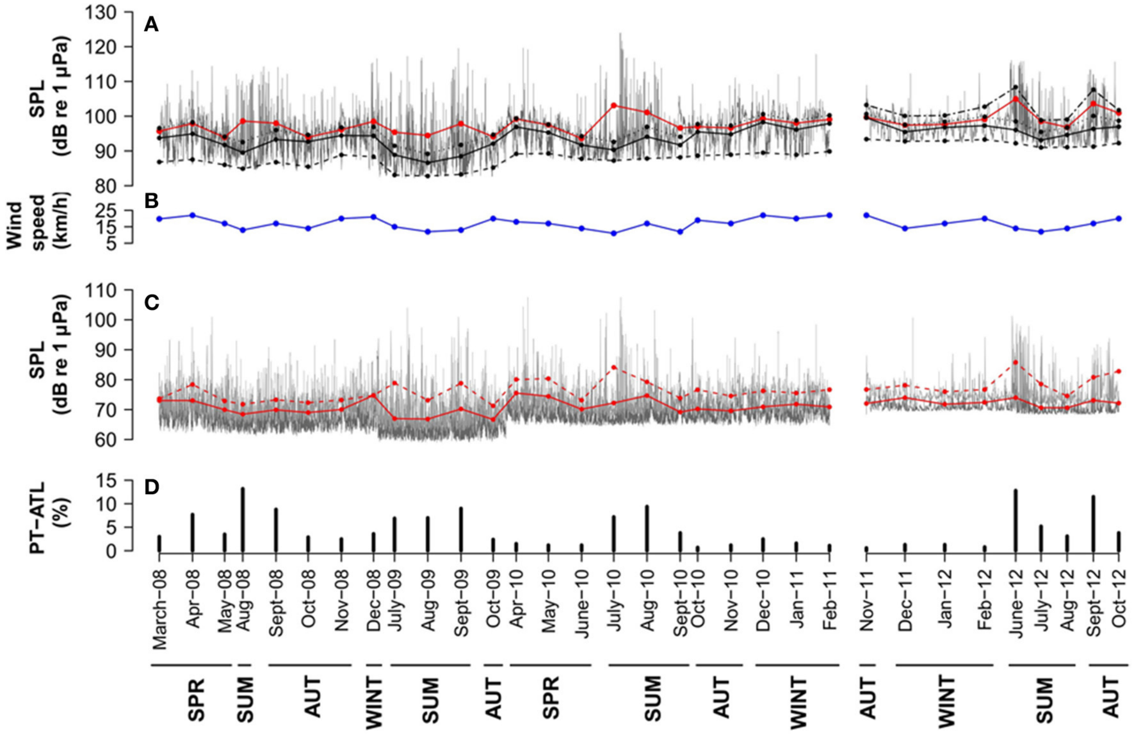

FIGURE 5 | Condor seamount: (A) hourly (gray lines) and monthly averages (red lines), medians (black lines) and 5th, 75th, and 95th percentiles (dashed black lines from bottom to top) SPLs in the 18–1,000 Hz frequency band. **(B)** monthly averaged wind speed (blue line). **(C)** hourly SPLs in the 63 Hz (dark gray lines) and 125 Hz (light gray lines) one-third octave bands and monthly averages (63 Hz: red line and 125 Hz: dashed red line). **(D)** monthly PT-ATL. Months are grouped in seasons below the x axis. Seasons are described as follows: SPR, Spring (March–May); SUM, Summer (June–August); AUT, Autumn (September–November) and WINT, Winter (December–February).

(0.03%) and June (0.07%) of 2012, while in Gigante, values >120 dB were recorded in 2008, with a maximum value of 0.12% in August, and in February 2011.

DISCUSSION

This work provides the first long-term characterization of low-frequency underwater noise levels at an important baleen whale mid-ocean habitat and discusses potential adverse effects on this cetacean group.

Noise levels at Condor seamount were higher than at Gigante and Açores seamounts and rises in monthly average broadband noise levels were mainly due to the presence of intermittent loud events such as boats. Median noise levels were more affected by wind-driven noise. In the absence of boats or with few boats, median and average levels were similar and wind became a major contributor to background noise.

The ATL methodology developed by Merchant et al. (2012b); to detect intermittent loud noise events attributed to boat presence has been successfully tested and applied in this study. Time period (W) over which minimum SPLs are calculated and threshold ceiling (C) are parameters that need readjustment depending on environmental acoustic characteristics and system duty cycle. We found that increasing C caused a decrease on the percentage of true and false positives but the extent of this variation differed between locations, depending on the acoustic characteristics of the environment. In our case, the same W worked well for all duty cycles but the adequate threshold ceiling was lower for higher duty cycles than for lower duty cycles (**Table 2**). In general, environments with a high presence of loud intermittent events and systems with lower duty cycles should require smaller W and higher C than quieter places and higher duty cycles in order to detect these events above minimum SPLs. The high correlation between boat presence at Condor seamount from logbook data and PT-ATL values from 2009 to 2011 indicates that this methodology can be used to describe boat presence in the study area. The lack of correlation in 2012 is likely explained by the limitations in boat detection distance using these methods and the fact that not all boat activity was registered in logbooks. We suspect that the high PT-ATL values found in June 2012 could be due to an increase in recreational activities.

The monthly variability in PT-ATL values found in Condor reflects this area's main recreational uses during late spring and summer. Also, the annual decrease in PT-ATL values in winter can be explained by the designation of the temporary protected area for research in force since 2010. Since this was implemented, demersal fisheries, which operate year round, are prohibited, thus explaining the lower presence of boats during the winter. On the other hand, recreational activities are gaining importance, particularly shark diving, an activity which started

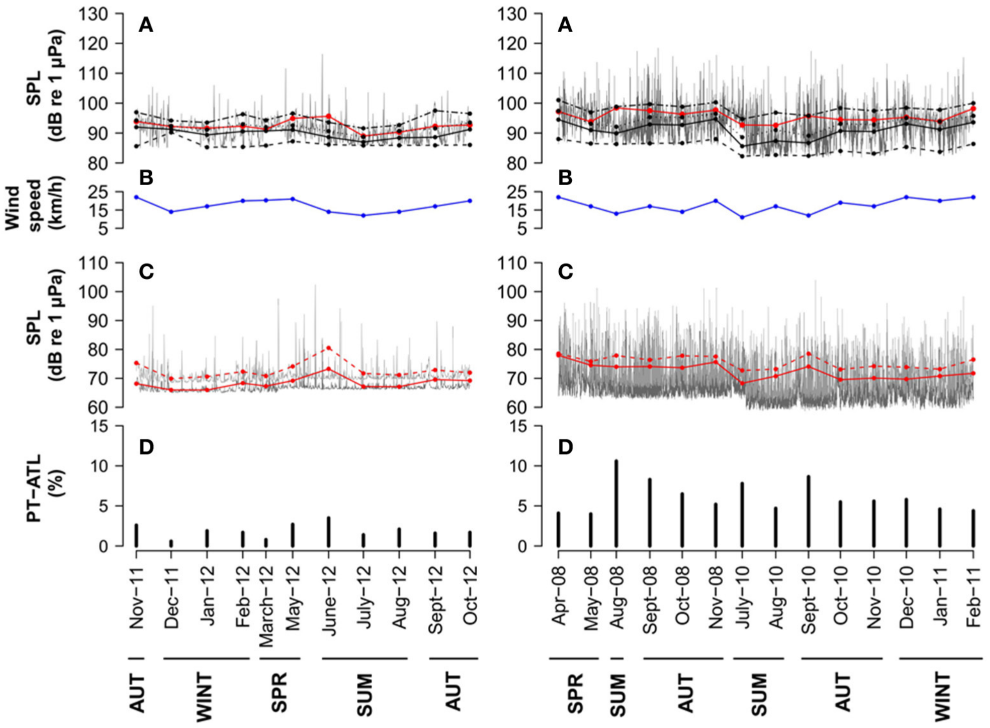

FIGURE 6 | Açores and Gigante seamount: (A) hourly (gray lines) and monthly averages (red lines), medians (black lines) and 5th, 75th, and 95th percentiles (dashed black lines from bottom to top) SPLs in the 1–1,000 Hz frequency band. **(B)** monthly averaged wind speed (blue line). **(C)** hourly SPLs in the 63 Hz (light gray lines) and 125 Hz (dark gray lines) one-third octave bands and monthly averages (63 Hz: red line and 125 Hz: dashed red line). **(D)** monthly PT-ATL. Months are grouped in seasons below the x axis. Seasons are described as follows: SPR, Spring (March–May); SUM, Summer (June–August); AUT, Autumn (September–November) and WINT, Winter (December–February).

experimentally in 2009 and that mostly operate in spring and summer (Ressurreição and Giacomello, 2013). The expeditions to dive with sharks at Condor were reported to double between 2011 and 2012 (Ressurreição and Giacomello, 2013), which might well explain why PT-ATL values increased in 2012. This activity also takes place in the Açores seamount, but to a lesser extent, which is reflected by a lower boat presence than in Condor. Gigante seamount shows a higher presence of boats throughout the year, as a result of the proximity of a marine traffic route used by commercial shipping and the presence of commercial fishing year-round in Gigante. Therefore, there is a great potential for using passive acoustic techniques to monitor boat activity in specific areas such as the ones in the study. This methodology, however, cannot be used to detect distant vessels and might not be adequate for areas with higher ship traffic where separation between continuous and intermittent events might not be possible.

For measuring the contribution of distant ship noise, the European MSFD (2008/56/EC, European Commission 2008) suggests the use of one-third octave bands, centered at 63 Hz and 125 Hz, which are included as indicators to assess the Good Environmental Status (GES) of the marine environment. In this study, Gigante shows the highest noise levels in the 63 Hz one-third octave band which can be explained by the proximity of a shipping lane mentioned in the above paragraph. Noise levels measured in the 125 Hz octave band better reflect local boat presence at Condor and Açores while at Gigante the difference between the two octave bands (63 and 125 Hz) is not very clear. This is mainly due to the difference in the type of vessels and distance of those to the hydrophone at each location. Comparison of spectrum levels indicates that Gigante has higher noise levels below 100 Hz, which is typical of distant large vessels such as tankers, while Condor and Açores have higher levels above 100 Hz, which is characteristic of smaller boats. Performance of one-third octave bands with distant shipping could not be assessed in this study because AIS data were not available for this period.

The maximum percentage of time with presence of boats found in this study is relatively low (13%). However, our results show that contribution of local boat noise to background noise levels ranged from 16–19 dB, depending on the study area, and on average was nearly 10 dB higher than wind contribution. This value is similar to those described in the literature where it is documented that below 1 kHz ship traffic regularly increases noise levels by 25 dB above background levels (Bassett et al., 2012). These increases in ambient noise might be sufficient to mask baleen whale calls unless they are able to compensate vocally, which is known as the Lombard effect (Lombard, 1911). There is some evidence that several species of mysticetes can, but sometimes do not, modify their vocalization's characteristics

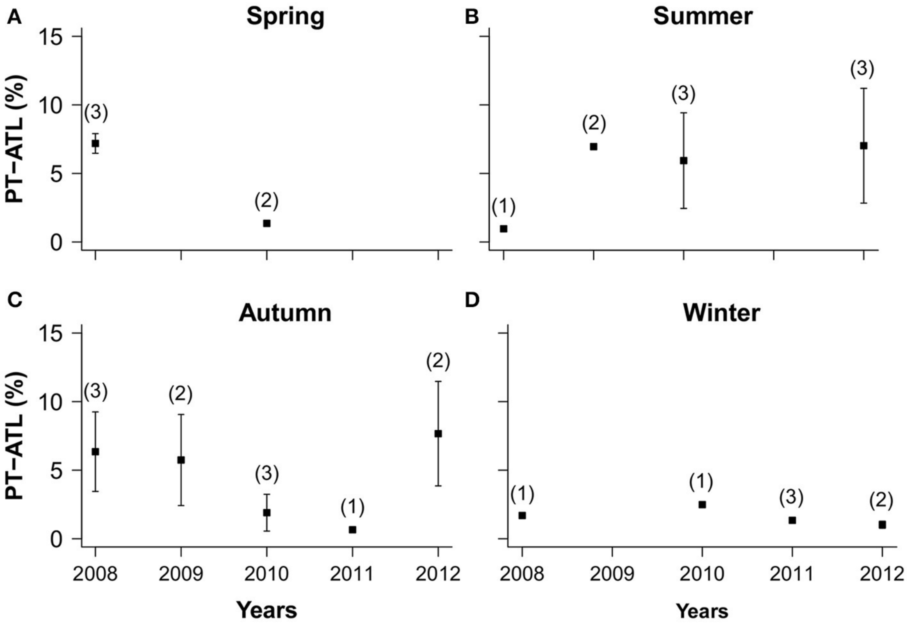

FIGURE 7 | Inter-annual variability in averaged seasonal PT-ATL values for Condor seamount and standard deviations (error bars). Numbers in brackets are number of months with data representing each of the following seasons: **(A)** Spring: March–June; **(B)** Summer: June–September; **(C)** Autumn: October–November; **(D)** Winter: December–February.

in response to shipping noise. Blue whales have been found to change the interval, types and amplitudes of their calls (McKenna, 2011; Melcón et al., 2012) while male fin whales seem to change their song characteristics (Castellote et al., 2012). Other baleen whale species such as gray whales (*Eschrichtius robustus*) also modify calling rates, received levels and percentage of calls (Dahlheim and Castellote, 2016), humpback whales sing shorter versions of their songs (Sousa-Lima et al., 2002) and North Atlantic right whales show short- and long-term changes in their calling behavior in response to increased low-frequency noise (Parks et al., 2007, 2009, 2010). However, other studies show that humpback whales respond to increases of noise levels produced by wind but do not compensate for higher levels of noise from vessels (Dunlop, 2016).

Auditory masking reduces the effective communication space between sender and receiver (Clark et al., 2009). A model developed by Tennessen and Parks (2016) demonstrated that a right whale is not able to hear an upcall from another whale if a ship passes at less than 25 Km, unless the calling whale increases the amplitude of the calls by 20 dB. Despite differences in call source levels between right whales and blue, fin and sei whales, they share similarities in call frequency ranges (e.g., Parks and Tyack, 2005; Sirović et al., 2007; Romagosa et al., 2015). Detection ranges of calls for these three species might be affected by passing ships in similar ways, which is of concern given the dependence of Balaenoperids on long range communication (Payne and Webb, 1971). Although their calls have been mainly attributed to male reproductive displays, whales also produce sounds outside their breeding grounds and season (Clark et al., 2002; Oleson et al., 2007; Vu et al., 2012). Blue whales are known to produce D calls during foraging within groups (McDonald et al., 2001; Stafford et al., 2005; Calambokidis et al., 2008) and fin whales produce "20-Hz pulse" calls that are likely to have a social purpose or a contact maintaining function when produced irregularly or as call-counter calls (McDonald et al., 1995; Edds-Walton, 1997). Baleen whale long-range calls could also be used for orientation purposes, as suggested by Payne and Webb (1971). In the Azores, preliminary analysis of acoustic data shows that blue and fin whales produce these types of calls when they are seen in spring as well as reproductive songs during the winter (unpublished data). Sei whales also vocalize during their migratory journey (Olsen et al., 2009; Prieto et al., 2014) through the Azores producing a well-known downsweep call for this species (Romagosa et al., 2015). Several studies indicate that blue, fin and sei whales are present around the archipelago, including in the deployment areas, mostly from February to May (Silva et al., 2014; Prieto et al., in press) which coincides with a lower presence of boats at Condor but with a higher presence of boats at Açores. As for the transiting area (Gigante), due to its more constant vessel traffic throughout the year, an overlap exists with the baleen whale northward migration in spring and summer, and possibly with the southward journey in late autumn.

The biological implications of masking for these three species, whether they compensate it by modifying vocal behavior or not, are still unclear. However, given the association of vocalizations to such vital processes (e.g., social, foraging, navigation, reproduction), masking could reduce the chance of finding partners to mate, the ability of finding food or even their navigational skills thus negatively affecting their reproductive success and ultimately its survival. Although some efforts have been made to develop masking models that can be incorporated into regulation strategies, more research is needed to better understand potential effects of this complex phenomena, hearing characteristics from different species and anti-masking strategies used by free-ranging animals (Erbe, 2002; Clark et al., 2009).

Ship noise can also cause behavioral responses to cetaceans and Southall et al. (2007) suggests using SPLs to assess it. This metric might not be the most appropriate way to look for consistent patterns of response but it is often measured or estimated because it is required by law in many European countries and the USA as part of their noise mitigation regulations. Also, many other variables such as location, nature and behavior of noise sources and characteristics and activity of the individual animal among others, can affect the nature and extent of responses (Ellison et al., 2012). Therefore, the percentage of time with SPL levels above 120 dB re 1 μPa was calculated based on the model from the NRC (2005) that established that marine mammals exposed to levels above this value might be affected by sound. The maximum monthly percentage time with levels above 120 dB re 1 μPa was 3.3% (at Condor seamount) which is very low considering that an animal is unlikely to remain in the same location for the entire month. However, deployment depth affect noise levels received by the hydrophone and percentages with levels above 120 dB re 1 μPa are certainly higher closer to the source which in this case is found at the surface. While this is a simplistic and limited approach, it can nevertheless give an initial sense of the time that noise levels in an area could induce behavioral responses on baleen whales.

Comparatively, average noise levels for the three noisiest months at Condor (100.1 ± 17.2 dB re 1 μPa), Açores (95.9 ± 7 dB re 1 μPa) and Gigante (96.2 ± 13 dB re 1 μPa) for the frequency band of 10–585 Hz are lower than those measured by Castellote et al. (2012) in areas of the Mediterranean, such as the Provençal (106.9 ± 5.3 dB re 1 μPa), Alboran (103.7 ± 2.5 dB re 1 μPa) and Balearic (105.2 ± 1.2 dB re 1 μPa) basins and the Strait of Gibraltar (112.5 ± 4 dB re 1 μPa). Also, median noise levels within the 10–25,000 Hz measured in winter at Trindade-Martin Vaz Archipelago (113.7 ± 11.4 dB re 1 μPa), another oceanic archipelago in the Southwestern Atlantic, are higher than those of Condor (105.3 ± 11.4 dB re 1 μPa) for the same frequency band (Bittencourt et al., 2016). Differences in this case might be explained by presence of snapping shrimp found to be an important noise contributor in shallow waters (Hildebrand, 2009).

Despite our findings suggesting the Azores is characterized by reduced underwater noise, we expect other areas in the archipelago closer to ferry routes, commercial shipping routes or routinely used by whale watching boats to be considerably noisier. Therefore, these measurements are representative only of these locations and further measurements and sound propagation modeling in other areas will be necessary to produce a detailed soundscape for the entire archipelago.

AUTHOR CONTRIBUTIONS

Conceived and designed the work: MR and MS. Collected the data: IC, ML, EG, and MS. Performed data analysis and interpretation: MR, NM, EG, TM, and MS. Wrote the paper: MR. Reviewed the manuscript and approved the final version; MR, IC, NM, ML, EG, TM, and MS.

FUNDING

Fundação para a Ciência e a Tecnologia (FCT) and Fundo Regional da Ciência e Tecnologia (FRCT), through research projects TRACE (PTDC/MAR/74071/2006), MAPCET (M2.1.2/F/012/2011), and FCT Exploratory project (IF/00943/2013/CP1199/CT0001), supported by funds from FEDER, the Competitiveness Factors Operational (COMPETE), QREN, POPH, European Social Fund, Portuguese Ministry for Science and Education, and Proconvergencia Açores/EU Program. We also acknowledge funds provided by FCT to MARE, through the strategic project UID/MAR/04292/2013, that also supported fees for this open access publication. MR is supported by a DRCT doctoral grant (M3.1.a/F/028/2015), IC was supported by a FCT doctoral grant (SFRH/BD/41192/2007) and MAS is supported by an FCT-Investigator contract (IF/00943/2013). TM is a member of CEA/UL (Funded by FCT - Fundação para a Ciência e a Tecnologia, Portugal, through the project UID/MAT/00006/2013).

ACKNOWLEDGMENTS

We are grateful to Rui Prieto, the skippers and crew members that helped with the deployment of the EARs. Data on boat presence were kindly provided by the Azores Fisheries Observer Program (POPA) (www.popaobserver.org) and by tourism operators (in the latter case an output of the projects CONDOR (EEA Grants PT-0040/2008) and SMaRT (M.2.1.2/029/2011)). We are also grateful to Ricardo Serrão Santos for his support and useful comments. Comments and suggestions from two reviewers significantly improved the present paper. This work is an output of research projects TRACE-PTDC/MAR/74071/2006, MAPCET-M2.1.2/F/012/2011, and of the FCT-Exploratory project IF/00943/2013/CP1199/CT0001.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2017.00109/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 28 April 2017
doi: 10.3389/fmars.2017.00088

Zoantharians (Hexacorallia: Zoantharia) Associated with Cold-Water Corals in the Azores Region: New Species and Associations in the Deep Sea

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OPEN ACCESS

Edited by:
Tony J. Pitcher,
University of British Columbia, Canada

Reviewed by:
Paul Snelgrove,
Memorial University of Newfoundland,
Canada
James Davis Reimer,
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Specialty section:
This article was submitted to
Deep-Sea Environments and Ecology,
a section of the journal
Frontiers in Marine Science

Received: 01 July 2016
Accepted: 13 March 2017
Published: 28 April 2017

Citation:
Carreiro-Silva M, Ocaña O,
Stanković D, Sampaio Í, Porteiro FM,
Fabri M-C and Stefanni S (2017)
Zoantharians (Hexacorallia:
Zoantharia) Associated with
Cold-Water Corals in the Azores
Region: New Species and
Associations in the Deep Sea.
Front. Mar. Sci. 4:88.
doi: 10.3389/fmars.2017.00088

Zoantharians are a group of cnidarians that are often found in association with marine invertebrates, including corals, in shallow and deep-sea environments. However, little is known about deep-sea zoantharian taxonomy, specificity and nature of their associations with their coral hosts. In this study, analyses of molecular data (mtDNA COI, 16S, and 12S rDNA) coupled with ecological and morphological characteristics were used to examine zoantharian specimens associated with cold-water corals (CWC) at depths between 110 and 800 m from seamounts and island slopes in the Azores region. The zoantharians examined were found living in association with stylasterids, antipatharians and octocorals. From the collected specimens, four new species were identified: (1) *Epizoanthus martinsae* sp. n. associated with the antipatharian *Leiopathes* sp.; (2) *Parazoanthus aliceae* sp. n. associated with the stylasterid *Errina dabneyi* (Pourtalès, 1871); (3) *Zibrowius alberti* sp. n. associated with octocorals of the family Primnoidae [*Paracalyptrophora josephinae* (Lindström, 1877)] and the family Plexauridae (*Dentomuricea* aff. *meteor* Grasshoff, 1977); (4) *Hurlizoanthus hirondelleae* sp. n. associated with the primnoid octocoral *Candidella imbricata* (Johnson, 1862). In addition, based on newly collected material, morphological and molecular data and phylogenic reconstruction, the zoantharian *Isozoanthus primnoidus* Carreiro-Silva, Braga-Henriques, Sampaio, de Matos, Porteiro & Ocaña, 2011, associated with the primnoid octocoral *Callogorgia verticillata* (Pallas, 1766), was reclassified as *Zibrowius primnoidus* comb. nov. The zoantharians, *Z. primnoidus* comb. nov., *Z. alberti* sp. n., and *H. hirondelleae* sp. n. associated with octocorals showed evidence of a parasitic relationship, where the zoantharian progressively eliminates gorgonian tissue and uses the gorgonian axis for structure and support, and coral sclerites for protection. In contrast, the zoantharian *P. aliceae* sp. n. associated with the stylasterid *E. dabneyi* and the zoantharian *E. martinsae* sp. n. associated with the antipatharian *Leiopathes* sp., appear to use the coral host only as support with no visible damage to the host. The monophyly of octocoral-associated zoantharians suggests that substrate specificity is tightly linked to the evolution of zoantharians.

Zibrowius alberti sp. n. urn:lsid:zoobank.org:act:8E186AD4-CA6E-419B-B46A-4C8D11C757DD
Hurlizoanthus hirondelleae sp. n. urn:lsid:zoobank.org:act:6737B10E-9E87-4BA0-9559-C22D49863732
Parazoanthus aliceae sp.n. urn:lsid:zoobank.org:act:3D3AA61D-E5CC-47DF-94F1-A4A2FF59ABEA
Epizoanthus martinsae sp. n. urn:lsid: zoobank.org:act:04686BB5-03D7-4132-B52B-CC89DF8EBFA8
urn:lsid:zoobank.org:pub:FED88229-30F9-481F-9155-FF481790AE5C

Keywords: antipatharians, gorgonians, molecular taxonomy, parasitic, phylogeny, stylasterids, Zoantharia

INTRODUCTION

Zoantharians (Cnidaria, Anthozoa, Hexacorallia, Zoantharia) are an order of benthic cnidarians that are found in most marine environments from shallow tropical coral reefs (e.g., Burnett et al., 1997; Reimer et al., 2008b, 2010b) to cold seeps (Reimer et al., 2007) and seamounts in the deep sea (Reimer et al., 2008a; Carreiro-Silva et al., 2011; Sinniger et al., 2013).

Until recently, zoantharian taxonomy was poorly known due to the paucity of standardized morphological characters, the large amount of intraspecific variation (Burnett et al., 1997; Reimer et al., 2004) and difficulties in examining internal morphology resulting from the presence of sand and detritus encrustated in the ectoderm and mesoglea of the body wall (Reimer et al., 2010c). Several studies have attempted to find new morphological and histological characters that efficiently discriminate between zoantharian genera and species. Characters such as the cnidome (Herberts, 1972; Ryland and Lancaster, 2004) and sphincter muscle anatomy (Lwowsky, 1913) have traditionally been used, but have not proven to be efficient and applicable to zoantharians over a wide range of taxa (Sinniger et al., 2010). However, studies using molecular techniques in combination with morphological data have begun to bring some standardization and reassessment to zoantharian taxonomy, resulting in the creation of new taxa (Reimer et al., 2008a; Sinniger and Häussermann, 2009; Sinniger et al., 2010), the merging of other taxa (e.g., Reimer et al., 2006), and the identification of the most useful morphological characters to Zoantharia systematics by mapping these traits onto the molecular phylogeny of the group (Swain et al., 2016).

In addition to genetic and morphological characters, the ecology of zoantharians and in particular the type of the substrate used by zoantharians, has been suggested as a useful character for zoantharian taxonomic identification (e.g., Sinniger et al., 2005; Reimer et al., 2008a; Sinniger et al., 2010). This is based on results of molecular phylogenetic studies suggesting a possible relationship between the group of organisms used as substrate and the evolution of the suborder Macrocnemina (comprising all the specimens examined in the present study; Sinniger et al., 2005, 2010, 2013; Montenegro et al., 2015b). Zoantharians, especially those belonging to the family Parazoanthidae Delage and Hérouard, 1901, appear to form monophyletic groups correlated to the organisms they colonize (such as hydrozoans, sponges, antipatharians or octocorals). In recent revisions of the family Parazoanthidae (Sinniger et al., 2010, 2013; Montenegro et al., 2015a,b) this character, together with DNA markers and morphological characteristics, were used to help define (1) a family of zoantharians associated with hydrozoans (family Hydrozoanthidae Sinniger, Reimer & Pawlowski, 2010) with the genera *Hydrozoanthus* Sinniger, Reimer & Pawlowski, 2010, and *Terrazoanthus* Reimer & Fujii, 2010; (2) a genus (*Antipathozoanthus* Sinniger, Reimer & Pawlowski, 2010) of zoantharians associated with antipatharians; (3) five genera (*Kulamanamana*, *Zibrowius*, *Hurlizoanthus*, *Kauluzoanthus,* and *Bullagummizoanthus* Sinniger, Ocaña & Baco, 2013) associated to deep-sea octocorals; and (4) the genera *Umimayanthus* Montenegro, Sinniger & Reimer, 2015, *Parazoanthus* Haddon and Shackleton, 1891 and the resurrected genus *Bergia* Duchassaing de Fonbressin and Michelotti, 1860, associated with sponges.

The Azores are recognized as a cold-water coral (CWC) hotspot in the NE Atlantic, with more than 160 species identified to date, and where deep-sea gorgonians, stylasterids, and black corals are the most conspicuous components, forming dense coral assemblages commonly referred to as "coral gardens" (Braga-Henriques et al., 2013; Tempera et al., 2013). A high number of epifaunal organisms such as crustaceans, polychaete worms, anemones, zoantharians, ophiuroids, crinoids and hydroids are associated with CWCs (Roberts et al., 2009). However, in many cases, their taxonomic identity is unknown at the species level, suggesting an important diversity among epifaunal organisms. Amongst these, zoantharians are very often associated with octocorals in coral garden areas. An important aspect of this association is the parasitic behavior of zoantharians toward their host octocorals (Carreiro-Silva et al., 2011; Sinniger et al., 2013), thus raising questions on their contribution to coral mortality, and on how they can affect coral population structure. In the Azores region, one such species, a parasitic zoantharian associated with the octocoral *Callogorgia verticillata* (Pallas, 1766), has been recently described as *Isozoanthus primnoidus* Carreiro-Silva, Braga-Henriques, Sampaio, Matos, Porteiro & Ocaña, 2011 (Carreiro-Silva et al., 2011). In the present paper we extend this study by using molecular data (mtDNA COI, 16S, and 12S rDNA) together with ecological and morphological characteristics to describe the diversity, phylogenetic relationship and coral-zoantharian relationship of four more epizoic zoantharians associated with octocorals and other CWCs in the seamounts and island slopes of the Azores region and one canyon in the Mediterranean Sea. In addition, based on newly collected material, morphological and molecular data and phylogenic reconstruction, *I. primnoidus* was reclassified as *Zibrowius primnoidus* comb. nov.

MATERIALS AND METHODS

Sample Collection

Zoantharian specimens from the Azores were obtained from by-catch material caught during scientific longline fishing cruises onboard of the RV "Arquipélago" (ARQDAÇO monitoring programme and DEECON project) and from the local longline fisheries fleet. Samples were collected at depths between 110 and 800 m from 12 locations in the Azores region (**Figure 1**). One additional zoantharian specimen was collected in the Cap Sicié canyon (Mediterranean Sea) in 2010 with the ROV Achille during the MEDSEACAN cruise (dive SI-ACH- P4) (Fabri et al., 2014). Immediately after collection, each zoantharian specimen was split into two fragments and preserved in 10% formalin for morphological, histological and microanatomy analysis and 96% ethanol for molecular studies. All type material is deposited in the reference collection (COLETA) of the Department of Oceanography and Fisheries, University of the Azores (DOP-UAz).

Morphological and Cytological Examinations

External Morphology

The external morphology of specimens was examined using preserved material and images of live specimens (only for zoantharians associated with the octocorals *Callogorgia verticillata* and the antipatharian *Leiopathes* sp.) maintained in aquaria at the DeepSeaLab facilities of DOP-UAz. Live specimens of zoantharians associated with *C. verticillata* and *Leiopathes* sp. were collected from the southern slope of the Faial-Pico Channel (38° 30'N 28°37'W) at depths of 320–360 m with the manned submersible "Lula" (Rebikoff-Niggeler Foundation) on September 2009.

Observations of zoantharian colonies were made using a dissecting microscope Leica MZ 16FA, and measurements taken using Image-J 1.45 software (Rasband, 2012). The following data were obtained for the characterization of zoantharians: for preserved specimens, polyp dimensions (oral disk diameter, polyp height), color of polyps, presence of particle encrustation on zoantharian's ectoderm (e.g., sand, foramiferan tests, sponge spicules, and coral sclerites) and coral host species. For live specimens (zoantharians associated with the octocoral *C. verticillata* and the antipatharian *Leiopathes* sp.), polyp dimensions of live polyps and tentacle number were also noted. Data on polyp dimensions are presented as the minimum-maximum ($n = 7$–38 polyps/colony, 1–3 colonies per species). In the case of zoantharians associated with gorgonians, the observed sclerites within the zoantharian specimens were compared with gorgonian sclerites after tissue removal using a sodium hypochlorite solution. In the case of the zoantharian associated with *C. verticillata*, morphological information presented in this paper, including observations and measurements on live specimens, is based on newly collected material in the Azores and Mediterranean, and complements previous information already included in the original description of the zoantharian in Carreiro-Silva et al. (2011).

Internal Morphology

Internal morphological examinations of the new zoantharian species using histological techniques were performed only

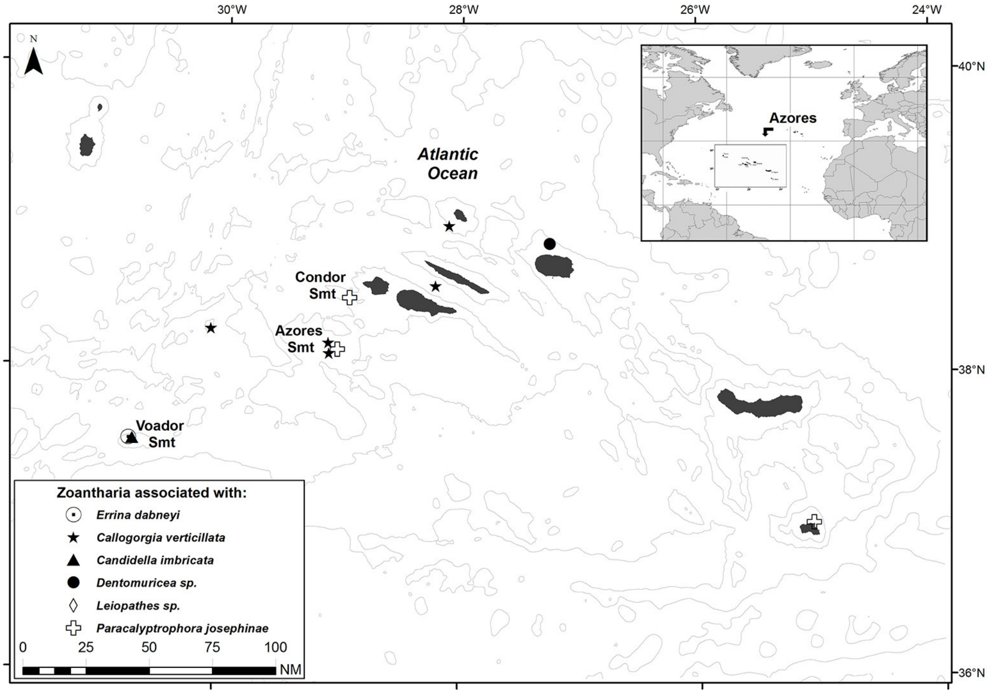

FIGURE 1 | Sampling sites of the zoantharians associated with the six cold-water corals under study in the Azores region.

for zoantharian specimens associated with the octocorals *C. verticillata* and *Paracalyptrophora josephinae* (Lindström, 1877) and the black coral *Leiopathes* sp. due to scarcity of material for other zoantharians. For the zoantharian species associated with the octocoral *Dentomuricea* aff. *meteor* Grasshoff, 1977 and the stylasterid *Errina dabneyi* (Pourtalès, 1871), anatomical and microanatomical details were studied using staining *in toto*. For histological examinations, individual polyps dissected from zoantharian colonies were decalcified for 4 h with RDF Mild Decalcifier (CellPath Ltd, UK) and desilicified for 2 h in 20% hydrofluoric acid, then washed in distilled water. Polyps were dehydrated in ethanol, cleared with xylene, embedded in paraffin, and sectioned. Serial 8-mm longitudinal and cross sections of polyps were stained with Mallory Trichrome. Cross sections were cut transversely across the column, at the level of the actinopharynx. Longitudinal sections were cut across the marginal sphincter muscle. Histological slides of zoantharian specimens were examined with a light microscope (Zeiss Jeneval, × 25). The following morphological characters and conditions were examined: mesentery condition, number, and form (in particular fifth mesentery from dorsal directive complete or incomplete); presence or absence of drag marks from debris; presence or absence of sand and debris in mesoglea; overall condition of tissue and cells and in particular the ectoderm and endoderm.

Nematocysts Observations

Undischarged nematocysts were identified and measured in squashed tissue preparations from the tentacles, column, pharynx, and mesenterial filaments of preserved specimens using glycerine gel. A minimum of two polyps for each species and all the colonies available were examined. Nematocysts were examined with a light microscope (Zeiss Jeneval ×1,000, oil immersion) equipped with a Nomarski differential interference contrast optic system. Images were captured using Delta Pix-Invenio 5S scanner. Cnidae were classified according to the terminology used by Ryland and Lancaster (2004). The analyses of the cnidome are summarized in **Table 1** where the ranges of length and width of nematocysts are reported.

DNA Extraction, PCR Amplification and Sequencing

Genomic DNA was extracted using the commercial kit Mag-Bind® Tissue DNA Kit (Omega Biotek) following the manufacturers' instructions. PCR amplification of the mitochondrial protein-coding gene COI was performed using primers specifically designed for zoantharians, COIZoanF and COIZoanR (Reimer et al., 2007); while for the 16S and 12S rDNA regions, the pairs of primers used were 16Sant1a/16SbmoH and 12S1a/12S3r, respectively (Sinniger et al., 2005). PCR reactions were performed in a 20 μl total-reaction volume with 10 μl of PCR Mastermix solution (Promega), 0.5 μl of each primer (10 μM), 8 μl of pure water and 1 μl of template DNA.

The thermal cycling profile for the three genomic regions started with an initial denaturation at 95°C for 3 min followed by 40 cycles of touch-down PCR (denaturation at 95°C for 30 s, annealing at 52–72°C for 1 min 35 s), and a final extension at 72°C for 7 min on a BioRad Mycycler thermal cycler. Non-template controls were included to all PCR reactions to detect any genomic DNA contamination. Electrophoresis of PCR products on a 1% agarose gel was performed to evaluate the integrity of the products. Finally, all amplified products were purified using ExoSAP-IT (USB Corporation) and sent for sequencing to the BMR Genomics (Padua, Italy) facility using the same set of primers. Newly obtained sequences were deposited in the NCBI database. GenBank accession numbers for all molecular markers and for each species used to reconstruct the phylogeny are reported in **Supplementary Table 1**.

Phylogenetic Analyses

Additional sequences of closely related species (**Supplementary Table 1**) were retrieved from the NCBI database to reconstruct the phylogeny of zoantharians from the Azores. All sequences were aligned using MAFFT v. 7 (Katoh and Standley, 2013) and sections with large indels were rearranged by eye. For the 16S, the V5 region was aligned following Sinniger et al's (2013) suggestions. In addition, indel events were coded as binary characters with SeqState (Müller, 2005) using simple-indel coding approach (SIC; Simmons and Ochoterena, 2000) and added to the existing alignment. Moreover, 16S and 12S rDNA alignments were also automatically edited by GBlock v. 0.91b (Castresana, 2000) to eliminate potentially poorly aligned positions; the configuration was set in agreement with the suggestions from Montenegro et al. (2015b), allowing small final blocks, gap positions between final blocks and less strict flanking positions.

For the phylogenetic investigation, the most appropriate nucleotide substitution model was selected from the hierarchical series of likelihood ratio test implemented in MEGA 4 (Tamura et al., 2007). Phylogenetic relationships were reconstructed for all three alignments (SIC, an alignment including indel coding; NoSIC, an alignment with no indel coding; and GBlock, a GBlock edited alignment) using Bayesian inference (BI) in MrBayes v. 3.2.6 (Ronquist et al., 2011), while the Maximum Likelihood (ML) in RAxML v. 8.2.8. (Stamatakis, 2014) approach was used only on the alignment with no indel coding; all phylogenetic reconstructions were run online using the CIPRES Science Gateway portal v. 3.3 (Miller et al., 2010). BI was done implementing the HKY+G model (Hasegawa et al., 1985; Yang, 1993) for DNA sequences and a binary model for the coded indel events, assuming unlinked parameters and rates for each gene and a site-specific rate model for the protein-coding COI gene. BI calculations were conducted with the help of the BEAGLE library (Ayres et al., 2012) and run for 20,000,000 generations until the standard deviation of split frequencies value was less than 0.05. For the ML approach, DNA sequences were analyzed in a partitioned dataset (COI, 16S, and 12S) following a RAxML Workflow interface and using the Maximum Likelihood/Thorough Bootstrap approach and GTR+gamma model, while an autoMRE criterion was used for bootstrapping (660 bootstrap iterations). In both approaches, representatives of the family Epizoanthidae Delage and Hérouard, 1901 were used

TABLE 1 | Types, relative abundances and sizes of cnidae of the new species described.

Tissue	Nematocyst type	*Zibrowius alberti* sp. n.	*Hurlizoanthus hirondelleae* sp. n.	*Parazoanthus aliceae* sp. n.	*Epizoanthus martinsae* sp. n.
Tentacles	Spirocysts	(15–20) × (2–5), 3/3, 10, vc (A)	(15–20) × (2–5), 1/1, 10, vc (A)	(15–30) × (2–5), 2/2, 10, vc (A)	(15–27) × (2–4), 2/2, 10, vc (A)
	b-mastigophore 1	(17–21) × (3–4),3/3, 20, c (B)	(17–19) × (3–4),1/1, 10, c (B)	(13–28) × (3–4),2/2, 20, c; (B)	(15–20) × (4–6), 2/2, 20, rc; (C)
	b-mastigophore 2			(17–27) × (3–4), 2/2, 20, c (C)	(19) × (2–3), 2/2, 6, uc;(D)
	b-mastigophore 3			(9–15) × (2–3), 2/2, 5, uc (D)	(14–20) × (2.5–3), 2/2, 20, rc; (E)
	Special b-mastigophore 4			(13–18) × (8), 2/2, 5, uc; (E)	
	Special b-mastigophore 5			(20–25) × (7–10), 2/2, 10, rc; (F</A>)	
	p-mastigophore				(12) × (3.5), 1/2, 1, r; (F)
	Holotrich 1		(16–17) × 3, 1/1, 3, rc (C)		(20–33) × (9–13),2/2, 40, c; (B)
	Holotrich 2		(8 × 3), 1/1, 1, r; (D)	(24–25) × (12), 2/2, 2, r;(G)	
Pharynx	b-mastigophore 1	(18 × 20), 3/3, 15, c (D)	(18–19) × 4, 1/1, 5, rc (E)	(17–21) × (3–4), 2/2, 20, c; (H)	(17–25) × (2–3), 2/2, 20, rc; (H)
	b-mastigophore 2			(17–27) × (3–4), 2/2, 15, c; (I)	(15–17) × (3–4), 2/2, 10, uc;(I)
	p-mastigophore	(19–21) × 5, 1/3, 3, r (C)			
	Holotrich 1	(9–3), 1/3, 1, r (E)	(14–17) × (3–4), 1/1, 10, c (F)	(15–24) × (8–11), 2/2, 10, rc; (J)	(22–35) × (9–17), 2/2, 2, c; (G)
	Holotrich 2			(10–13) × (3–4), 2/2, 10, rc; (K)	(9) × (3), 1/2, 1, r; (J)
Filaments	b-mastigophore 1	(16–20) × (3–3.5), 3/3, 15, rc (F)	(18–20) × (3–4), 1/1, 4, rc; (G)	(19–22) × (3–4), 2/2, 10, rc; (L)	(16–20) × (4–5), 2/2, 20, c; (N)
	b-mastigophore 2			(20–23) × (3), 2/2, 5, uc;(M)	(15–18) × (3–4), 2/2, 15, rc; (O)
	Special b-mastigophore			(15–16) × (6–7), 2/2, 5, uc; (P)	
	p-mastigophore	(15–20) × (4–6), 3/3, 25,rc (G)	(16–20) × (5–7), 1/1, 5, rc (H)	(13–20) × (4–5), 2/2, 10, rc; (N)	(16–20) × (4–5), 2/2, 20, c; (M)
	Holotrich 1	(9) × (3), 1/3, 3, uc (H)		(15–23) × (7–10), 2/2, 15, c; (O)	(25–33) × (10–15), 2/2, 40, vc; (K)
	Holotrich 2				(15–16) × (2), 2/2, 3, uc (L);
	Holotrich 3			(1–11) × (3–4), 2/2, 10, rc; (Q)	
	Alien 1		(37–40) × (10–12), 1/1, 2, r (I)		
	Alien 2		(37–40) × (10–12), 1/1, 2, r (J)		
Body wall	b-mastigophore			(17–22) × (3–4), 2/2, 5, uc; (R)	
	Special b-mastigophore			(13–17) × (5–7), 2/2, 15, rc; (T)	(9–13) × (4–5), 2/2, 20, rc (Q)
	Holotrich 1	(30–35) × (17–18), 3/3, 5, uc (I)	(30–32) × (11–17), 1/1, 5, rc;(K)	(19–23) × (7–10), 2/2, 20, c; (S)	(22–25) × (10–11), 2/2, 4, uc; (P)
	Holotrich 2		(10–12) × 4, 1/1, 2, r (L)		
	Holotrich 3			(25–30) × (10–15), 2/2, 20, c; (U)	
	Holotrich 4			(9) × (3), 2/2, 3, r. (V)	

Number ranges indicate cnidae dimensions (length × width) in μm, followed by the ratio of the number of individual polyps examined having a particular type of cnidae to the total number examined; and the number of measured capsules. Abbreviations: r, rare; u, uncommon; rc, relatively common; c, common; vc, very common. Capital letters refer to ***Figure 4****.*

as an outgroup and inferred trees were viewed with Figtree v. 1.4.2 (Rambaut, 2014).

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/." The LSID for this publication is: urn:lsid:zoobank.org:pub: FED88229-30F9-481F-9155-FF481790AE5C. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the digital repository PubMed Central. The supraspecific nomenclature of the zoantharians followed the recent revision of the order Zoantharia in Low et al. (2016). For valid synonyms of families and genera of the order Zoantharia the reader is referred to Low et al. (2016).

RESULTS

Systematics

Phylum Cnidaria Hatschek, 1888
    Class Anthozoa Ehrenberg, 1831
    Subclass Hexacorallia Haeckel, 1896
    Order Zoantharia Gray, 1832

Suborder Macrocnemina Haddon and Shackleton, 1891

Diagnosis: Zoantharians characterized by a complete fifth pair of mesenteries.

Family Parazoanthidae Delage and Hérouard, 1901

Diagnosis: Macrocnemic zoantharians that have an endodermal sphincter muscle. Most species in this family associated with other organisms as substrate.

Genus *Zibrowius* Sinniger, Ocaña & Baco, 2013

Type Species: *Zibrowius ammophilus* Sinniger, Ocaña & Baco, 2013.

Diagnosis: Sand-encrusted, arborescent fan-shaped colonies, golden skeleton, well developed coenenchyme completely covering the host, can be confused with *Kulamanamana* Sinniger, Ocaña & Baco, 2013, but are easily distinguished by the presence of sand encrustation in the ectoderm, and characteristic insertion/deletion pattern in the 16S V5 region *sensu* Sinniger et al. (2005).

Zibrowius primnoidus comb. nov.

Figures 2–4.

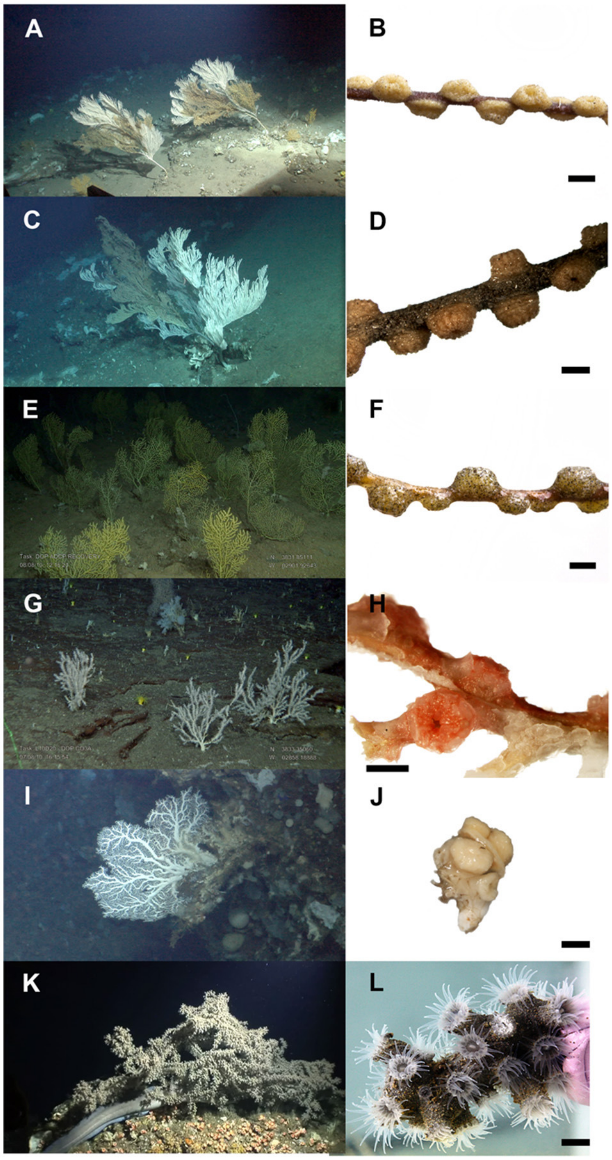

FIGURE 2 | Photographs of zoantharians and respective cold-water coral hosts in the Azores. (A) octocoral *Callogorgia verticillata*; and **(B)** associated zoantharian *Zibrowius primnoidus* comb. nov. Specimen DOP-804 (Holotype); **(C)** octocoral *Paracalyptrophora josephinae*; and **(D)** associated zoantharian *Zibrowius alberti* sp. n. Specimen DOP-3050 (Holotype); **(E)** octocoral *Dentomuricea* aff. *meteor*, and **(F)** associated zoantharian *Zibrowius alberti* sp. n. Specimen DOP-5332 (Paratype); **(G)** octocoral *Candidella imbricata* and **(H)** associated zoantharian *Hurlizoanthus hirondelleae* sp. n. Specimen DOP-4098 (Holotype); **(I)** stylasterid *Errina dabneyi* and **(J)** associated zoantharian *Parazoanthus aliceae* sp. n. Specimen DOP-4090 (Holotype); **(K)** antipatharian *Leiopathes* sp. and **(L)** associated zoantharian *Epizoanthus martinsae* sp. n. Specimen DOP-3609 (Holotype). Scale bar = 2 mm for **(B,D,F,H)** and 4 mm for **(L)**. Photo credits: CORAZON project/Rebikoff-Niggeler Foundation **(A,C,I,K)**; CoralFISH/CONDOR projects **(E,G)**.

Isozoanthus primnoidus Carreiro-Silva, Braga-Henriques, Sampaio, de Matos, Porteiro & Ocaña, 2011, pp. 409,410, **Figures 2–5**, **Table 1**.

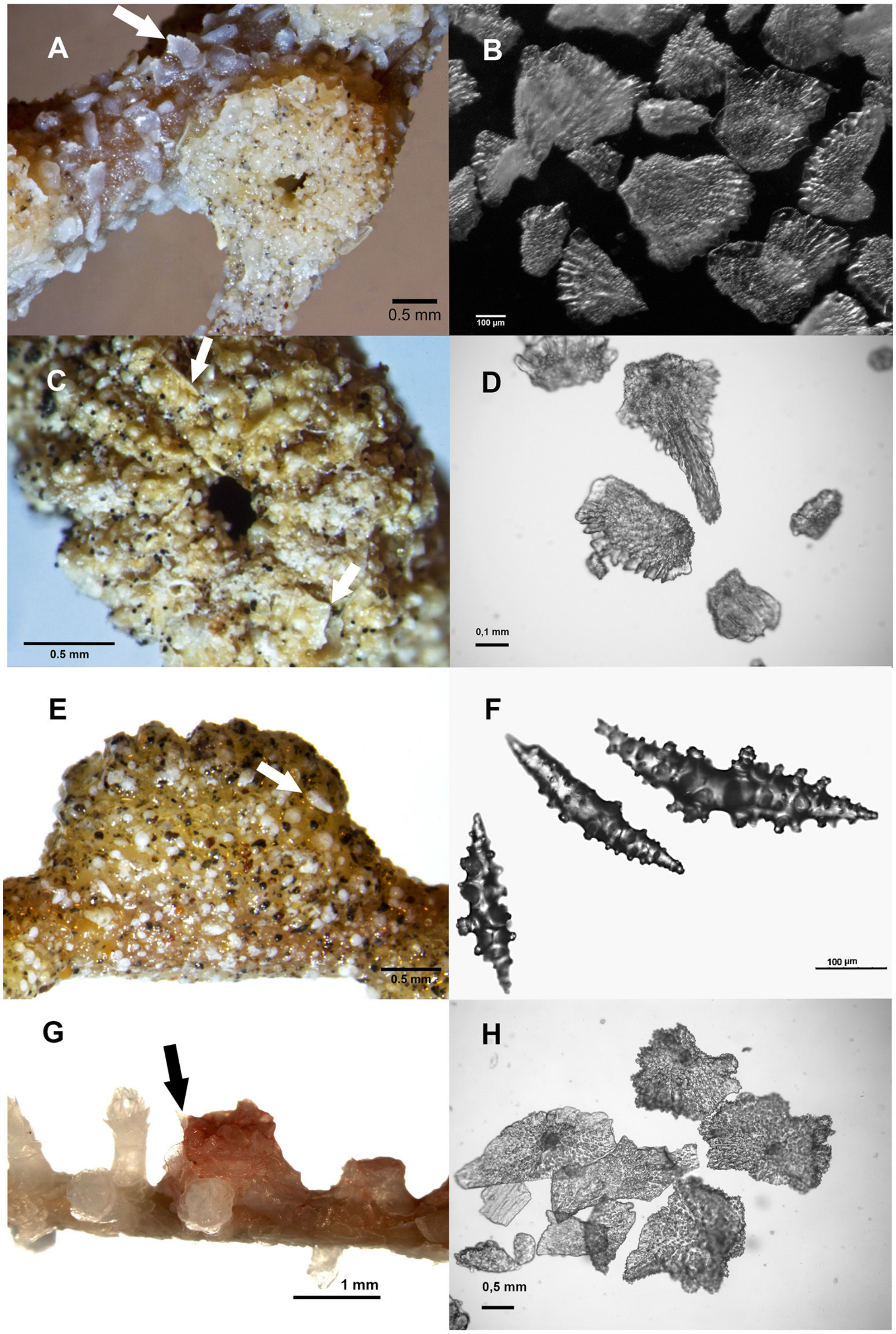

FIGURE 3 | Zoantharian polyps showing encrustations in the ectoderm including octocoral sclerites (arrow) and sclerites of the octocoral hosts for comparison: (A) zoantharian *Zibrowius primnoidus* comb. nov. Specimen DOP-804 (Holotype); **(B)** detail of sclerites of the octocoral *Callogorgia verticillata*; **(C)** zoantharian *Zibrowius alberti* sp. n. growing on the octocoral *Paracalyptrophora josephinae*. Specimen DOP-3050 (Holotype); **(D)** detail of sclerites of *P. josephinae*; **(E)** *Z. alberti* growing on the octocoral *Dentomuricea* aff. *meteor*. Specimen DOP-5332 (Paratype) **(F)** detail of sclerites of *D.* aff. *meteor*; **(G)** *Hurlizoanthus hirondelleae* sp. n. Specimen DOP-4098 (Holotype); **(H)** detail of sclerites of the octocoral *Candidella imbricata*.

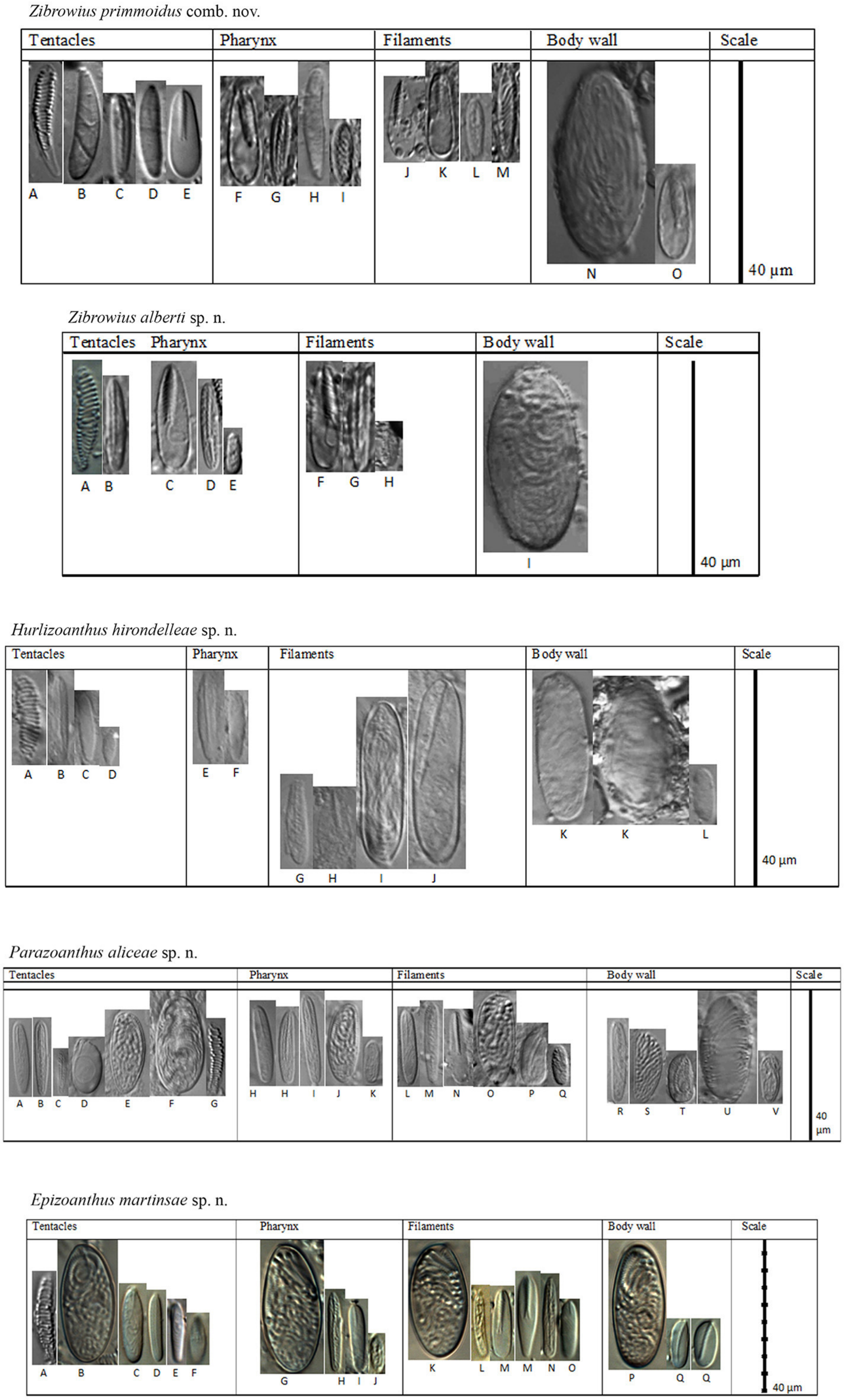

FIGURE 4 | Cnidae in tentacles, pharynx, filaments and body wall of *Zibrowius primnoidus* comb. nov, *Zibrowius alberti* sp. n. and *Hurlizoanthus hirondelleae* sp. n., *Parazoanthus aliceae* sp. n., and *Epizoanthus martinsae* sp. n. respectively. Letters correspond to the cnidae listed in **Table 1**.

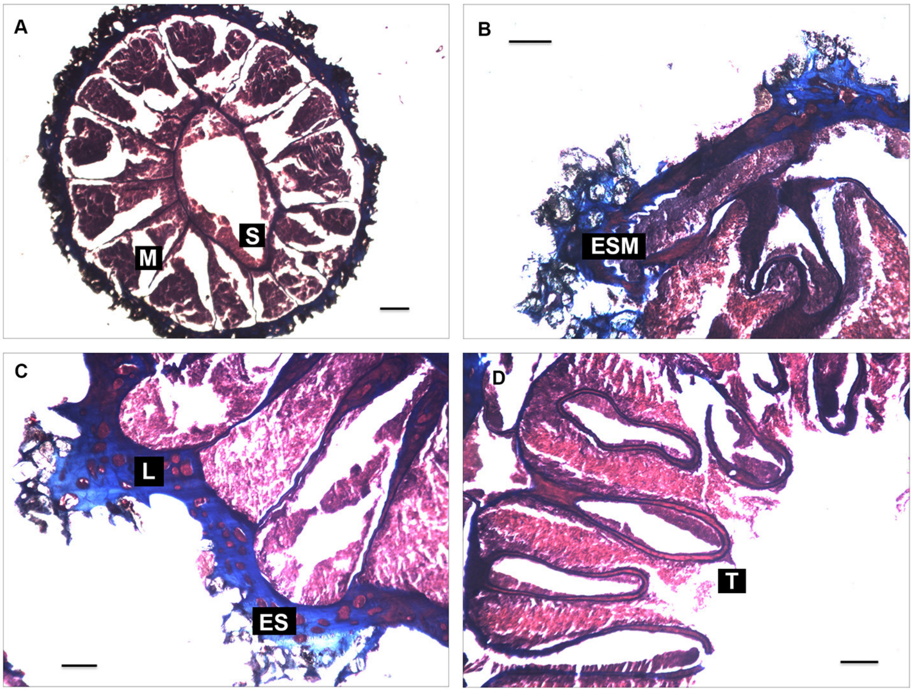

FIGURE 5 | Histological sections of *Zibrowius alberti* sp. n. (A) siphonoglyph (S) and mesenterial disposition (M); **(B)** endodermal sphincter muscle (ESM); **(C)** mesogloea of the body-wall with a complex lacunae system (L) and encircling sinus (ES); **(D)** weak tentacles musculature (T) and endodermal intrusion in their mesoglea. Cross sections of contracted polyps are shown at the region of the actinopharynx **(A)**; capitulum **(C)**, and the tentacles **(D)**. Longitudinal sections at the region of the capitulum are shown in **(B)**. Scale bar: 100 μm.

Material Examined

Holotype

Atlantic Ocean, Condor Seamount, 38N°32′N 29°06′W, depth 293 m, 26 June 2008, zoantharian associated with the octocoral *Callogorgia verticillata* (Pallas, 1766), fragment of 43 small polyps (formalin-fixed) and fragment of 7 polyps (ethanol-fixed), DOP-804.

Paratypes

Atlantic Ocean, Condor Seamount, 38°08′N 29°05′W, depths 274–293 m, 17 September 2006, zoantharian associated with *C. verticillata*, fragment with 32 polyps (formalin-fixed) and 6 polyps (ethanol-fixed) DOP-3242; Atlantic Ocean, Açor Seamount, 38°17′N 28°52′W, depth 368 m, 11 September 2007, zoantharian associated with *C. verticillata*, fragment with 41 polyps (formalin-fixed) and 7 polyps (ethanol-fixed) DOP-3051. Mediterranean, Cap Sicié canyon (Off Toulon, France), 43°01′N 5°89′E, depth 260 m, 14 April 2010, zoantharian associated with *C. verticillata*, fragments with 5 and 6 polyps (ethanol-fixed) Si-ACH-P4-1, Si-ACH-P4-2, respectively.

Sequences: see **Supplementary Table 1**.

Description

Diagnosis

Colonial zoantharian found at the surface of the octocoral *Callogorgia verticillata*, often in an orthogonal arrangement around the octocoral axis (**Figures 2A,B**). Presence of encrustations in the polyp's ectoderm. Endodermal sphincter forming a wide sinus, mesogloea with a large number of lacunae left behind by dissolved mineral particles. Presence of large holotrichs in the polyp's body wall and p-mastigophores in the tentacles and body wall.

External Anatomy

In life, capitulum and oral disc are light brown with short translucent tentacles. In preserved samples, polyps are light brown and connected by a thin coenenchyme growing over the gorgonian axis (**Figure 2B**). Polyps occur at intervals of approximately 1–1.5 polyps in diameter, often in an orthogonal arrangement. Living polyps have an oral disc 3–4 mm in diameter, with a column diameter of 2–3 mm and height of 3–4 mm. In preserved specimens, contracted polyps are 1.8–3.0 mm in diameter and extending to 1.0–2.1 mm above the coenenchyme; proximal part of the polyp is slightly broader than the distal part (**Figure 2B**). Two rows of 18–26 transparent tentacles (smaller, immature polyps can have fewer) are pointed; length of tentacles are shorter than the expanded oral disk diameter. Pharynx is oval and orange. Ectoderm and outer mesogloea are densely encrusted with mineral particles, gorgonian sclerites, foraminiferan tests, and sponge spicules, and therefore appearing "flecked" with white (**Figure 3A**); sclerites were confirmed to be from *C. verticillata* (**Figure 3B**).

Internal Anatomy

Mesenteries in a macrocnemic arrangement into three to four cycles of mesenteries, of which the 3° and 4° are incomplete mesentaries. Musculature poorly developed; retractor muscles are not present in mesenteries; parietobasilar muscles are weak, forming very small pennons; stronger ectodermal musculature in tentacles. Sphincter is endodermal but short and concentrated in the upper part of the column, forming a wide sinus; siphonoglyph is conspicuous and prominent. There is an absence of lacunae canals system and an encircling sinus. Mesogloea of the body wall presents a large number of lacunae formed by dissolved mineral particles and host sclerites. Lacunae are less numerous and larger in the connected coenenchyme. There was no indication of the presence of zooxanthellae.

Cnidae

Large holotrichs (holotrich 1) were the most characteristic nematocyst observed in this species, and were very common in the ectoderm of the body wall (**Figure 4**, see also Table 1 and Figure 5 in Carreiro-Silva et al., 2011). Presence of p-mastigophores in the body wall was scarce, as were the special b-mastigophores in the tentacles.

Biological Interaction

Found in association with primnoid octocoral *C. verticillata*, Carreiro-Silva et al. (2011) observed it in association with 17% (nine zoantharian bearing colonies/53 total colonies) of examined colonies. It can cover up to 14 ± 5% (mean ± st. dev., $n = 6$) of the external surface of the octocoral colony. There is strong evidence of parasitic behavior by the zoantharian (see Discussion section). In aquaria, the species displays bioluminescence when touched.

Distribution

Reported in the Azores region, Northeast Atlantic, at depths of 110–800 m with ocean temperatures ranging from 10°C to 15°C, and from the Mediterranean Sea at 260 m depth with temperatures ranging from 13°C to 14°C also in association with *C. verticillata*.

Zibrowius alberti sp. n.

Figures 2–5, **Table 1**.

urn:lsid:zoobank.org:act:8E186AD4-CA6E-419B-B46A-4C8D11C757DD.

Etymology: This species name is dedicated to Prince Albert I of Monaco for his promotion of the oceanographic sciences in the late 19th to early 20th centuries, and for his oceanographic campaigns in the Azores which contributed to the increased knowledge of CWCs and associated fauna in the region.

Material Examined

Holotype

Atlantic Ocean, Condor Seamount, 38°50′N 28°93′W, depth 360 m, 15 April 2007, zoantharian associated with the octocoral *Paracalyptrophora josephinae* (Lindström, 1877) (family Primnoidae), fragment of 30 polyps (formalin-fixed) and 5 polyps (ethanol-fixed) DOP-3050.

Paratypes

Atlantic Ocean, Terceira, 38°07′N 27°25′W, depth 304 m, 4 Junho 2010, zoantharian associated with the octocoral *Dentomuricea* aff. *meteor* Grasshoff, 1977 (family Plexauridae), fragment of 42 polyps (formalin-fixed) and fragment of 8 polyps (ethanol-fixed) DOP-5332; Atlantic Ocean, Santa Maria, 37°02′N 25°06′W, depths 350 m, 21 April 2007, zoantharian associated with *P. josephinae*, fragment of 23 polyps (formalin-fixed) and fragment of 9 polyps (ethanol-fixed) DOP-3049; Atlantic Ocean, Açor Seamount, 38°15′N 29°03′W, depth 307 m, 23 April 2007, zoantharian associated with *P. josephinae*, fragment of 20 polyps (formalin-fixed) and fragment of 3 polyps (ethanol-fixed) DOP-3042.

Sequences: see **Supplementary Table 1**.

Description

Diagnosis

Colonial zoantharian found at the surface of the octocorals *Paracalyptrophora josephinae* and *Dentomuricea* aff. *meteor*, often in an orthogonal arrangement around the gorgonian axis (**Figures 2D,F**). Presence of encrustations in the polyp's ectoderm. The endodermal sphincter forms a wide sinus, its mesogloea with a large number of lacunae with endodermic content and lacunae system. There is a presence of large holotrichs in the body wall and p-mastigophores with well-marked filaments.

External Anatomy

No observations were made on live specimens. In preserved samples, polyps were orange-brown, connected by thin coenenchyme growing over the gorgonian axis (**Figures 2D,F**). Polyps occur at intervals of approximately 1–1.5 polyp diameters, often in an orthogonal arrangement. In preserved specimens, contracted polyps are 1.9–4.1 mm in diameter and extending to 0.6–2.5 mm above the coenenchyme; the proximal part of the polyp is slightly broader than the distal part (**Figures 2D,F**); there are 11–14 capitular ridges on closed polyps. Ectoderm and outer mesogloea are densely encrusted with mineral particles, gorgonian sclerites, foraminiferan tests, and sponge spicules, and therefore appear "flecked" with white (**Figures 3C,E**); sclerites were confirmed to be from the gorgonian host (**Figures 3D,F**). In larger specimens, there are 24 tentacles, which are arranged in three tentacle cycles, and an additional extra incomplete cycle may also be present in some specimens.

Internal Anatomy

Mesenteries in macrocnemic arrangement (**Figure 5A**), distributed in seven pairs of complete mesenteries and five pairs of incomplete mesenteries (24 mesenteries in total). The sphincter is endodermal (**Figure 5B**) but short and concentrated in the upper part of the column, forming a wide sinus and enlarged pennons; its siphonoglyph is conspicuous. Mesogloea of the body wall presents a large number of lacunae with endodermic content (**Figure 5C**), very few of which present dissolved mineral particles and host sclerites. Lacunae system with encircling sinus in the mesogloea of the body wall. Endodermal intrusion is commonly observed in the mesogloea of the sphincter, mesenteries, pharynx and tentacles. Musculature is poorly developed; retractor and parietobasilar muscles are not present in mesenteries or are very weak as observed with stereomicroscopy; there is only weak ectodermal musculature in tentacles (**Figure 5D**). There was no indication of the presence of zooxanthellae.

Cnidae

Large holotrichs (holotrich 1) and p-mastigophores are present with a well-marked filament and are the most important nematocyst characteristics observed in this species (**Table 1** and **Figure 4**).

Biological Interaction

This species is found in association with the primnoid octocoral *P. josephinae* and the plexaurid octocoral *D.* aff. *meteor*. *Z. alberti* was associated with 20% (three zoantharian bearing colonies/15 total colonies) of *P. josephinae* colonies examined. Unfortunately, zoantharian-bearing specimens of *P. josephinae* were broken due to damage during capture, and we could not accurately estimate the external surface of *P. josephinae* covered by *Z. alberti*. Only one *Z. alberti* was found in association with *D.* aff. *meteor*. There was strong evidence of parasitic behavior by the zoantharian (see Discussion section).

Distribution

So far this species has only been reported in the Azores region, Northeast Atlantic, at depths of 300–360 m with ocean temperatures ranging from 13°C to 15°C.

Genus *Hurlizoanthus* Sinniger, Ocaña & Baco, 2013

Type Species: *Hurlizoanthus parrishi* Sinniger, Ocaña & Baco, 2013.

Diagnosis: Macrocnemic genus associated with primnoids. Characteristic insertion/deletion pattern in the 16S V5 region *sensu* Sinniger et al. (2005).

Hurlizoanthus hirondelleae sp. n.

Figures 2–4, **Table 1**.

urn:lsid:zoobank.org:act:6737B10E-9E87-4BA0-9559-C22D49863732.

Etymology

This species name is dedicated to the research yacht *Hirondelle* used by Prince Albert I of Monaco during his oceanographic campaigns in the Azores.

Material Examined

Holotype

Atlantic Ocean, Voador Seamount, 37°53′N 30°71′W, depth 256 m, 26 July 2010, zoantharian associated with the octocoral *Candidella imbricata* (Johnson, 1862) (family Primnoidae), fragment of 2 polyps (ethanol-fixed), DOP-4098.

Sequences: see **Supplementary Table 1**.

Description

Diagnosis

This colonial zoantharian is found at the surface of the octocoral *Candidella imbricata* often in an orthogonal arrangement around the gorgonian axis (**Figures 2G,H**). No mineral encrustations occur in the polyp's ectoderm. There is a short endodermal sphincter. There is the presence of large holotrichs in the body wall and p-mastigophores with a well-marked filament.

External Anatomy

No observations were made of live specimens. In preserved samples, polyps were pinkish to light-red, connected by a thin coenenchyme growing over the gorgonian axis (**Figure 2H**). Polyp color may not correspond to the original color, but instead may be the result of preservation, as has been reported for other zoantharians (e.g., Sinniger et al., 2013). Polyps occur at intervals of approximately 1 polyp in diameter, often in an orthogonal arrangement. In preserved specimens, contracted polyps are 2.2–3.9 mm in diameter and extend to 0.9–1.7 mm above the coenenchyme; proximal part of the polyp is slightly broader than the distal part (**Figure 2H**). The ectoderm and outer mesogloea are densely encrusted with gorgonian sclerites (**Figure 3G**). No other particles were evident in the ectoderm. Sclerites were confirmed to be from the gorgonian host (**Figure 3H**).

Internal Anatomy

Mesenteries are in macrocnemic arrangement, with at least 25 mesenteries observed under the microscope. No specific number of mesenteries was estimated due to the scarcity of material. Musculature is poorly developed as a whole; there are no retractor and parietobasilar developments. There is a short endodermal sphincter, however, further detail was not possible due to the retracted state of the polyps. Siphonoglyph is conspicuous. No zooxanthellae present.

Cnidae

The most important nematocyst characteristics observed in this species are large holotrichs (holotrich 1) and the presence of p-mastigophores with a well-marked filament (**Table 1** and **Figure 4**). Due to the scarcity of material, we only observed nematocysts from one specimen. Therefore, future observations could reveal new cnidae characteristics for this species.

Biological Interaction

This species is found in association with the primnoid octocoral *C. imbricata*. Only one specimen of *H. hirondelleae* was found in association with *C. imbricata*. Therefore, we assume that the prevalence of this association is rare. There is strong evidence of parasitic behavior by the zoantharian (see Discussion section).

Distribution

So far, this species has only been reported in the Azores region, Northeast Atlantic, at a water depth of 256 m with ocean temperatures ranging from 10°C to 15°C.

Genus *Parazoanthus* Haddon and Shackleton, 1891

Type Species: *Palythoa axinella* Schimdt, 1862.

Diagnosis: Colonial zoantharians characterized by a mesogleal lacuna and by canals forming a "ring sinus" in distal part of polyp. Fine mineral particles are incorporated in polyps.

Parazoanthus aliceae sp.n.

Figures 2–4, **Table 1**.

urn:lsid:zoobank.org:act:3D3AA61D-E5CC-47DF-94F1-A4A2FF59ABEA.

Etymology

This species name is dedicated to another research yacht of Prince Albert I of Monaco, *Princess Alice*, used during his oceanographic campaigns in the Azores, and during which the homonymous seamount was discovered.

Material Examined

Holotype

Atlantic Ocean, Voador Seamount, 37°54′N 30°74′W, depth 293 m, 26 Julho 2010, associated with the stylasterid *Errina dabneyi* (Pourtalès, 1871) (Hydrozoa, family Stylasteridae), fragment of 2 polyps (ethanol-fixed), DOP-4090.

Sequences: see **Supplementary Table 1**.

Description

Diagnosis

This colonial zoantharian is found at the surface of the stylasterid *Errina dabneyi* (**Figures 2I,J**). Polyps are grouped by a thin coenenchyme and with a presence of encrustations in the ectoderm. There is an enlarged endodermal sphincter. Large holotrichs are present in all the tissues and there are special spirulae in most tissues.

External Anatomy

In preserved specimens, contracted polyps are 1.5–3.7-mm in diameter and extend to 0.8–3.2 mm above the coenenchyme; column is cylindrical (**Figure 2J**). No capitular ridges were visible. Ectoderm and outer mesogloea are encrusted with mineral particles.

Internal Anatomy

Mesenteries in macrocnemic arrangement, there are at least 30 mesenteries observed under the binocular. No specific number of mesenteries was possible due to scarcity of material. Some mesenteries present well developed retractor in the middle of the mesenteries. There is an enlarged endodermal sphincter. Siphonoglyph is conspicuous. No zooxanthellae are present.

Cnidae

Numerous categories of nematocysts are the main character, with large holotrichs (holotrich 1) in all the tissues including the presence of special b-mastigophores (**Table 1** and **Figure 4**).

Biological Interactions

It is found on the surface of the skeleton of the stylasterid *E. dabneyi*. There is no evidence of parasitic behavior.

Distribution

So far this species is only reported in the Azores region, Northeast Atlantic, at the depth of 293 m with ocean temperatures ranging from 13°C to 14°C.

Family Epizoanthidae Delage and Hérouard, 1901

Diagnosis: Characterized by a simple mesogloeal sphincter muscle, this family includes the genera *Epizoanthus* Gray, 1867, *Paleozoanthus* Carlgren, 1924, and *Thoracactis* Gravier, 1918. The genus *Palaeozoanthus* has not been found or examined in detail since its original description (Carlgren, 1924), while *Thoracactis topsenti* Gravier, 1918 is the sole representative of its genus and is an epibiont on sponges at 800–1100 meters around the Cape Verde Islands (Gravier, 1918). The type genus of Epizoanthidae, *Epizoanthus*, includes species that have epibiotic associations with hermit crabs (Ates, 2003; Reimer et al., 2010b; Schejter and Mantelatto, 2011), molluscs (Rees, 1967), eunicid worms (Sinniger et al., 2005; Kise and Reimer, 2016), or the stalks of glass sponges (hexactinellids) (Beaulieu, 2001). There are some cases of free-living species reported (*Epizoanthus lindahli* Carlgren, 1913, *Epizoanthus vagus,* Herberts, 1972). Polyps usually strongly encrusted with sand. In colonial species, polyps are linked by stolons or by a continuous coenenchyme. There are no symbioses with *Symbiodinium* zooxanthellae.

Genus *Epizoanthus* Gray, 1867

Type Species: *Dysidea papillosa* Johnston, 1842.

Diagnosis: Generally as for the family. Distinct from *Paleozoanthus* (Gravier, 1918) by its non-fertile micro-mesenteries (Carlgren, 1924, see also Sinniger and Häussermann, 2009). Only one specimen is known from the genus *Paleozoanthus* and it was not conserved well enough for genus distinction (Sinniger et al., 2005). Furthermore, *Epizoanthus* is distinct from the genus *Thoracactis* by presenting polyps joined by a common coenenchyme, in contrast with *Thoracactis* which shows isolated polyps without apparent coenenchyme connection.

Epizoanthus martinsae sp. n.

Figures 2–4, **6**, **Table 1**.

Nomenclatural act recorded at Zoobank: urn:lsid:zoobank.org:act:04686BB5-03D7-4132-B52B-CC89DF8EBFA8.

Etymology

The name of this species is dedicated to Dr. Helen Martins, researcher at the Department of Oceanography and Fisheries of the University of the Azores for her contribution to the advancement of marine science in the Azores through her research and dedication to the Azorean scientific journal *Arquipélago*.

Material Examined

Holotype

Atlantic Ocean, Faial-Pico Channel, 38°49′N 28°61′W, depth 360 m, 23 September 2009, zoantharian associated with the antipatharian *Leiopathes* sp. (Anthozoa, family Leiopathidae),

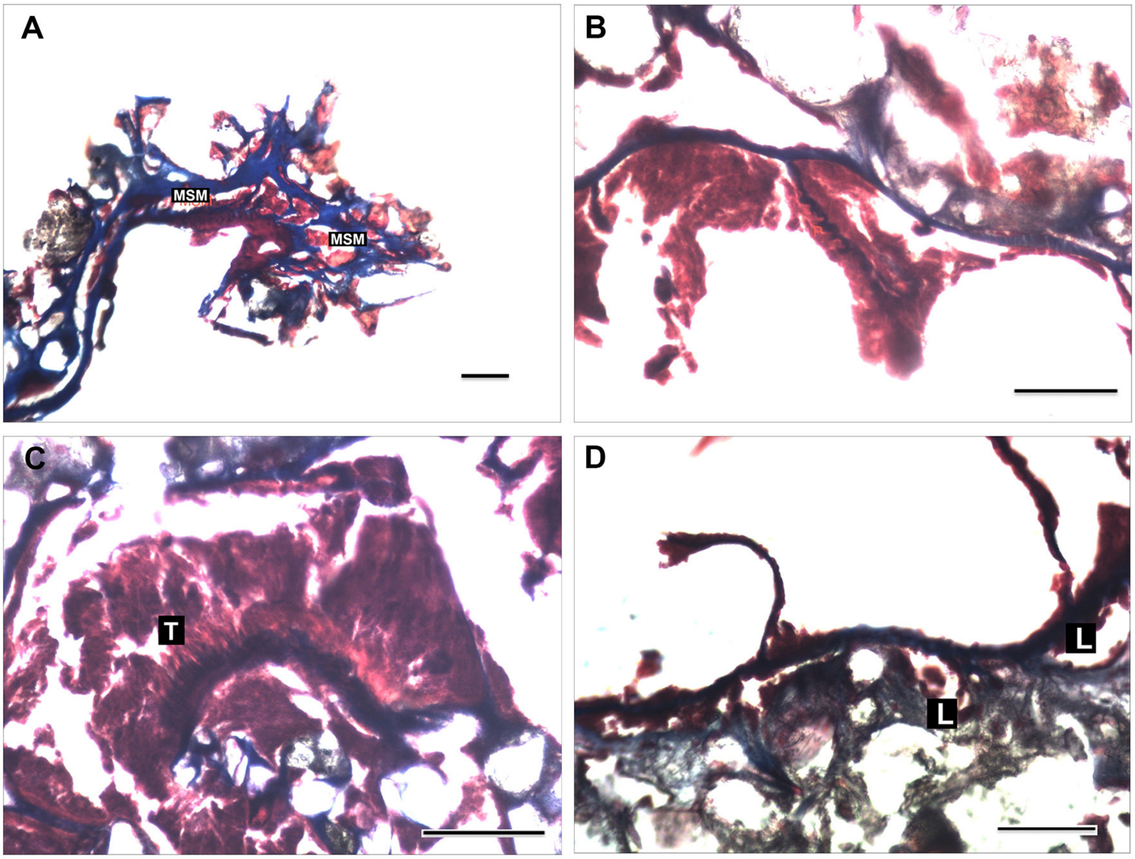

FIGURE 6 | Histological sections of *Epizoanthus martinsae* sp. n. (A) mesogloeal sphincter muscle (MSM); **(B)** retractor pennons (P) of the mesenteries; **(C)** tentacles musculature (T); **(D)** structure of the mesogloeal body wall showing enlarged lacunae with endodermic content. Longitudinal section of contracted polyps at the region of the capitulum is shown in **(A)**. Cross sections at the region of the mesenteries are shown in **(B,D)**, and of the tentacles **(C)**. Scale bar: 100 μm.

fragment of approximately of 10 polyps (formalin-fixed) and 6 polyps (ethanol-fixed), DOP-3609.

Sequences: see **Supplementary Table 1**.

Description

Diagnosis

Colonial zoantharian found at the surface of the black coral *Leiopathes* sp. (**Figures 2K,L**). Polyps with encrustations in the ectoderm and grouped by a thin coenenchyme forming a compact unit. It has a very short mesogloeal sphincter. Mesogloeal of the body wall has enlarged lacunae. Presence of large holotrichs in all tissues and special spirulae in the body wall.

External Anatomy

On live specimens, polyps are brown with two rows of transparent tentacles (**Figure 2L**). In preserved samples, dark brown polyps are connected by a thin coenenchyme growing over the *Leiopathes* sp. axis. Living polyps have an oral disc 4–5 mm in diameter, column diameter 3–4 mm, height 6–8 mm; column cylindrical. In preserved specimens, contracted polyps are 3–4 mm in diameter and extend to 5–7 mm above the coenenchyme; column is cylindrical (**Figure 2L**). There are two rows of 14–17 transparent tentacles (smaller, immature polyps can have fewer), with circular knobs at tips; length of tentacles is the same length than the expanded oral disk diameter. Pharynx is oval and whitish. Column is dark brown due to heavy encrustations of sand grains. Encrustations are more abundant in the ectoderm, and extend into the mesoglea.

Internal Anatomy

Mesenteries are in a macrocnemic arrangement, distributed in 12 pairs of complete mesenteries, 12 pairs of incomplete mesenteries and several pairs of very low development mesenteries; we counted up to 31 mesenteries. There is a very short mesogleal sphincter (**Figure 6A**). Musculature poorly developed; retractor muscle present, with some pennons well arranged in the mesoglea (**Figure 6B**); the parietobasilar muscle is undistinguished. Ectodermal tentacles musculature is well developed and arranged in numerous small pennons (**Figure 6C**). The mesogloea of the body wall presents enlarged lacunae with endodermic contents (**Figure 6D**). There was no indication of the presence of zooxanthellae.

Cnidae

High diversity of nematocysts is characteristic in this species, the presence of large holotrichs (holotrich 1) in all the tissues and the presence of small special b-mastigophores in the body wall being the key characters regarding the cnidae (**Table 1** and **Figure 4**).

Biological Interactions

Found on skeletons of the black coral *Leiopathes* sp. There is no evidence of parasitic behavior. In aquaria, it was found to colonize rocks and aquarium walls.

Distribution

So far it has only been reported in the Azores region, Northeast Atlantic, at water depths of 360 m with ocean temperatures ranging from 13°C to 15°C.

Phylogenetic Results

The sequence alignment was 2,067 bp long: 1,114 bp for 16S rDNA, 686 bp for 12S rDNA and 267 bp for COI. Indel coding with SIC approach resulted in an additional 78 binary characters for 12S rDNA and 36 for 16S rDNA that were all added to the existing alignment. After GBlock editing the 16S rDNA alignment shrunk to 50% off its original length (560 bp) and the 12S to 92% (636 bp).

The BI and ML trees had well-supported nodes corresponding to most of the recognized genera (**Table 2**). One of the four new species of zoantharians reported for the Azores was found to belong to the family Epizoanthidae and three species to the family Parazoanthidae (**Figure 7**, **Supplementary Figures 1**, **2**). Within the genus *Epizoanthus,* specimen DOP-3609 from Faial-Pico Channel classified as *Epizoanthus martinsae* sp. n. was nested within a clade together with the genetically similar *Epizoanthus arenaceus* (Delle Chiaje, 1823), *Epizoanthus vagus* Herberts, 1972, and *Epizoanthus paxi* Abel, 1955.

Inside Parazoanthidae, the first split corresponded to the separation of *Isozoanthus* Carlgren in Chun, 1903 from the rest of the family representatives. Within Parazoanthidae, all octocoral-associated zoantharians grouped together in a well-supported monophyletic group distinct of *Parazoanthus* Haddon and Shackleton, 1891, *Umimayanthus* and *Antipathozoanthus* species. This clade includes representatives of the genus *Savalia* Nardo, 1844, *Kauluzoanthus* Sinniger Ocaña & Baco, 2013, *Bullagummizoanthus* Sinniger Ocaña & Baco, 2013, *Kulamanamana* Sinniger Ocaña & Baco, 2013, *Corallizoanthus* Reimer in Reimer Nonaka Sinniger & Iwase, 2008, *Hurlizoanthus* Sinniger Ocaña & Baco, 2013, and *Zibrowius* Sinniger Ocaña & Baco, 2013. Seven of our specimens fell into the *Zibrowius* clade, where they grouped into two lineages according to the SIC and NoSIC alignments. One of these lineages (specimens: DOP-3242, DOP-804, Si-ACH-P4-1, Si-ACH-P4-2) is classified as *Zibrowius primnoidus* comb. nov., a recently described species from the Azores that is associated with the gorgonian *Callogorgia verticillata* and previously placed into the genus *Isozoanthus* (Carreiro-Silva et al., 2011; for the correct generic placement see also the Systematics results section and the Discussion section), while the second lineage (specimens: DOP-3049, 3050, 5332) is classified as the new species *Zibrowius alberti* sp. n., closely related to *Zibrowius ammophilus* Sinniger Ocaña & Baco, 2013. The specimen DOP-3242 of Z. *primnoidu*s differed from its conspecific by a single nucleotide substitution in the 12S rDNA fragment, while the COI and 16S were identical. The genus *Isozoanthus* represented by the type species *Isozoanthus giganteus* Carlgren in Chun, 1903 (12S, 16S) and *Isozoanthus sulcatus* Gosse, 1859 (COI) concatenated in a single sequence (**Supplementary Table 1**) represented by a well-defined branch formed after a deep first split within Parazoanthidae. This branch is well separated from *Z. primnoidus*.

TABLE 2 | Bayesian posterior probabilities for selected clades inferred from phylogenetic trees reconstructed from different alignments: SIC alignment, indel events were coded as binary characters and appended to the existing alignment; NoSIC alignment, indel events were not additional coded and included to the existing alignment; GBlock alignment, potentially poorly aligned positions were excluded altogether from the alignment.

Clades	SIC	NoSIC	GBlock
Zibrowius	1.00	1.00	1.00
Hurlizoanthus	1.00	1.00	0.98
Z+Hu	0.97	0.99	0.97
C+Ku	0.99	0.99	0.99
Z+Hu+C+Ku	0.95	0.96	0.91
Z+Hu+C+Ku+Bu	0.93	0.99	0.97
Z+Hu+C+Ku+Bu+Ka	0.86	/	/
Z+Hu+C+Ku+Bu+Ka+S	0.98	0.97	0.98
Hy	1.00	1.00	1.00
Hy+Be	0.98	0.96	/
PSS+Hy+Be	0.92	0.90	0.84*
Ps+Pd	0.83	0.89	1.00
Ps+Pd+PSS+Hy+Be	0.83	/	/
Umimayanthus	0.96	/	/
Antipathozoanthus	1.00	1.00	1.00
Pdae&Hdae (excluding I)	1.00	1.00	1.00
Pdae&Hdae (including I)	1.00	1.00	1.00
Epizoanthidae	1.00	1.00	1.00

The presented clades were selected from the phylogenetic tree in ***Figure 7****: Z, Zibrowius; Hu, Hurlizoanthus; C, Corallizoanthus tsukaharai; Ku, Kulamanamana haumeaae; Bu, Bullagummizoathus emilyacardiaarum; Ka, Kauluzoanthus kerbyii; S, Savalia; Hy, Hydrozoanthus; Be, Bergia puertoricense; PSS, Parazoanthus sensu stricto; Ps, Parazoanthus swiftii; Pd, Parazoanthus darwini; Pdae, Parazoanthidae; Hde, Hydrozoanthidae; I, Isozoanthus. According to the GBlock alignment, Be formed a poorly supported clade with three representatives of Umimayanthus (****Supplementary Figure 2****), thus the clade PSS+Hy was observed instead of the clade PSS+Hy+Be (*).*

Phylogenetic analyses also indicate that the zoantharian associated with the primnoid octocoral *Candidella imbricata* constitutes a new species within the recently described genus *Hurlizoanthus* of the family Parazoanthidae (Sinniger et al., 2013). *Hurlizoanthus hirondelleae* sp. n. is represented by one specimen (DOP-4098) collected in Voador Seamount.

While the support for and within most of the other genera and lineages that are also analyzed *(Antipathozoanthu*s, *Hydrozoanthus, Bergia, Parazoanthu*s *sensu stricto* and *"Parazoanthus darwini* Reimer & Fujii, 2010 + *Parazoanthus swiftii* Duchassaing de Fonbressin and Michelotti, 1860") is good in all the phylogenetic trees, the relationships between them could not always be well resolved. Nevertheless, specimen (DOP-4090) from the Voador Seamount clearly falls within the *Parazoanthus* s. str. clade and represents a

FIGURE 7 | Bayesian phylogenetic tree obtained using concatenated sequences (COI, 16S, and 12S) and indel events coded as binary characters. Values at branches represent Bayesian posterior probabilities and bootstrap values obtained for the Maximum Likelihood tree. Nodes where Bayesian posterior probability was under 0.50 are collapsed, while nodes with only Bayesian support and no bootstrap values were not inferred with the Maximum Likelihood approach. Samples collected in this study are listed in brackets next to the species names, while (*) marks the sequences collected from the NCBI database; list of species with associated Genbank accession numbers is available in **Supplementary Table 1**.

new species, *Parazoanthus aliceae* sp. n., found in association with the stylasterid *Errina dabneyi.* Furthermore, the genus *Umimayanthus* was well-supported only in the BI tree constructed from the SIC alignment.

DISCUSSION

The Azores are considered a CWC biodiversity hotspot, particularly with regards to the sub-class Octocorallia (e.g., soft corals and gorgonians) (Braga-Henriques et al., 2013). Comparably less is known about the epifaunal organisms associated to octocorals and other coral taxa and the biological interactions (symbiosis, competition, predation) between these two groups of organisms (Buhl-Mortensen et al., 2010). Within this context, the present study contributes to increase the knowledge on the diversity of the zoantharians associated with CWCs, with the description of four new zoantharian species, and the nature of their association to their coral host. Similar to the pattern of increased biodiversity in azooxanthellate corals species in deeper waters (Cairns, 2007; Watling et al., 2011), the diversity of zoantharian species appears to follow the same trend of increased diversity in deeper areas, suggesting there is undescribed diversity at the species level among epifaunal organisms in the deep sea. This diversity may be under-evaluated when descriptions are based on morphology only. Indeed, genetic tools can help to distinguish between cryptic species that are species with similar morphologies but strong genetic differences.

Phylogenetic reconstruction using three mitochondrial DNA markers (COI, 16S, and 12S) provided well-supported trees resolving the relationship within Parazoanthidae and Epizoanthidae families (**Figure 7**), with topology supported by ecological and morphological characteristics (Sinniger et al., 2005, 2010, 2013; Reimer et al., 2008a; Montenegro et al., 2015b). These relationships were best resolved by concatenating the three markers and using phylogenetic information carried by indel events (BI). This type of information was shown to be very important for zoantharian phylogeny as it allows distinguishing among some genera (Sinniger et al., 2005, 2010). Strong phylogenetic signals were provided by the variable regions within the 16S and 12S fragments, portions of the genes reported in Sinniger et al. (2005) as informative at intergeneric level. Furthermore, our phylogeny confirms: (1) agreement with the re-classification and erection of the genus *Hydrozoanthus* as proposed by Sinniger et al. (2010); (2) agreement with the re-classification and construction of the genus *Umimayanthus* as proposed by Montenegro et al. (2015b); (3) agreement with the resurrection of the genus *Bergia* as proposed by Montenegro et al. (2015a); (4) uniqueness of the *Parazoanthus swiftii* and *Parazoanthus darwini* clade, which forms a basal separation in regard to the *Parazoanthus* s. str. clade in the BI tree reconstructed from the SIC alignment; and (5) strong support for the *Isozoanthus* lineage independent from the rest of the Parazoanthidae, as pointed out by Sinniger et al. (2010, 2013).

Parazoanthidae

The genus *Zibrowius*, recently described from Hawaii (Sinniger et al., 2013), also includes *Zibrowius alberti* sp.n. and *Zibrowius primnoidus* comb. nov. (Carreiro-Silva et al., 2011). The re-classification of the latter species, which was originally classified as *Isozoanthus*, is in agreement with the revised morphology, anatomy and molecular phylogeny. This re-classification is supported by the association with a primnoid octocoral (as is also the case with *Hurlizoanthus hirondelleae* sp. n.), marked morphological differences between this species and other *Isozoanthus* (large ectodermal nematocysts and the mesogleal structure of the body wall) and the phylogenetic reconstruction, which clearly positions this species within the *Zibrowius* genus. The identification of *Z. primnoidus* from Cap Sicié canyon (off Toulon, France) found in association with the octocoral *Callogorgia verticillata*, also confirmed the presence of this species in the Mediterranean, thus expanding its known geographic range. Unreliability of the morphological characters traditionally used to distinguish *Isozoanthus* (i.e., the lack or absence of the mesogloeal ring sinus system) from other parazoanthids was also shown to be unreliable in the case of *Hydrozoanthus antumbrosus* (Swain, 2009a). The latter is a symbiotic zoantharian which was first described as belonging to the genus *Isozoanthus* but it was more related to *Parazoanthus* s. str. according to molecular data (Swain, 2009a) and was later transfer to a newly erected genus *Hydrozoanthus* (Sinniger et al., 2010). In an effort to integrate modern molecular data with traditional morphological research, Swain et al. (2016) reviewed and identified the morphological characters most useful to systematics in Zoanthidea by mapping these traits onto the molecular phylogeny of the group. These authors identified traditionally targeted (fifth mesenteries, marginal muscle arrangement, encircling sinus) and novel (fissure morphology, basal canals of the mesenteries) morphological features, as the most important characters necessary for reunification and revision of Zoanthidea systematics. Useful morphological characters identified for the genus *Isozoanthus* included fissured capitulum and hypertrophic retractor muscles of the microdirectives, which should be targeted in future studies. In addition, the characterization of the cnidome in *Isozoanthus* could also aid in the correct identification of the genus.

The newly described zoantharian *Zibrowius alberti* sp. n. was found associated with the octocorals *Paracalyptrophora josephinae* and *Dentomuricea* aff. *meteor* and it presents unique mesogleal and cnidom features, such as mesogloea with a large number of lacunae with endodermic content and lacunae system, and the presence of large holotrichs in the body wall and p-mastigophores with a well-marked filament. Molecular data indicated that this species is more closely related to *Zibrowius ammophilus* although in its appearance (polyp size, color, and presence of particles in the body wall) it is more similar to *Z. primnoidus*.

The genus *Hurlizoanthus* is characterized by zoantharians associated with the primnoid octocorals. Adding *Hurlizoanthus hirondelleae* sp. n. has consolidated its monophyly, despite being in contrast with the recommendation of Sinniger et al. (2013), where merging *Hurlizoanthus parishi* Sinniger, Ocaña & Baco, 2013 and *Z. primnoidus* (previously *Isozoanthus primnoidus*) in a single genus was suggested based on their morphology and ecology. Furthermore, the color of *H. parrishi* and *H. hirondelleae* sp. n. polyps are different from *Zibrowius* species (white to light pink vs. orange to brownish, respectively) and *Hurlizoanthus* holds a thin layer of sand particles on the ectoderm (or not at all) in comparison to heavy encrustations present in *Zibrowius*. In the original description of the genus *Hurlizoanthus* the diagnostic character was the association with primnoid corals. This feature is no longer unique as it is also valid for the genus *Zibrowius*, therefore it is now recommended to use the degree of encrustation and characteristic insertion/deletion pattern in the 16S V5 region (Sinniger et al., 2013) as discriminant characters between these two genera.

According to the most recently accepted definition of the genus *Parazoanthus* (Low et al., 2016), the genus includes zoantharians often associated with sponges but not Hydrozoa and lacking skeletal secretion. However, the new species *Parazoanthus aliceae* sp. n., observed growing on the hydrocoral *Errina dabneyi* (Hydrozoa, family Stylasteridae), falls into the clade *Parazoanthus* s. str. (a.k.a. clade A, in Sinniger et al., 2010) together with *Parazoanthus elongatus* McMurrich, 1904, *Parazoanthus juan-fernandezii* Carlgren, 1922, *Parazoanthus capensis* Duerden, 1907, *Parazoanthus anguicomus* Norman, 1869, and *Parazoanthus axinellae* (Schmidt, 1862), species associated to sponges and rocks (Sinniger et al., 2010). The reason for this apparent incongruity may be related to the fact that *P. aliceae* sp. n. was found to colonize dead portions of *E. dabneyi* skeleton. Thus *P. aliceae* sp. n. appears to use the hydrocoral solely as substrata, instead of forming a symbiotic association with hydrozoans as described by Sinniger et al. (2005), Swain (2009b) and Sinniger et al. (2005), but this may need further examination. Indeed, *P. aliceae* sp. n. differs greatly from its closest relatives in terms of morphology to such a degree that one could suggest placing it in a new genus. However, molecular phylogenetics and especially short patristic distances clearly indicate a very close relationship with *P. juan-fernandezii* and *P. elongatus* (**Figure 7**). Such a discrepancy between molecular and morphological data for the genus *Parazoanthus* further emphasizes the need to identify and standardize the morphological characters used in Zoantharia systematics (Swain et al., 2016). The new species presents a large variety of nematocysts as the main character, (including several b-mastigophore categories absent from the other species in the same clade) large holotrichs in all tissues and at least two different categories of homotrich in all the analyzed tissues. In addition, *P. elongatus* and *P. juan-fernandezii* are reported at shallow depths (10–40 m) in the Pacific, while similar depths are reported for *P. axinellae, P. capensis,* and *P. swiftii* in the Mediterranean Sea, Indian and Atlantic Oceans. *P. anguicomus* is a North Atlantic species growing on sponges and other substrata (stones, worm tubes, coral debris) at depths between 20 and 400 m (see Manuel, 1981). However, it differs from *P. aliceae* sp. n. by having two categories of holotrichs in its body wall—one larger and the other broader (40–53 × 19–25 μm; 23–35 × 13–19 μm, length × width), and by having more encrustations in the ectoderm.

There are also other deep-sea *Parazoanthus* species for which sequences are not yet available, but which could possibly belong to this *Parazoanthus* s. str. clade. One such species is *Parazoanthus haddoni* Carlgren, 1913, a zoantharian that grows on sponges and presents larger holotrichs (41–46 × 17–18 μm length × width) in the body wall in comparison with *P. aliceae* sp. n., which has developed two categories of smaller holotrichs in the same tissue (25–30 × 10–15 μm; 19–23 × 7–10 μm length × width) but also other cnidae categories. Even though cnidae show great promise for taxonomic delimitation, they should be used with caution as some types of cnidae found in *P. aliceae* sp. n. were also reported from *Antipathozoanthus macaronesicus* (Ocaña and Brito, 2004). However, the latter grows on hydroids (Ocaña et al., 2007) and it was never found on hydrocorals.

There has been continuous effort with the aim of resolving the paraphyly of *Parazoanthus* with the description of new genera: *Antipathozoanthus*, *Hydrozoanthus*, *Bergia,* and *Umimayanthus* (Sinniger et al., 2010; Montenegro et al., 2015a,b), and the discovery of new species is providing stronger support to the structure of the groupings. In our phylogenetic reconstruction there is a monophyletic clade (also observed by Montenegro et al., 2015b) formed by *P. swiftii* and *P. darwini*, a basal cluster of the *Parazoanthus* s. str. clade. This clade is well supported by the molecular data, but the morphology needs further investigation before proper taxonomic reassessment can be conducted for this clade. However, according to the literature (Reimer and Fujii, 2010), *P. swiftii* and *P. darwini* share similarities in both polyp and coenenchyme color but *P. swiftii* has shorter and fewer tentacles; and while *P. darwini* presents special spirulae (not holotrich sensu Reimer and Fujii, 2010) no detailed information on the morphology of cnidae of *P. swiftii* is available. In addition, *P. swiftii* differs from *P. darwini* by being found more often associated with sponges, while *P. darwini* can sometimes cover rock surfaces. Moreover, these species occur in geographic distinct areas (*P. swiftii* in the Caribbean and *P. darwini* in the Galapagos).

From all the specimens' sequences included into the phylogenetic reconstruction, placement of representatives belonging to *Umimayanthus* varied the most when comparing phylogenetic trees built from the different alignments. While all the representatives from these genera formed a well-supported clade according to the SIC alignment (0.96 posterior probability), their monophyly was not supported according to the NoSIC or the GBlock alignment (**Supplementary Figures 1**, **2**). As the formation of the genus *Umimayanthus* was mostly based on the presence of highly conservative and unique indels in the V5 region (Montenegro et al., 2015b) such discrepancies are not unexpected. Namely, the SIC alignment also included indel events coded as binary characters, the NoSIC alignment did not utilize phylogenetic information carried by the indel events in such a way, while the Gblock alignment had such potentially poorly aligned positions excluded altogether.

The zoantharian *Bergia puertoricense* (West, 1979) (formerly known as *Parazoanthus* clade C sensu Sinniger et al., 2010) forms a well-defined lineage and stands out as a sister species to the *Hydrozoanthus* clade. The genus *Hydrozoanthus* was described on the basis of substrate specificity and characteristic patterns in DNA sequences (specific insertions and deletions in the 16S rDNA, especially in the V5 region as defined in Sinniger et al., 2005, 2010). However, our phylogenetic reconstructions of all three alignments (SIC, NoSIC, and Gblock, **Table 2**) clearly indicate that this genus is well-nested within the Parazoanthidae at least according to the phylogeny of mitochondrial DNA. While limited support for such positioning also comes from the Gblocks alignment (0.84 posterior probabilities; **Table 2**) which excludes poorly aligned positions (16S rDNA alignment was shrunk to only 50% off its original length) such positioning of the *Hydrozoanthus* is not supported by the phylogenetic reconstruction based on COI, ITS, and 16S rDNA in the original description of this genus (Sinniger et al., 2010). However, reconstruction of higher level phylogeny within Zoantharia is beyond the scope of this study and should also include representatives from other families accompanied with a detailed revision of their morphology and anatomy. Furthermore, to resolve the relationships within Parazoanthidae and to identify true paraphylies future efforts should be focused on establishing the correct species tree using a multilocus approach with a multispecies coalescent model and not just relying on mtDNA and limited number of nuclear loci.

Epizoanthidae

The zoantharian *Epizoanthus martinsae* sp. n. growing on portions of dead skeletons of black coral *Leiopathes* sp. clustered as a sister species of *Epizoanthus arenaceus*, *Epizoanthus paxi* and *Epizoanthus vagus*, which are zoantharians that form no specific relationship with living organisms, and are commonly found attached to rocky bottoms and gastropod shells (Costello et al., 2001). *E. arenaceus* is morphologically distinct from these species by the presence of a strong sphincter and, among other less important cnidome differences, the absence of an extra category of wide b-mastigophores in the tentacles and the body wall (see Herberts, 1972). *E. paxi* is quite different from *E. martinsae* sp. n. by the presence of strong sphincter and smaller holotrichs in its tissues, especially in the tentacles (see Pax and Müller, 1962; Gili et al., 1987). *E. vagus* presents an extended sphincter along the column and disposed in the center of the mesoglea, meanwhile *E. martinsae's* sphincter is shorter, covering almost all the mesogloea width. *E. vagus* has smaller holotrichs in the tentacles and pharynx than those present in *E. martinsae* sp. n. and does not have two or three different b-mastigophore categories in the tissues (see Herberts, 1972).

Nature of the Association between Zoantharians and Their Coral Hosts

Substrate specificity corroborates the structure of the tree associating a unique type of host (or typology of substrate) to each of the monophyletic clade of zoantharians: antipatharians to *Antipathozoanthus*, sponges to *Umimayanthus*, hydrozoans to *Hydrozoanthus*, octocorals to the large clade housing *Zibrowius*, *Hurlizoanthus*, *Corallizoanthus*, *Kulamanamana*, *Bullagummizoanthus*, *Kauluzoanthus,* and *Savalia* (Sinniger et al., 2005, 2010, 2013; Reimer et al., 2008a; Montenegro et al., 2015b). In contrast, species within the genus *Epizoanthus* do not appear to form monophyletic groups according to the type of substrate used, being often associated with gastropod shells (regularly inhabited by pagurid crustaceans), tube worms, stalks of glass sponges or living on rocks or dead organisms (e.g., Reimer et al., 2010a; Kise and Reimer, 2016).

The nature of the symbiotic association between zoantharians and their hosts varies along the mutualism-parasitism continuum. While the association between zoantharians and hydrozoans is often thought to be commensal or even potentially mutualistic (e.g., Swain, 2009a,b; Di Camillo et al., 2010), zoantharians associated with gorgonians and black corals are mostly considered as parasitic (Ocaña and Brito, 2004; Reimer and Fujii, 2010; Sinniger et al., 2010, 2013; Carreiro-Silva et al., 2011; Bo et al., 2012). In many cases, coral colonization by zoantharians may result in the complete death of the host. This is the case of the zoantharians *Antipathozoanthus* cf. *hickmani* Reimer & Fujii, 2010, and *Terrazoanthus onoi* Reimer & Fujii, 2010 that colonizes the black corals *Myriopathes panamensis* (Verrill, 1869) and *Antipathes galapagensis* Deichmann, 1941 in Ecuador in the Pacific Ocean (Bo et al., 2012). Reaching the organic axis of the host for mechanical support is the final colonization effect for most parasitic zoantharians, benefiting the zoantharians by raising them well above the substratum into faster flowing water that can be filtered, while avoiding the investment of energy to build their own skeleton (Ocaña et al., 1995; Ocaña and Brito, 2004). The parasitic behavior of the zoantharian *Savalia savaglia* (Bertoloni, 1819) toward their host octocorals (*Paramuricea clavata*, *Eunicella* spp.) represents an extreme case of parasitism (Ocaña and Brito, 2004). In this case, when the host is completely engulfed by the zoantharian, *S. savaglia* becomes able to produce a hard layered proteinaceous skeleton deposited on the host skeleton that can reach large sizes (up to 2 m high, with a main trunk diameter up to 14 cm; Bell, 1891) and attain 2,700 years of age (Roark et al., 2006), becoming itself an important component of coral gardens where it provides structural habitat for a large number of associated fauna species (Cerrano et al., 2010).

The symbiotic association between zoantharians and octocorals observed in the present study and reported in Carreiro-Silva et al. (2011) for *Zibrowius primnoidus* (previously known as *Isozoanthus. primnoidus*) and *Callogorgia verticillata,* suggests parasitic relationships with their hosts. Support for a parasitic behavior is based on the following observations: (1) zoantharians covering gorgonian polyps and coenenchyme damaging the host tissue and forcing the gorgonian polyps to live only on the axis; and (2) incorporation of gorgonian sclerites in the zoantharian tissue (**Figure 3**, see also Figure 3 in Carreiro-Silva et al., 2011). Therefore, these observations suggest that zoantharians progressively eliminate gorgonian tissue, keeping the gorgonian axis as support, while coral sclerites are used for protection, although the complete overgrowth and death of the octocoral host was never observed. Nevertheless, observations made in aquaria confirm that these zoantharians are able to survive in the absence of their coral host, feeding on particles in the water column.

In contrast, zoantharians associated with the antipatharian *Leiopathes* sp. and the hydrocoral *Errina dabneyi* reported in the present study appear to use the coral host only as support, often colonizing dead portions of their skeleton, with no visible damage to the host tissue.

A similar parasitic relationship between a zoantharian and a deep-sea gorgonian has been described for *Epizoanthus* sp. and the primnoid octocoral *Primnoa resedaeformis* (Gunnerus, 1763) in the Northeast Channel (Buhl-Mortensen and Mortensen, 2005; Mortensen et al., 2005). Those authors observed what they classified as *Epizoanthus* sp. gradually overgrowing and killing *P. resedaeformis*. Mortensen et al. (2005) suggested that the degree of incidence of this zoantharian is related to gorgonian damage by fishing, with *Epizoanthus* sp. colonizing tissue-abraded areas and taking over large parts of the gorgonian skeleton.

We found the greatest incidence of zoantharians to occur on *C. verticillata* and *Paracalyptrophora josephinae*, two octocorals that are most often captured or damaged during long line fishing operations in the Azores (Sampaio et al., 2012). However, based on our data, we cannot determine whether a similar relationship exists between gorgonian damage caused by fishing and the degree of colonization by zoantharians. All octocoral specimens examined in this study were collected within fishing grounds, so we have no comparison with areas closed to fishing. Future studies comparing number of colonized *C. verticillata* colonies inside and outside fishing areas will help to clarify the effect of fisheries on the degree of colonization by zoantharians.

CONCLUSIONS

Our study contributes to a better understanding of the zoantharian diversity associated with CWCs in deep-sea environments (see also Carreiro-Silva et al., 2011; Sinniger et al., 2013), highlighting the need for further research on the diversity of anthozoans and other epizoic groups of species associated with deep-sea ecosystems. Our phylogenetic reconstruction confirmed the relationship between zoantharian taxonomy and the type of substrate selected for settlement (Sinniger et al., 2005, 2010, 2013; Reimer et al., 2008a; Montenegro et al., 2015b) and suggests that the different epizoic clades described here have long evolutionary histories in association with their hosts. The phylogenic tree identified four well-supported monophyletic groups within the family Parazoanthidae, one representing all octocorals associated with zoantharians, one representing zoantharians associated with living colonies of antipatharians (genus *Antipathozoanthus*), two representing zoantharians associated with sponges (genus *Umimayanthus,* and genera *Parazoanthus* and *Bergia*) and one with hydrozoans *(*Hydrozoanthidae, *Hydrozoanthus*). Furthermore, our phylogenetic reconstructions confirmed the conclusion of several other authors that *Isozoanthus* (zoantharians associated with non-living substrates) forms a well-defined lineage that should not be included within the Parazoanthidae (Sinniger et al., 2010, 2013).

Understanding the speciation processes and distribution of these zoantharians will contribute to a better knowledge of the past oceanographic patterns in the worldwide oceans as well as contributing to developing efficient impact assessment methods in relation to deep-sea resource exploitation. In addition, given the parasitic behavior displayed by octocoral-associated zoantharians, a better knowledge on the effect of fishing and climate change on the severity of parasitic association is required to predict changes in octocoral populations in the future.

Because of difficult access, the deep-sea remains one of the least explored regions of the oceans (Mora et al., 2011), thus it is likely that many other species of zoantharians and other epizoic organisms in these environments still remain to be discovered.

ETHICS STATEMENT

The study was exempt from ethics committee because it used invertebrate organisms that are not endangered species.

AUTHOR CONTRIBUTIONS

Conceived and designed the study: MCS, SS. Sampling: MCS, ÍS, MF. Histological and morphological examinations: OO, MCS, ÍS. Molecular analyses: SS, DS. External morphology: MC, OO, ÍS. Analyzed the data: MCS, OO, SS, DS, ÍS, MF. Contributed reagents/materials/analysis tools: MCS, FP, OO, SS. Wrote the paper: MCS with contribution from OO, SS, DS, MF, FP, ÍS.

ACKNOWLEDGMENTS

This study was supported by the European Union's Seventh Framework Programme (FP7/2007-2013) through a Marie-Curie IRG Fellowship to MCS (CoralChange, project no 231109), project CoralFISH (FP7 ENV/2007/1/21314), the Portuguese funded project CORAZON (PTDC/MAR/72169/2006) and CONDOR project [supported by a grant from Iceland, Liechtenstein, Norway through the EEA Financial Mechanism (PT0040/2008)]. This work is a contribution to the ATLAS project and has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement no. 678760. The paper reflects the authors' views and the European Union is not responsible for any use that may be made of the information it contains. MCS was supported by an invited scientist grant by Fundação para a Ciência e a Tecnologia (FCT) through the strategic project (FCT/UID/MAR/04292/2013) granted to MARE. ÍS was supported by an FCT PhD grant (SFRH/BD/101113/2014). The authors wish to thank the monitoring programme ARQDAÇO funded by the Regional Government of the Azores and DEECON project (ESF proposal No 06-EuroDEEP-FP-008 and SFRH-EuroDEEP/0002/2007), for providing specimens. The authors are also grateful to Ricardo Medeiros for map elaboration, Rodrigo Sá da Bandeira and Maria Rakka for help with figures elaboration and Domitilia Rosa, Valentina Matos, and Andreia Braga-Henriques for their help with the histological techniques. The Rebikoff-Niggeler Foundation is gratefully acknowledged for their *in situ* photographs and collection of zoantharian live specimens taken within the CORAZON project. Special thanks go to Lea-Anne Henry for her precious help proofreading English language and grammar, and Bert Hoeksema, Kei Matsuyama, and Max Wisshak for helping with nomenclature questions.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2017.00088/full#supplementary-material

Supplementary Figure 1 | Bayesian phylogenetic tree obtained using concatenated sequences (COI, 16S, and 12S) and no indel coding approach (NoSIC alignment). Values at branches represent Bayesian posterior probabilities. Nodes where Bayesian posterior probability was under 0.50 are collapsed. Samples collected in this study are listed in brackets next to the species names, while (∗) marks the sequences collected from the NCBI database; list of species with associated Genbank accession numbers is available in **Supplementary Table 1**.

Supplementary Figure 2 | Bayesian phylogenetic tree obtained using strict alignment of concatenated sequences (COI, 16S, and 12S) edited by Gblock (Gblock alignment). Values at branches represent Bayesian posterior probabilities. Nodes where Bayesian posterior probability was under 0.50 are collapsed. Samples collected in this study are listed in brackets next to the species names, while (∗) marks the sequences collected from the NCBI database; list of species with associated Genbank accession numbers is available in **Supplementary Table 1**.

Supplementary Table 1 | List of species with associated genbank accession number for each of the markers used to build the phylogenetic trees.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 06 November 2017
doi: 10.3389/fmars.2017.00354

Review of the Diversity, Ecology, and Conservation of Elasmobranchs in the Azores Region, Mid-North Atlantic

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A vulnerable species group, such as, the elasmobranchs, in a data-deficient context presents a complicated management problem. Evidence suggests that the Azores islands, a remote archipelago on the Mid-Atlantic Ridge, serve essential functions in the life-history of species across taxa. The diversity of marine resources within its EEZ are exploited by local to international fleets, and the full extent of fishing pressure can often be underestimated. Although sharks and rays appear to be of minor importance in the fishery, the possibilities of illegal, unreported, and unregulated fishing raises concerns about these threatened species. However, this group has failed to attract management attention, visible in the lack of regional studies focused on biodiversity, ecology, or threats of elasmobranchs. Our work attempts to review and update the information on elasmobranchs of the Azores and identify potential threats, mainly by the local fisheries. We aim to highlight knowledge gaps that require further research and conservation actions. We (1) update the annotated checklist of elasmobranch species, (2) compare species distribution across a biogeographically similar section of the North Atlantic, and (3) analyze the interaction of elasmobranch species with local fisheries. We confirm 61 chondrichthyan species for the Azores (39 sharks, 17 rays, and 5 chimaeras), adding 19 species to the previous annotated checklist of 1997. The Azores elasmobranch species assemblage most resembles Madeira, the neighboring Macaronesian archipelago. Biogeographic affinities between the chosen regions of the North Atlantic are reflected in the taxonomic structure of families. Although underestimated in the local fisheries, elasmobranchs constitute a regular but highly variable portion of total landings. Misreporting and misidentification is perhaps the greatest concern in the local fisheries records, further aggravated by few existing catch regulations for elasmobranchs. Local knowledge indicates that the Azores serves as essential habitat for at least a few species in coastal areas and shallow seamounts, and potentially so for a number of deep-sea elasmobranchs. The intersection of fishery threats and local essential habitat functions around the archipelago warrants greater research effort and studies.

Keywords: Mid-Atlantic Ridge, vulnerable species, Elasmobranchii, annotated species checklist, fisheries, essential fish habitat

OPEN ACCESS

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Specialty section:
This article was submitted to Deep-Sea Environments and Ecology, a section of the journal Frontiers in Marine Science

Received: *07 November 2016*
Accepted: *20 October 2017*
Published: *06 November 2017*

Citation:
Das D and Afonso P (2017) Review of the Diversity, Ecology, and Conservation of Elasmobranchs in the Azores Region, Mid-North Atlantic.
Front. Mar. Sci. 4:354.
doi: 10.3389/fmars.2017.00354

INTRODUCTION

The isolation of oceanic islands from continental masses often creates a unique gathering of species (Sandin et al., 2008; Kier et al., 2009; Kulbicki et al., 2013). Higher productivity regimes that are typically found around oceanic islands result in greater marine biodiversity compared with the surrounding open ocean (Doty and Oguri, 1956; Gove et al., 2016). Like for terrestrial fauna and flora (Patiño et al., 2015), islands can connect marine populations by forming ecological "stepping stones" across ocean basins (Joyeux et al., 2001; Hobbs et al., 2010). They often function as critical stops on the ontogenetic or annual migratory route of species, serving as important breeding (Carr et al., 1974; Olavarría et al., 2007) or feeding (Ashmole and Ashmole, 1967; Engel and Martin, 2009) grounds.

The unique traits of marine ecosystems around oceanic islands render them more vulnerable, deserving superior conservation and management. For instance, the populations and function of predatory species that play an essential role in maintaining ecological balance and ecosystem vitality. The top-down control of lower trophic-level species and ecosystem functions can be seriously disrupted in case of declines in predator populations (Pace et al., 1999). Elasmobranchs (sharks and rays) are a key group of marine predators, suspected to mediate trophic cascades as top or meso- predatory species (Myers et al., 2007; Baum and Worm, 2009; Heithaus et al., 2012). In recent years, these species have attracted increasing scientific concern due to the large declines in their population abundances (FAO, 1999; Baum and Myers, 2004; Ferretti et al., 2008, 2010) and a greater understanding of their ecological importance (Heupel et al., 2014) and high vulnerability to extinction risk (Camhi et al., 2008; García et al., 2008; Dulvy et al., 2014).

The main direct threat to elasmobranch species is fisheries exploitation, leading in some cases to extirpation and shifts in local species assemblages (Ward and Myers, 2005; Sguotti et al., 2016). These species exhibit density-dependent recruitment and K-strategy life history traits (Compagno, 1990; Hoenig and Gruber, 1990; Frisk et al., 2001) expressed in greater longevity, slower maturation, and lower fecundity. This makes them considerably more vulnerable to exploitation pressure than teleost counterparts. Elasmobranch species are often weakly regulated by fisheries management since they have little commercial significance, both in catch volume and monetary value (Bonfil, 1994; Stevens, 2000; Dulvy et al., 2008; Ferretti et al., 2010; Techera and Klein, 2011). Expansion and mechanization of fisheries over the last half-century marked a remarkable increase in fish catches (Swartz et al., 2010), sharks, and rays being no exception (Barker and Schluessel, 2005; Ferretti et al., 2010). Yet, elasmobranch catches and landings are not recorded in detail (Ferretti et al., 2010; Musick and Musick, 2011) obscuring the extent of threat to these species (Stevens, 2000; Dulvy et al., 2014).

The Azores are a group of remote oceanic islands situated on the Mid-Atlantic Ridge surrounded by depths regularly exceeding 1,500 m (Santos et al., 1995). These islands function as essential habitats for a variety of marine life. The dynamic bathymetry around the islands includes distinctive features such as, seamounts and ridges that harbor vulnerable marine ecosystems such as, cold-water coral gardens, hydrothermal vents, and deep-sea sponge aggregations (Abecasis et al., 2015; Pham et al., 2015). Evidence suggests that several charismatic species like marine birds (León et al., 2005), cetaceans (Silva et al., 2014), oceanic elasmobranchs (Afonso et al., 2014; Thorrold et al., 2014; Vandeperre et al., 2014b, 2016; Queiroz et al., 2016), and fishes (Druon et al., 2016) use the archipelago as a feeding, mating, or breeding ground. Large cetaceans (Silva et al., 2014; Tobeña et al., 2016) and fishes (Kohler et al., 1998; Hilborn et al., 2010) alike frequent these waters during their seasonal migrations.

The exclusive economic zone (EEZ) of the archipelago occupies an expansive one million square kilometers, where a 100 nautical miles (NM) buffer from the coast is currently reserved for the regional and national fleet beyond which other European fleets are authorized to operate (European Council, 2003). International and regional legislation also regulate the use of fishing nets in the area (European Council, 2005), banning the use of bottom and pelagic trawls within an area roughly coinciding with the EEZ (European Council, 1995). The local fishery is typically artisanal and essentially composed of small (<15 m) vessels using hooks and lines (longlines, handlines, pole-and-line; Pinho and Menezes, 2009; Carvalho et al., 2011; Morato, 2012). Gillnets and traps are limited to inshore coastal fishes and crustaceans. Despite the cautious nature of the local fishery, foreign pelagic longline vessels from Portuguese mainland and the EU operate unsupervised within the EEZ. These vessels land directly in mainland ports, without reporting Azorean catches to regional authorities (Pham et al., 2013). At the local scale, fishing activity is mostly concentrated around island slopes and seamounts (Pinho and Menezes, 2009), exposing non-target species with higher vulnerability to fisheries pressure (Morato et al., 2006). The true extent of fisheries extraction and its potential impact within the EEZ is thus greatly underestimated.

This situation raises conservation and management concerns for local shark and ray populations that are not always protected by catch regulations but are particularly susceptible owning to their life-history strategies (Afonso et al., 2014). Despite these concerns, a comprehensive overview of the elasmobranch assemblage and current threats, and the importance of this region for their populations has not been attempted, until now. Literature on elasmobranchs from the Azores is limited to a handful of species-specific accounts. Studies on ecology or biodiversity often overlook elasmobranchs as their primary focus. To address this knowledge gap, the current work has three main objectives: first, to provide an updated and annotated checklist of chondrichthyan species from the Azores region; second, to verify the uniqueness of the Azorean elasmobranch assemblage and resolve the biogeographical affinities with other comparable regions in the North Atlantic; and finally, to present an overview of potential vulnerabilities using information from local fisheries, regional extinction risk indices, and local ecological scientific knowledge.

METHODS

Checklist

Using the last complete annotated checklist from the region (Santos et al., 1997) as our starting point, we reviewed the list of Chondrichthyes (Elasmobranchii and Holocephali) found in the Azores EEZ. Additions and deletions were made strictly using primary scientific data, where the species were identified directly by its authors. This included results from experimental fisheries surveys, underwater visual surveys and other published literature describing the biodiversity within the Azores EEZ. The results were compared with the FAO Fisheries Catalogue for the region (Ebert and Stehmann, 2013) as a measure of global knowledge about the region. Clarifications regarding taxonomy and species occurrence were sought from local experts where necessary.

The primary sources used were:

- Scientific fishing surveys using bottom longlines carried out by the Department of Oceanography and Fisheries, University of Azores (DOP/UAz), Horta (Menezes et al., 2006, 2012; Menezes and Giacomello, 2013; Menezes, 2014) around the nine islands and important seamounts in the Azores EEZ;
- The MAR-ECO project by the Census of Marine Life (Fossen et al., 2008; Wenneck et al., 2008), using vertical and bottom longlines deployed within the regional EEZ limits;
- An exploratory fishing survey of orange roughy (*Hoplostethus atlanticus*) in the Azores using trawl fishing (Melo and Menezes, 2002), important for species not caught using longlines;
- Underwater visual census conducted by researchers of the Institute of Marine Research (IMAR—University of the Azores) each year in the shallow-water areas around the islands and offshore seamounts (Afonso et al., 2013; Schmiing et al., 2013; Afonso, unpublished data).

Species were classified into four classes to designate their presumed frequency of occurrence. The different classes were differentiated by color codes as follows:

- Commonly encountered species were designated green—these species have multiple records and no known taxonomic conflicts;
- Species that occur occasionally around the Azores were yellow —they are rarely recorded despite susceptibility to commonly used fishing gears;
- Species with scant records, probably due to observational constraints were orange—these species only appear in fishing surveys using trawl gears (Melo and Menezes, 2002; Kukuev, 2006; Kukuev and Pavlov, 2008) or were captured in gillnets before the fishery was regulated (Azevedo et al., 2003; Fergusson et al., 2008);
- Species with uncertain identification were designated red.

Note on Systematic Arrangement

Elasmobranch taxonomy is a work in progress, with changes in nomenclature almost every year (Weigmann, 2016). Two classification schemes have predominated elasmobranch taxonomy (Naylor et al., 2005; Nelson, 2006). One places batoids (rays) as a sister group of dorsoventrally flattened sharks (sawsharks and angelsharks), which together are placed within the superorder Squalimorphii along with Squaliformes and Hexanchiformes (Compagno et al., 2005). The other, which considers Batoidea separated from the Selachii (all sharks; Naylor et al., 2005) and supported by recent molecular evidence (Heinicke et al., 2009; Naylor et al., 2012) is adopted here (see Weigmann, 2016 for details). Subclass Holocephali was included to provide a complete overview. The sequence of orders and families adopted here follows Nelson et al. (2016).

Elasmobranch Assemblage and Biogeography

The updated species list was then used to analyze the biogeographical relationship of the Azorean elasmobranch assemblage within the North Atlantic. In order to maintain analytical coherence through a broad comparable environmental envelope, we focused our analysis on the section of the Atlantic bounded by the 42°N (northern extent of Azores EEZ) and 26°N (south of the Canary Islands) latitudes, thus including the Macaronesian archipelagos of Madeira and the Canaries, and the continental margins of the Atlantic to the east (Iberian Peninsula) and west (United States east coast). This section of the North Atlantic was assumed to represent the highest potential biogeographic affinity of species present in the Azores. Tropical regions such as, the archipelago of Cape Verde and Caribbean islands were excluded being separate biogeographic regions (Floeter et al., 2008) and owing to the few highly-migratory species shared between these sections of the North Atlantic.

Species lists of the other regions were adapted from regional annotated checklists (Brito et al., 2002; Wirtz et al., 2008; Wirtz, 2011) and recently published literature [Freitas and Biscoito, 2007; Ferreira et al., 2008; Freitas et al., 2011; Kyne et al., 2012 (only species from NWA); Ebert and Stehmann, 2013; Delgado et al., 2017], augmented by local expert knowledge where possible (P. Pascual IEO/Canaries, pers. comm. 2017; M. Freitas OOM/Madeira, pers. comm. 2017). Updated, comprehensive, region-specific annotated checklists were often not available, leading to a certain probability of erroneous species records. However, these were not considered to significantly affect the overall biogeographic pattern.

First, we focused on the elasmobranch species occurring in the Azores and how they are shared with the study areas across the North Atlantic. We added current knowledge on migratory habits of these species (Fowler, 2014) to overlay the observed biogeographic patterns. Next, we built a presence-absence table of all species by region, and analyzed biogeographic similarities using cluster analysis. The dissimilarity matrix was constructed with binary distances, and unweighted agglomerative method (UPGMA) used to build the dendrogram. All calculations were executed in RStudio® software environment using the "base" package. The structure of elasmobranch assemblages divided by family was used to understand which species groups influence similarities and differences between regions.

Possible Threats and Vulnerabilities

To determine threats to elasmobranchs at the regional level, we focused on the landing records of local fisheries; since there is no clear evidence of habitat destruction, pollution, or other factors threatening the local elasmobranch assemblage. The goal was to identify gear types more likely to land elasmobranchs and the species landed by these gears. Analysis of the landing records also provides the opportunity to recognize potential inaccuracies in the registration process itself. Local fisheries began recording elasmobranch landings in greater taxonomic resolution in official statistics since the mid-1990s. Thus, we chose a 19-year period from 1996 until 2014 to analyze how the local fishery interacts with elasmobranchs, using temporally aggregated landing information.

Landing records are collected from the auction houses (*lotas*) or point-of-first sale from all nine islands of the archipelago. It is maintained by Lotaçor SA in collaboration with the Department of Oceanography and Fisheries of the University of the Azores. The dataset used in this study was extracted from the Lotaçor database, structured by year, month, gear type ("*métier*"), and weight landed (kilograms) of each landing within the study period. A subset of this data included the weight of elasmobranch species per landing. Elasmobranchs appeared in the database under their local names with corresponding documentation on scientific names (Lotaçor, 2015).

Having no direct information on catch or effort, we scaled the impact of different métiers using two indicators. The first indicator was the weight of elasmobranchs landed proportional to other species by each métier. The weight of non-elasmobranch species was used as proxy for effort since they are often the target or more lucrative species. Thus, métiers with higher proportional weight landed of elasmobranchs, i.e., weight per unit effort (WPUE), could be preferentially landing these species. The second indicator was the frequency of elasmobranch landings per métier, measured as a percentage of total landings. Using the total number of landings per métier as a proxy for effort, métiers with higher percentage of landings with elasmobranchs, or landings per unit effort (LPUE), would be those more partial to these species.

WPUE was calculated by aggregating the total weight and elasmobranch weight landed by each métier for every month in the study period, separately. The weight of other species was obtained by subtracting weight of elasmobranchs from the total weight, and the ratio obtained for landed weight of elasmobranchs to other species. The arithmetic mean of the ratios was used to reduce the influence of disproportionately large values, and standard deviation used as an indication of variability. Similarly for LPUE values, the total number of landings per métier and the number of landings with elasmobranchs were aggregated to obtain the frequency of elasmobranch landings. All calculations and data analysis was executed in RStudio®.

The métiers were then separated into two categories to facilitate meaningful comparisons. One category featured métiers with higher elasmobranch LPUE (both proportional weight and landing frequency), thus greater tendency to catch and land these species, and a second category for métiers that land less elasmobranchs. The species composition of the two groups was analyzed separately. We used average weight of species per landing to identify species that are landed infrequently but could require greater management attention.

The species landed by the local fisheries were then related to their regional IUCN Red List (Nieto et al., 2015) status as a proxy for potential conservation concern. This analysis was then complemented with an evaluation of information collected opportunistically and mostly available through gray literature or unpublished data on known and putative essential fish habitats (EFH), to preliminarily identify potential areas of greater overlap with fisheries.

RESULTS

Annotated Species Checklist

Our literature search confirmed 61 chondrichthyans from the Azores EEZ (39 sharks, 17 batoids, and 5 chimaeras; **Table 1**), of which four species still require taxonomic clarification. The previous annotated checklist (Santos et al., 1997) included 44 species identified from the Azores. Thus, our study adds 19 species (40%) to that list and removes two species following taxonomic corrections. Six species presumed to commonly occur in the Azores did not feature or were considered uncertain in the earlier checklist. We compiled an annotated checklist of the species that do not appear in the main checklist of Santos et al. (1997), which is presented here. The species for which a declared first record could not be found were marked with an asterisk (*).

Elasmobranch Species Appearing in the Appendix to the Checklist in Santos et al. (1997) that are Confirmed in the Current Checklist

NB: The appendix in Santos et al. (1997) included: (i) species whose occurrence in the Azores needs further confirmation besides the references already found in the literature; (ii) species whose identification criteria are doubtful; (iii) littoral species whose occurrences are presumably exceptional; and/or (iv) species recorded at the outer limits of the Azorean EEZ.

Lamniformes

Alopiidae

Alopias superciliosus Lowe, 1841

Santos et al. (1997) report one specimen of this species recorded from south of the Azores EEZ, which is considered a first record of the species from the region. A 1999 study on shark bycatch from pelagic longline fisheries mentions the presence of this species based on the author's personal observations (Simões, 1999). The occurrence of this species in the region has since been confirmed by experimental pelagic longlines (Martins, 2013), and observer logbook data from commercial longlines operating in the region (Fernandez-Carvalho et al., 2015).

Frequency of occurrence: Green (common)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): Yes

Depth range (Ebert and Stehmann, 2013): 300-500 m (day); 10-100 m (night)

Local gear susceptibility: Pelagic longlines

TABLE 1 | Final species checklist with color codes; green: common, yellow: rare, orange: rare due to gear constraints, red: uncertain identification.

Order	Family	Species	Author	Frequency of occurrence
SUBCLASS–HOLOCEPHALI				
Chimaeriformes	Rhinochimaeridae	*Rhinochimaera atlantica*	Holt and Byrne, 1909	🟧
	Chimaeridae	*Chimaera monstrosa*	Linnaeus, 1758	🟥
		Chimaera opalescens	Luchetti et al., 2011	🟥
		Hydrolagus affinis	de Brito Capello, 1868	🟩
		Hydrolagus pallidus	Hardy and Stehmann, 1990	🟩
SUBCLASS–EUSELACHII				
Division–Selachii				
Orectolobiformes	Rhincodontidae	*Rhincodon typus*	Smith, 1828	🟩
Lamniformes	Odontaspididae	*Odontaspis ferox*	Risso, 1810	🟧
	Alopiidae	*Alopias superciliosus*	Lowe, 1841	🟩
	Cetorhinidae	*Cetorhinus maximus*	Gunnerus, 1765	🟧
	Lamnidae	*Carcharodon carcharias*	Linnaeus, 1758	🟩
		Isurus oxyrinchus	Rafinesque, 1810	🟩
		Isurus paucus	Guitart, 1966	🟨
		Lamna nasus	Bonnaterre, 1788	🟨
Carcharhiniformes	Pentanchidae	*Apristurus laurussonii*	Saemundsson, 1922	🟩
		Galeus murinus	Collett, 1904	🟩
	Pseudotriakidae	*Pseudotriakis microdon*	de Brito Capello, 1868	🟩
	Triakidae	*Galeorhinus galeus*	Linnaeus, 1758	🟩
	Carcharhinidae	*Carcharhinus galapagensis*	Snodgrass and Heller, 1905	🟩
		Carcharhinus longimanus	Poey, 1861	🟨
		Galeocerdo cuvier	Péron and Lesueur, 1822	🟨
		Prionace glauca	Linnaeus, 1758	🟨
	Sphyrnidae	*Sphyrna zygaena*	Linnaeus, 1758	🟩
Hexanchiformes	Chlamydoselachidae	*Chlamydoselachus anguineus*	Garman, 1884	🟧
	Hexanchidae	*Heptranchias perlo*	Bonnaterre, 1788	🟩
		Hexanchus griseus	Bonnaterre, 1788	🟩
Squaliformes	Centrophoridae	*Centrophorus granulosus*	Bloch and Schneider, 1801	🟩
		Centrophorus lusitanicus	Barbosa du Bocage and de Brito Capello, 1864	🟨
		Centrophorus squamosus	Bonnaterre, 1788	🟩
		Deania calcea	Lowe, 1839	🟩
		Deania profundorum	Smith and Radcliffe, 1912	🟩
	Etmopteridae	*Centroscyllium fabricii*	Reinhardt, 1825	🟨
		Etmopterus princeps	Collett, 1904	🟩
		Etmopterus pusillus	Lowe, 1839	🟩
		Etmopterus spinax	Linnaeus, 1758	🟩
	Somniosidae	*Centroscymnus coelolepis*	Barbosa du Bocage and de Brito Capello, 1864	🟩
		Centroscymnus crepidater	Barbosa du Bocage and de Brito Capello, 1864	🟩
		Centroscymnus owstonii	Garman, 1906	🟩
		Scymnodalatias garricki	Kukuev and Konovalenko, 1988	🟧
		Somniosus microcephalus	Bloch and Schneider, 1801	🟨
		Somniosus rostratus	Risso, 1827	🟨
		Zameus squamulosus	Günther, 1877	🟨
	Oxynotidae	*Oxynotus paradoxus*	Frade, 1929	🟧
	Dalatiidae	*Dalatias licha*	Bonnaterre, 1788	🟩
		Squaliolus laticaudus	Smith and Radcliffe, 1912	🟩
DIVISION: BATOMORPHI				
Torpediniformes	Torpedinidae	*Tetronarce nobiliana*	Bonaparte, 1835	🟧
Rajiformes	Rajidae	*Dipturus cf. intermedius*	Parnell, 1837	🟥

(Continued)

TABLE 1 | Continued

Order	Family	Species	Author	Frequency of occurrence
		Dipturus oxyrinchus	Linnaeus, 1758	🟩
		Leucoraja fullonica	Linnaeus, 1758	🟩
		Raja brachyura	Lafont, 1871	🟨
		Raja clavata	Linnaeus, 1758	🟩
		Rajella bigelowi	Stehmann, 1978	🟧
		Bathyraja pallida	Forster, 1967	🟨
		Bathyraja richardsoni	Garrick, 1961	🟩
Myliobatiformes	Dasyatidae	*Bathytoshia cf. centroura*	Garman, 1880	🟥
		Dasyatis pastinaca	Linnaeus, 1758	🟩
		Pteroplatytrygon violacea	Bonaparte, 1832	🟩
		Taeniurops grabatus	Geoffroy Saint-Hilaire, 1817	🟩
	Myliobatidae	*Myliobatis aquila*	Linnaeus, 1758	🟩
	Mobulidae	*Mobula birostris*	Walbaum, 1792	🟩
		Mobula mobular	Bonnaterre, 1788	🟩
		Mobula tarapacana	Philippi, 1892	🟩

Local primary literature where species appears: (Simões, 1999; Martins, 2013).

Carcharhiniformes

Pentanchidae

Apristurus laurussonii (Saemundsson, 1922)

The first published record of *A. maderensis*, now synonymous with *A. laurussonii* (Eschmeyer et al., 2017), appears in an *in-situ* study by Saldanha and Biscoito (1997). This record was considered provisional by the authors due to difficulties in identifying members of genus *Apristurus* (Saldanha and Biscoito, 1997). The presence of this species was confirmed in Azores EEZ was during an experimental fishing expedition of Atlantic orange roughy (*H. atlanticus*) (Melo and Menezes, 2002; Menezes et al., 2012). *Apristurus manis* is also suspected to occur here (Melo and Menezes, 2002), however remains unconfirmed owing to the difficulty in identifying members of this genus (Gui Menezes IMAR/Azores, pers. comm. 2016).

Frequency of occurrence: Green (common)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No

Depth range (Ebert and Stehmann, 2013): 560–2,060 m

Local gear susceptibility: Bottom trawls

Local primary literature where species appears: Appears as *A. maderensis* or *A. laurussonii* (Saldanha and Biscoito, 1997; Melo and Menezes, 2002; Menezes et al., 2012).

Rajiformes

Rajidae

Dipturus cf. intermedius (Parnell, 1837)

Dipturus batis appears in the appendix of Santos et al. (1997) as requiring further documentation from the region. The presence of *D. batis* has since been confirmed by experimental fisheries studies (Menezes et al., 2006; Menezes and Giacomello, 2013; Menezes, 2014), and is regarded as "common" in the Azores (Menezes et al., 2006, suppl. mat.). In 2011, this species was revealed to be a cryptic species complex of two separate species *D. flossada* and *D. intermedius* (Iglésias et al., 2010). It is still uncertain which of the two species is present in Azores. Preliminary morphological studies indicate the species is probably *Dipturus intermedius* (G. Menezes IMAR/Azores, pers. comm. 2016). However, genetic studies are required to confirm this hypothesis.

Frequency of occurrence: Red (species identification uncertain)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): Possible

Depth range (Ebert and Stehmann, 2013): 200–600 m (∼1,500 m)

Local gear susceptibility: Bottom longlines

Local primary literature where species appears: Appears as *D. batis* (Menezes et al., 2006; Menezes and Giacomello, 2013)

Dipturus oxyrinchus (Linnaeus, 1758)

D. oxyrinchus featured in the appendix of Santos et al. (1997) owing to the lack of primary references from the Azores and only one dried specimen deposited at a regional museum. Experimental fishing and longline surveys confirm the presence of this species in the region.

Frequency of occurrence: Green (common)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No

Depth range (Ebert and Stehmann, 2013): 90–900 m

Local gear susceptibility: Bottom longlines

Local primary literature where species appears: (Menezes, 2003; Menezes et al., 2006; Menezes and Giacomello, 2013).

Myliobatiformes

Dasyatidae

Bathytoshia cf. centroura (Mitchill, 1815)

Two specimens of *Dasyatis centroura* are recorded in Santos et al. (1997), leading the authors to recommend further investigation of the species from the region. The presence of this species was confirmed as occurring frequently in the region (Afonso et al., 2013). This species was recently moved to the resurrected genus *Bathytoshia* (Last et al., 2016a,b). *B. centroura* is supposed to be present on the western margin of the Atlantic, while the species in north-east Atlantic are the brown stingray *B. lata* (Last P. et al., 2016). Considering the central position of the Azores, further investigation is required to ascertain whether *B. lata* or *B. centroura* is present in the region.

Frequency of occurrence: Red (species identification uncertain)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No (for *D. centroura*) (NB: No records of either *B. lata* or *B. centroura* from the region in Last P. et al., 2016)

Depth range (Ebert and Stehmann, 2013): Not available

Local gear susceptibility: Bottom longlines?

Local primary literature where species appears: Confirmed for *D. centroura* (Afonso et al., 2013).

Elasmobranch Species That Do Not Appear in the Checklist Santos et al. (1997) That Are Confirmed in the Current Checklist

Chimaeriformes

Rhinochimaeridae

Rhinochimaera atlantica Holt and Byrne, 1909

The first published record of this species occurs in Melo and Menezes (2002) from an experimental bottom-trawl fishery survey.

Frequency of occurrence: Orange (observation constraint)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No

Depth range (Ebert and Stehmann, 2013): 400–1,500 m

Local gear susceptibility: Bottom trawls

Local primary literature where species appears: (Melo and Menezes, 2002; Menezes et al., 2012)

Chimaeridae

*Chimaera opalescens** (Luchetti et al., 2011)

A recently described Holocephalan that is known only since 2011 (Luchetti et al., 2011). It is suspected that records of *Chimaera monstrosa* from the region might be misidentified *C. opalescens* (Diana Catarino IMAR/Azores, pers. comm. 2016). *C. opalescens* has been observed near seamounts in North-East Atlantic (Vieira and Cunha, 2014) but the presence of this species in the region is not yet confirmed in published literature.

Frequency of occurrence: Red (species identification uncertain)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): Not available

Depth range (Ebert and Stehmann, 2013): Not available

Local gear susceptibility: ?

Local source: D. Catarino (IMAR/Azores) pers. comm. 2016.

Lamniformes

Lamnidae

Isurus paucus Guitart, 1966

The first published record of this species from the Mid-Atlantic Ridge is based on two specimens caught north-west of the Azores (Queiroz et al., 2008). This is a naturally rare species, with one study reporting catch ratio of one long-fin mako shark *I. paucus* caught for 364 short-fin mako sharks *I. oxyrinchus* (Mucientes et al., 2013) based on logbook data of commercial longliners. Within Azores EEZ, a regional study using pelagic longlines reports two specimens (Martins, 2013).

Frequency of occurrence: Yellow (rare)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): Possible

Depth range (Ebert and Stehmann, 2013): 120–240 m

Local gear susceptibility: Pelagic longlines

Local primary literature where species appears: (Martins, 2013).

Carcharhiniformes

Pentanchidae

Galeus murinus (Collett, 1904)

First published record of this species in the Azores EEZ was a single specimen caught at a depth of around 1,000 m by longline surveys (Menezes et al., 2006). This species seems to have increased in occurrence in recent years (G. Menezes IMAR/Azores, pers. comm. 2016), and is well documented in local primary literature.

Frequency of occurrence: Green (common)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No

Depth range (Ebert and Stehmann, 2013): 380–1,250 m

Gear susceptibility: Bottom longlines

Local primary literature where species appears: (Menezes et al., 2006, 2012; Fossen et al., 2008; Menezes and Giacomello, 2013).

Hexanchiformes

Chlamydoselachidae

Chlamydoselachus anguineus Garman, 1884

This rare deepsea species was first recorded from the Azores when an experimental fishing expedition of Atlantic orange roughy (*H. atlanticus*) caught one individual (Melo and Menezes, 2002; Menezes et al., 2012). Another experimental fishing study reported a catch of 34 specimens in one haul from a seamount north of the Azores (Kukuev and Pavlov, 2008) confirming their occurrence on the MAR.

Frequency of occurrence: Orange (observation constraint)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No (yes for MAR)

Depth range (Ebert and Stehmann, 2013): 20–1,500 m

Local gear susceptibility: Bottom trawls

Local primary literature where species appears: (Melo and Menezes, 2002).

Squaliformes

Centrophoridae

*Centrophorus lusitanicus** du Bocage and de Brito Capello, 1864 Barbosa

This is a poorly known and rarely sampled species, often confused with its congener *C. granulosus* (Veríssimo et al., 2014). A scientific survey of landing centers in mainland Portugal does not record the occurrence of *C. lusitanicus*

(Veríssimo et al., 2014). Locally this species has not been caught in the scientific demersal fisheries surveys, but was recorded extensively in the local fisheries from 2009 to 2014. The presence of this species has only recently been confirmed from the Azores (F. Porteiro DRAM/Azores, pers. comm. 2017) but is presumably rare.

Frequency of occurrence: Yellow (rare)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No

Depth range (Ebert and Stehmann, 2013): 300–1,400 m

Local gear susceptibility: Bottom longlines

Local primary literature where species appears: Not available

Etmopteridae

*Centroscyllium fabricii** (Reinhardt, 1825)

This species is rarely recorded in regional demersal fisheries surveys, but is confirmed to occur in the region.

Frequency of occurrence: Yellow (rare)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No

Depth range (Ebert and Stehmann, 2013): 300–1,400 m

Local gear susceptibility: Bottom longlines

Local primary literature where species appears: (Menezes and Giacomello, 2013; Menezes, 2014).

Somniosidae

*Somniosus microcephalus** (Bloch and Schneider, 1801)

This cold-water species occurs infrequently in the Azores EEZ, with 2 individuals reported from bottom longline surveys north of the Azores (Fossen et al., 2008) and one individual captured in a bottom trawl survey (Menezes et al., 2012).

Frequency of occurrence: Yellow (rare)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No

Depth range (Ebert and Stehmann, 2013): < 1,400 m

Gear susceptibility: Bottom longlines and trawls

Local primary literature where species appears: (Fossen et al., 2008; Menezes et al., 2012).

Somniosus rostratus (Risso, 1827)

First published record from the Azores of one individual in Menezes et al. (2006). Rarely occurs in the region but confirmed by experimental fishing.

Frequency of occurrence: Yellow (rare)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No

Depth range (Ebert and Stehmann, 2013): 180–2,200 m

Local gear susceptibility: Bottom longlines

Local primary literature where species appears: (Wenneck et al., 2008; Menezes, 2014)

*Zameus squamulosus** (Günther, 1877)

Synonymous with *Scymnodon obscurus* (Eschmeyer et al., 2017) which appears in regional demersal fisheries survey records.

Frequency of occurrence: Yellow (rare)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): No

Depth range (Ebert and Stehmann, 2013): 300–1,400 m

Gear susceptibility: Bottom longlines and trawls

Local primary literature where species appears: Appears as *S. obscurus* (Menezes et al., 2012; Menezes, 2014).

Rajiformes

Arhynchobatidae

Bathyraja pallida (Forster, 1967)

This species is captured infrequently, known from only 12 specimens (Orlov et al., 2006). The first published record for the Mid-Atlantic Ridge appears in the MAR-ECO expedition, with two individuals captured north of the Azores (Fossen et al., 2008). It is confirmed to occur within the Azores EEZ (G. Menezes IMAR/Azores, pers. comm. 2016).

Frequency of occurrence: Yellow (rare)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): Possible

Depth range (Ebert and Stehmann, 2013): 1,879–2,950 m

Local gear susceptibility: Bottom longlines

Local primary literature where species appears: (Fossen et al., 2008).

Bathyraja richardsoni (Garrick, 1961)

First published record from the region appears in bottom trawl survey for Atlantic orange roughy (Menezes et al., 2012). Very deep sea species (recorded between 2,050 and 2,200 m in Menezes et al. (2012), but appears to be common in the MAR region (Orlov et al., 2006).

Frequency of occurrence: Green (common)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): Yes (for MAR)

Depth range (Ebert and Stehmann, 2013): 526–2,951 m (for MAR)

Local gear susceptibility: Bottom longlines

Local primary literature where species appears: (Fossen et al., 2008; Menezes et al., 2012).

Myliobatiformes

Myliobatidae

Mobula tarapacana (Philippi, 1892)

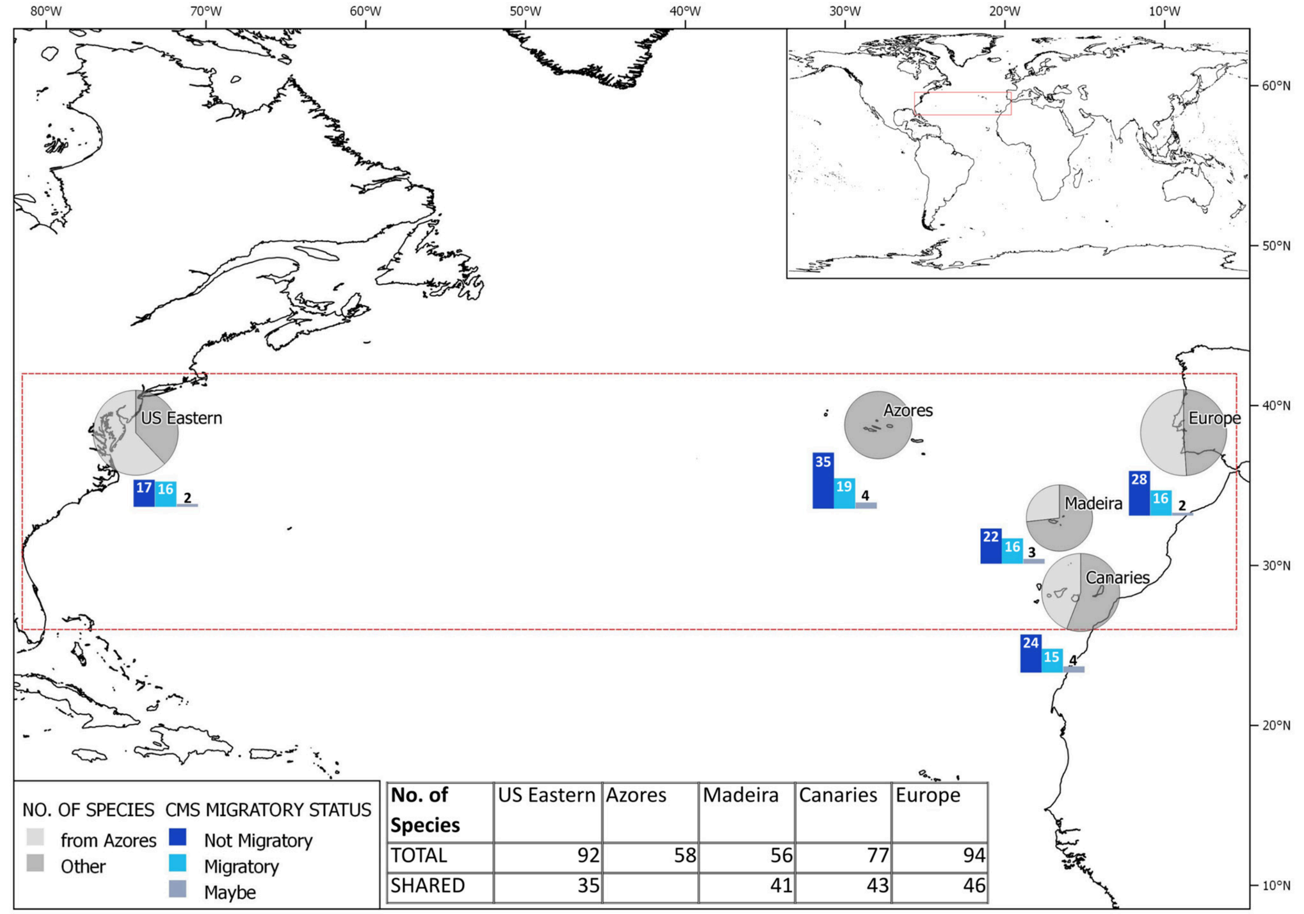
Mobula mobular was regularly recorded in the Azores until Sobral and Afonso (2014) rectified most of these sightings to actually be sickle-fin mobula ray (*Mobula tarapacana*) using photographic data. The authors found that this warm-water species is frequent during summer aggregations over shallow Azorean seamounts, whereas *M. mobular* in fact rarely occurs in the EEZ. The same authors noted that a clarification of sightings of the latter was needed given that *M. mobular* is thought to be restricted to the Mediterranean, while the closely-related *M. japanica* is circumglobal (Poortvliet et al., 2015). This was recently resolved to be a single species with the designation *M. mobular* based on molecular data (White and Last, 2012; White et al., 2017), and is thus here retained as the valid species for the region together with *M. tarapacana*.

Frequency of occurrence: Green (common)

Record for Azores in FAO Fish Finder (Ebert and Stehmann, 2013): Not available [NB: No records for the region for *M. tarapanca* and *M. mobular* (Last P. et al., 2016)]

Depth range (Ebert and Stehmann, 2013): Not available

Gear susceptibility: ?



No. of Species	US Eastern	Azores	Madeira	Canaries	Europe
TOTAL	92	58	56	77	94
SHARED	35		41	43	46

FIGURE 1 | Distribution of species shared between the Azores and the study regions in the North Atlantic, and their currently known migratory status. The size of the circles are relative to total species diversity.

Local primary literature where species appears: (Sobral and Afonso, 2014).

Elasmobranch Species That Appear in the Checklist Santos et al. (1997) but Were Not Confirmed in the Current Checklist

Alopias vulpinus (Bonnaterre, 1788)

Records of *Alopias superciliosus* were quite probably misidentified as *A. vulpinus*. A shark bycatch study from pelagic longline fisheries states *A. vulpinus* reported in landings data, while the author personally records *A. superciliosus* (Simões, 1999). This species that is known to occur much closer to continental landmass has not been recorded in observer data or in pelagic longline experiments (P. Afonso, unpublished data).

Raja maderensis Lowe, 1838

Raja maderensis is reported to occur in the Azores (Santos et al., 1997; Weigmann, 2016) but genetic studies show that a morphotype of *R. clavata*, a species known to exhibit phenotypic plasticity (Aloncle, 1966; Chevolot et al., 2006), is present in these waters (Ball et al., 2016). Hence, records of *R. madarensis* are now considered *R. clavata* (G. Menezes IMAR/Azores, pers. comm. 2016).

Biogeographic Similarities

Since the distribution of *C. opalescens*, *B.* cf. *centroura* and *D.* cf. *intermedius* are still uncertain, the remaining 58 species were used to compare biogeographic affinities of the Azores with the rest of the North Atlantic. About one-third of elasmobranch species of the United States east coast occur in the Azores, while the archipelago shares more than half of the species of continental Europe (**Figure 1**). Elasmobranch species composition in the Azores was dominated by non-migratory species, majority of which were same as eastern North Atlantic. Migratory species that occur in the Azores were evenly present across the North Atlantic, with a slightly lower number of these species occurring in the Canaries.

The elasmobranch assemblage was most similar between the Azores archipelago and Madeira (**Figure 2**), with Madeira sharing almost three-quarters of the species with the Azores (**Figure 1**). The diversity of elasmobranch families of these two regions was comparable as well (**Figure 3**). Deepwater

Squaliformes dominated in species diversity in both regions. However, Madeira had a greater number of carcharhinids while Azores had a higher count of lamniforms.

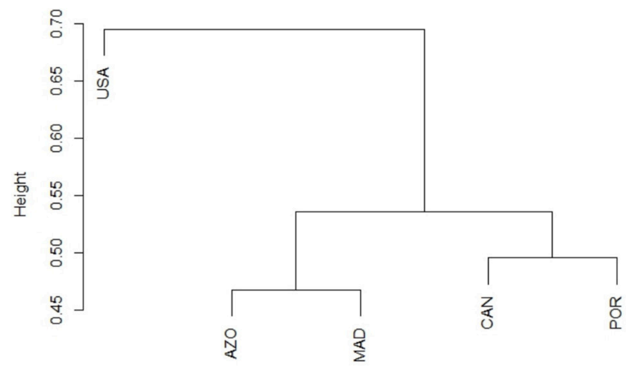


FIGURE 2 | Similarity between biogeographic regions by cluster analysis; y-axis represents binary distances. USA, United States east coast; AZO, Azores; MAD, Madeira; CAN, Canaries; POR, Portugal continental shelf.

Not all archipelagos of the Macaronesian biogeographic unit clustered together; the Canaries and Portugal continental shelf formed a separate group (**Figure 2**). The species diversity (**Figure 1**) and composition of elasmobranch families (**Figure 3**) of the Canaries was more similar to mainland Portugal than to Madeira and Azores, even if family diversity was lower than the continental margin. Other evident points of difference were the greater diversity of families in the order Carcharhinidae and dominance of rajids on the continental margin as compared to the Canaries.

There was a clear separation between the elasmobranch species composition of the western and eastern halves of the North Atlantic (**Figure 2**). Elasmobranch assemblage structure by family indicated that the two continental margins had high, but contrasting species diversity. The western margin was dominated by requiem sharks (Carcharhinids) and a high diversity of Myliobatiformes (Dasyatidae to Urotrygonidae) (**Figure 3**). On the contrary, the eastern continental species assemblage was dominated by Rajiformes. Deepwater species also differ visibly between the eastern and western halves of the North Atlantic. In particular, Squaliformes (Centrophoridae

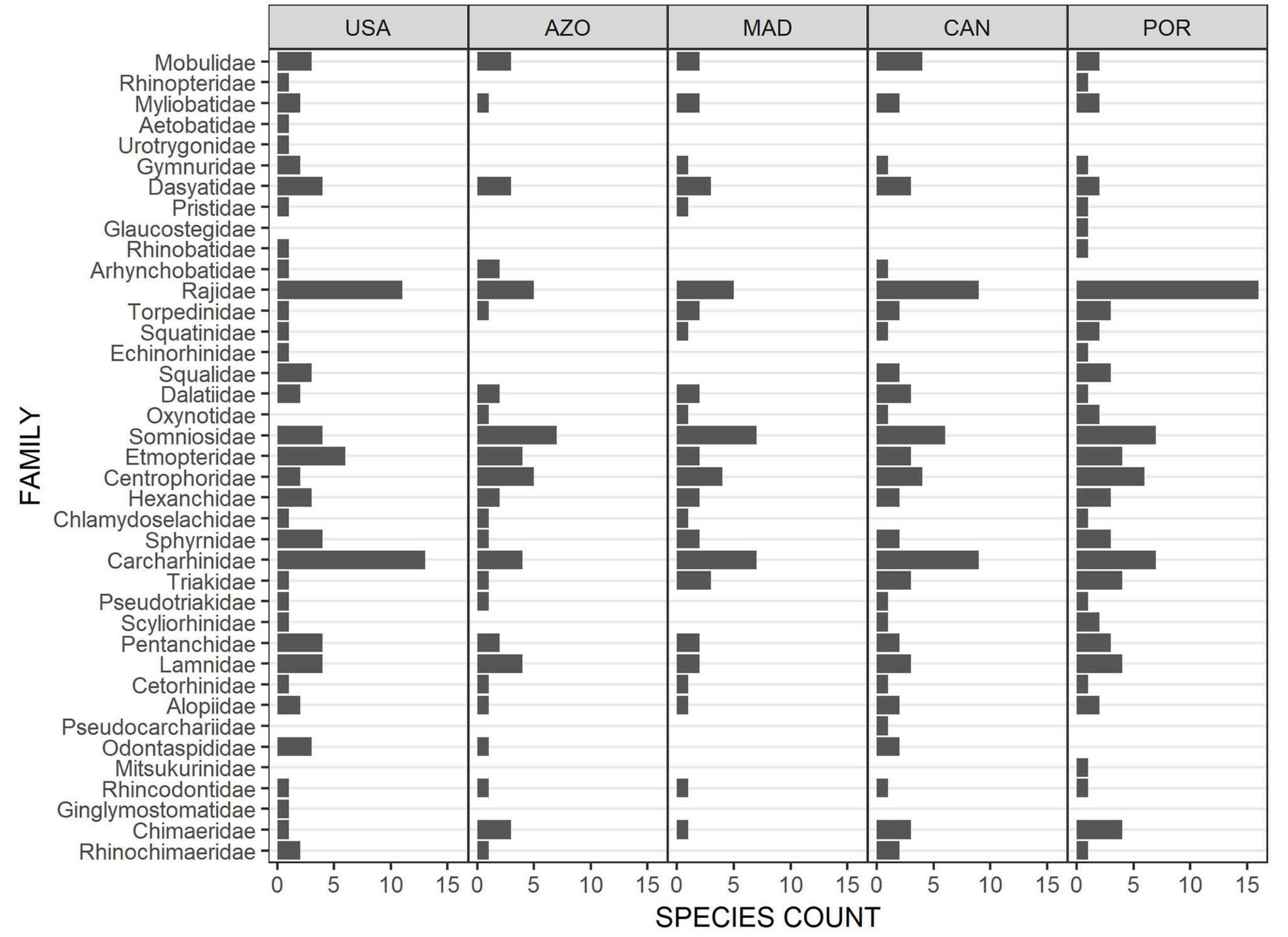


FIGURE 3 | Configuration of elasmobranch diversity by families across the North Atlantic. USA, United States east coast; AZO, Azores; MAD, Madeira; CAN, Canaries; POR, Portugal continental shelf.

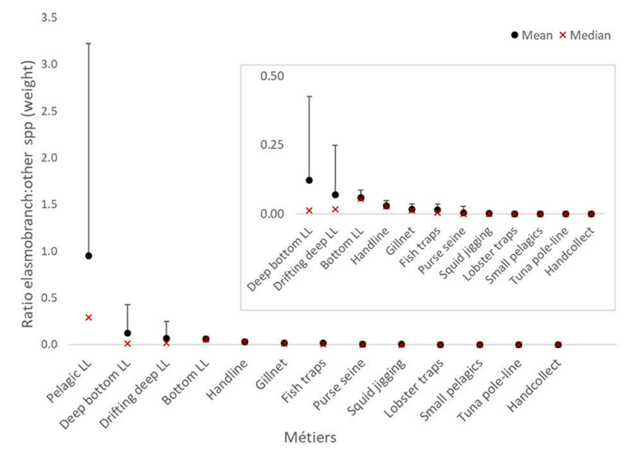


FIGURE 4 | Proportional weight landed of elasmobranchs per unit weight of other species, by fishery métier. INSET, After removing métier pelagic longline.

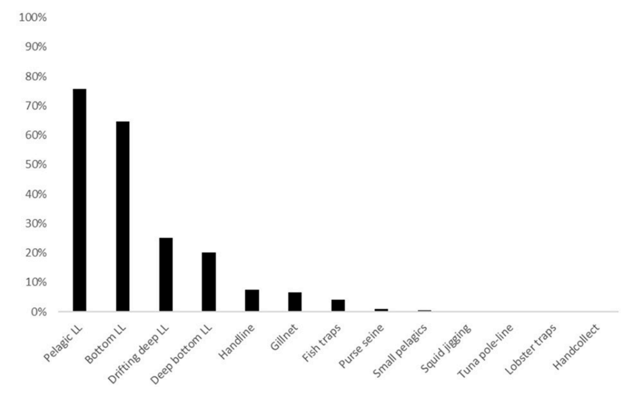


FIGURE 5 | Frequency of elasmobranch landings (% of total landings) per métier.

to Squalidae) had strikingly low species diversity in the west compared to the central and eastern parts.

Local Threats and Vulnerabilities

Interactions with Local Fisheries

Local vessels operating within the Azores EEZ landed elasmobranchs regularly, but landings were highly variable within and across métiers. All longline gears had greater landings of elasmobranchs per unit effort (proportional weight and frequency), even when compared to other métiers using hooks such as handlines (**Figure 4**). The tuna pole and line fishery, also using hooks, had no elasmobranch landings.

Pelagic longlines landed by far the largest quantity, proportion (average 0.95 kg elasmobranch WPUE, **Figure 4**) and frequency (75.6% LPUE, **Figure 5**) of elasmobranchs. This proportion varied substantially with year, the maximum reaching 20.6 kg elasmobranch per kg of other species. Bottom longlines showed a comparable frequency of elasmobranch landings (64.7% LPUE) but landed smaller proportion weight (<0.1 kg elasmobranch WPUE). In comparison, both the deeper bottom and drifting deep longlines recorded only a quarter or less of the landings that included elasmobranchs.

Handlines, gillnets, and fish traps landed between 0.05 and 0.01 kg elasmobranch WPUE with less than 10% elasmobranch LPUE. Six of the 13 métiers recorded in the local fisheries database had minimal interaction with elasmobranchs (<0.01 WPUE, **Figure 4**; and <1% LPUE, **Figure 5**) and were excluded from further analyses.

Species Composition by Métier and Related Red List Status

The longline gears were analyzed separate from the other métiers for species composition by average weight per landing. The average weight per landing of most species was associated with a great degree of variability, deep bottom longline recorded the highest average weight (>1,500 kg/landing) for a species appearing as *Centrophorus lusitanicus*, categorized as Endangered in the European Red List (Nieto et al., 2015). The other species with high average weight per landing were *Dalatias licha* (611.5 kg/landing), *Deania calcea* (272.6 kg/landing), and *Centrophorus granulosus* (141.6 kg/landing; **Figure 6A**). The first two species have been categorized as Endangered by the regional Red List, while *C. granulosus* is listed as Critically Endangered. The landings of the pelagic longline was singularly dominated by blue shark *Prionace glauca* (**Figure 6B**; 753.4 kg/landing). However, this amount varied considerably along the study period. Other species like short-fin mako shark *Isurus oxyrinchus* were landed in much smaller quantities (147.3 kg/landing). The circumglobal big-eyed thresher shark *Alopias superciliosus* registered only one landing (154.3 kg). *P. glauca* is regionally assessed as Near Threatened, while *I. oxyrinchus* and *A. superciliosus* are assessed Data Deficient and Endangered, respectively. The bottom longline recorded the highest diversity of species landed (**Figure 6C**), with high but variable landing of *C. lusitanicus* (625.9 kg/landing). This was followed by a species recorded as *Deania hystricosa* (83.4 kg/landing) that does not appear in our regional species checklist and is listed as Data Deficient in the regional Red List. Elasmobranch landings of the drifting deep longline had lower average weight than the other longline gear, with maximum average weight of *C. granulosus* (398.9 kg/landing). Four of the eight species landed by this métier are recorded only once (**Figure 6D**).

The elasmobranch landings of the remaining métiers visibly differed in species composition from the longline métiers. Instead of a few species dominating landings, multiple species were landed in comparable quantities. Handlines landed the highest diversity of species, with slope species (e.g., genus *Deania* and *Centrophorus*) landed in greater average weight than coastal species (e.g., *Dasyatis pastinaca*, *Raja clavata*, *Galeorhinus galeus*). A one-time landing of a species with no corresponding Latin name (local name "sapata quilha," tentatively designated as *Deania* spp.) was the maximum average weight of this métier (**Figure 7A**). The apex predator sixgill shark *Hexanchus griseus* had high average elasmobranch weight in handlines

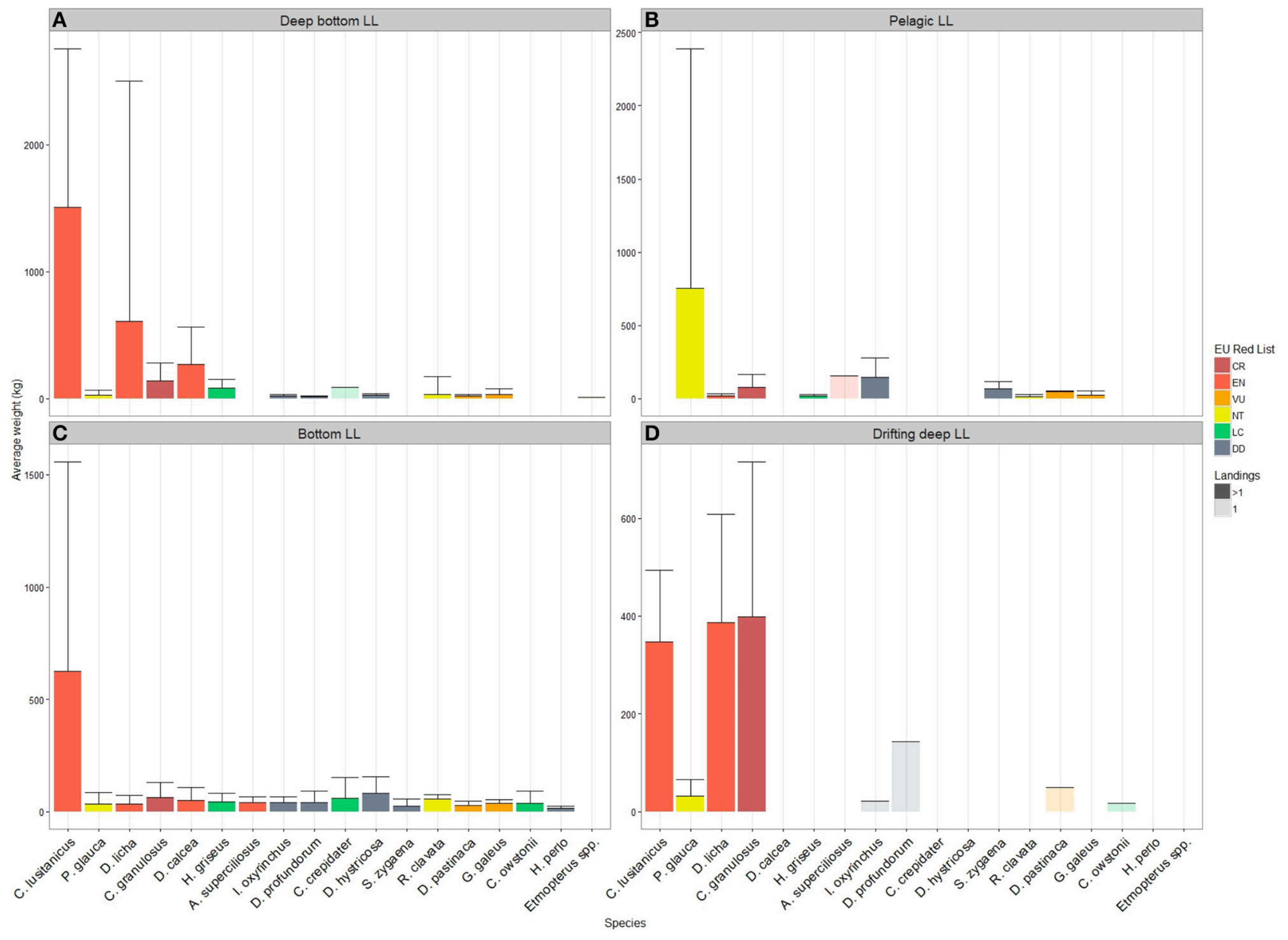


FIGURE 6 | Species composition, by regional Red List status, and average weight per landing of métiers using longlines; semi-transparent bars for species with only one landing record. NB, Y-axis different for each panel. **(A)** Deep bottom longline, **(B)** Pelagic longline, **(C)** Bottom longline, **(D)** Drifting bottom longline.

(174.5 kg/landing) and gillnets (53.9 kg/landing), but with substantial variance. Other species landed by gillnets included the coastal *G. galeus*, regionally Vulnerable (30.1 kg/landing) but also oceanic *I. oxyrinchus* (30.1 kg/landing), *P. glauca* (22.3 kg/landing) and *Sphyrna zygaena*, assessed DD, (15.3 kg/landing) (**Figure 7B**). Species such as tope shark *G. galeus* and thornback ray *R. clavata*, as well as mako shark *I. oxyrinchus*, were more important in average weight per elasmobranch landing of fish traps (**Figure 7C**).

Vulnerability and EFHs

Azorean fisheries broadly target all the three main marine habitat types in the region: coastal (gillnets and handlines), island slopes and seamounts (handlines, drifting deep, and fixed bottom/deep bottom longlines) and pelagic (surface longlines). The sparse empirical information available suggests the presence of EFH for elasmobranchs in each of these three habitats, including nurseries and adult aggregation sites inshore and in the open-ocean, and deepwater ray egg deposition sites (J. Pichazek, pers comm. 2017). Blue sharks use the region's pelagic environment as a nursery for small juveniles that remain in the area for up to 2 years, and maybe even as a pupping ground (Vandeperre et al., 2014a,b, 2016). Sightings and long-term acoustic tagging data also show that smooth hammerhead shark *S. zygaena* uses the inshore coastal areas around some of the islands as nursery habitats (PA, unpublished data). Occasional sightings and incidental catches of pregnant females in the summer suggest that these nurseries are most possibly pupping grounds as well (PA, unpublished data). Similarly, juvenile tope sharks also aggregate in discrete coastal areas as revealed by occasional high catches in experimental fishing sets (G. Menezes pers. comm. 2016). Certain shallow seamounts are well-known aggregating sites for adult devil rays (*M. tarapacana*) that are observed over consecutive years (Sobral and Afonso, 2014). The function of these aggregations is yet unknown, but these could well be mating sites (Sobral, 2013). The deepwater frilled shark *Chlamydoselachus anguineus* is speculated to use seamounts in the Azores EEZ as a mating site (Kukuev and Pavlov, 2008), though this hypothesis is based on a single fishing haul.

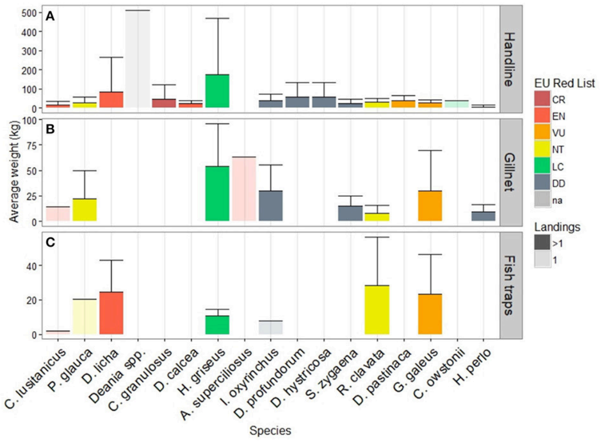


FIGURE 7 | Species composition, by regional Red List status, and average weight per landing of remaing métiers (considering only landings with elasmobranch); semi-transparent bars for species with only one landing record. NB, Y-axis different for each panel. **(A)** Handline, **(B)** Gillnets, **(C)** Fish traps.

DISCUSSION

A Diverse Elasmobranch Assemblage around a Remote Archipelago

The species composition of the chondrichthyan assemblage around the Azores is dominated by species that are either oceanic or deep-sea, reflecting the dominant marine habitat surrounding the archipelago. The fact that they are underwhelmingly known becomes evident in the lack or misrepresentation of species occurrence records in regional and global species catalogs. However, the Azorean elasmobranch assemblage emerges as more diverse than expected. Most of the new species additions are a result of nearly two decades of additional sampling effort and the use of different sampling gears. Species like the frilled shark *C. anguineus* and broadnose chimera *Rhinochimaera atlantica*, for example, were only obtained in experimental deep-water trawl nets (Melo and Menezes, 2002). More importantly, technological advancements over the last two decades and an increasing interest in the deep ocean (Costello et al., 2010) have allowed sampling at greater depths in more remote locations. Nevertheless, better known and accessible areas like coasts and nearby seamounts also revealed new additions. Evidence shows that morphologically similar species have been misidentified due to prevalent assumptions. For example, coastal stingrays are often identified as the common stingray *D. pastinaca*. A similar looking species, until now considered to be roughtail stingray *D. centroura* (Afonso et al., 2013), also occurs in the region. Recently, this species has undergone a reclassification to two different species (Last et al., 2016b), prompting the need to re-identify and reconsider the relative abundance of the two morphologically similar species present in the Azores EEZ. A similar story occurred for the devil rays *M. tarapacana* and *M. mobular*, and was resolved to yield unexpected results (Sobral and Afonso, 2014).

Continental margins are often richer in biodiversity because of their greater productivity and older geological age. It is thus not surprising that the elasmobranch species on the Azores archipelago are less diverse compared to the continental margins of the Atlantic, a trend common to bony fishes as well (Santos et al., 1995, 1997; e.g., Almada et al., 2013). Despite the low diversity, the Azores elasmobranch species assemblage have a wider provenance, especially when compared with the other Macaronesian archipelagos. This result may be explained by the fact that the Azores region is considered to represent a transition zone (ecotone) between cold and warm temperate waters, where the Gulf Stream provides a warmer input than would be normal at this latitude. This transitional signature explains why half the demersal fish (*sensu lato*, including elasmobranchs) assemblage is composed of species of subtropical origin (Menezes et al., 2006), and which also account for nearly 90% of the more rare fish occurrences (Afonso et al., 2013). Our results provide renewed support to this scenario by showing that the region falls in the boundary between the southern limit of cold-water species like deepwater skates (genus *Bathyraja*) and Greenland shark *Somniosus microcephalus*, and the northern limit of tropical and sub-tropical species like whale shark *Rhincodon typus*, sicklefin devil-ray *M. tarapacana* or round sting ray *Taeniura grabata*. The importance of this region as a fringe habitat is bound to increase with possible shifts in global distribution (Afonso et al., 2013), thus highlighting the need for continued monitoring of the elasmobranch species assemblage around the Azores EEZ.

Biogeographic studies showed that the Azores have greater proportion of coastal fish species from outside north-east Atlantic compared to the entire Lusitanian province (Almada et al., 2013). Shallow water fauna of the Azores also constitutes species with origins in the east as well as the west of the Atlantic basin (Santos et al., 1995). Similarly, the elasmobranch diversity in the Azores also claims different regional affiliations in the North Atlantic. Highly migratory sharks like blue and mako sharks travel from the eastern coast of North America to the Mid-Atlantic Ridge, close to the Azores (Vandeperre et al., 2014a, 2016; Queiroz et al., 2016). The Azores and associated Mid-Atlantic Ridge maybe an important migratory corridor and feeding ground for some pelagic elasmobranch species (Gore et al., 2008; Wögerbauer et al., 2015; Doherty et al., 2017). Conversely, the biogeographic pattern of non-migratory deep-sea sharks and rays seems to highlight the potential barrier posed by abyssal plains, as well as the possible role of seamounts as dispersal “stepping stones.” Comprehensive genetic and telemetry studies can shed light on the role of the wider Azores region in connecting both sides of the Atlantic basin for species of different habitat ecology.

Essential Fish Habitats and Interaction with Local Fisheries

Local fisheries in the Azores operate at a much smaller scale compared to mainland Portugal and other European fleets, where elasmobranch landings can be almost 20 times greater by weight (Correia et al., 2016). However, the interaction between elasmobranchs and the fishery is far from simple. A recent study of elasmobranch fisheries in the Azores identified four main species–tope shark, thornback ray, blue shark, and short-fin mako shark–to be important to the local fishery (Torres et al., 2016). This study overlooked other elasmobranch species that do not dominate official landing records by weight. Our results show that the local fishery in fact involves other species, landed sporadically but in considerable volume. These less frequent species demand greater management attention due to their higher extinction risk and, perhaps more importantly, high discard potential.

The Demersal Fisheries

The kite-fin shark *D. licha* was the only deep-sea elasmobranch commercially targeted by the local fishery, with landings to the tune of 900 t in the 1980s (ICES, 2015). The fishery has since declined, while it is still not certain whether the decrease in landings was due to falling population abundance or market demand. Within our study period, landings of species *C. lusitanicus* dominate by average weight, even though this species is known to be rare and is seldom encountered in landing centers (Veríssimo et al., 2014). The implementation of zero total allowable catch (TAC) of *C. squamosus* and *C. granulosus* by the European Commission in 2012 led to masking the landings of these species as *C. lusitanicus* in mainland Portugal (ICES, 2015; Correia et al., 2016). Our results suggest that similar misreporting occurred in the Azores as well.

Records from the deepwater drifting longline fishery targeting black scabbardfish are similarly riddled with inconsistencies. Observer reports from the experimental fishery in the Azores (Machete et al., 2011) allow a direct comparison of catch and reported landings between 1999 and 2005. The catch of elasmobranchs from the experimental fishery was dominated by *C. squamosus* (Machete et al., 2011, suppl. mat.), which does not even appear in the official landings. Instead, the largest landings of a deep-sea shark species from this fishery was attributed to *C. lusitanicus*.

Regionally abundant species such as the demersal lantern sharks *Etmopterus* spp. also do not appear in the landing records, however is locally the most abundant elasmobranch genus in fishing surveys (Wenneck et al., 2008; Menezes, 2014). Current discard estimates calculate that around 300 mt of this species group is discarded for every 10 kg recorded in landings (Pham et al., 2013). Evidence suggests that lanternshark species are declining due to commercial fishing in Southern Portugal, where they are frequently discarded as well (Coelho, 2007). The extent of unreported and unregulated fishing could seriously affect the population of these two species, assessed as near threatened (*E. spinax*) and data deficient (*E. pussilus*) for European populations (Nieto et al., 2015).

The landings of deepwater sharks present an interesting case influenced strongly by legislation as well as commercial value. Misreporting and unreported discards are notorious problems in landing records from deep-sea fisheries (Musick and Musick, 2011; ICES, 2015). This highlights the immediate need to account for the unreported and discarded catch from the demersal fisheries for deep-water sharks, in light of the planned implementation of the EU Landings Obligation act.

Oceanic Pelagic Fisheries

In the Azores EEZ, the fisheries pressure on blue shark is severely underestimated in local records, as a majority of the catches are landed in ports outside the Azores. Our results show that, within the local fishery, reported landings of blue shark can be 20 times higher than landings of other species by weight. These results do not consider the discard or unreported landings, estimated to be up to 80% more than reported landings (Pham et al., 2013).

Blue shark catch by surface longlines has generally not been considered a grave threat to the population status (Cortés et al., 2010; ICCAT, 2015). However, catch analysis from surface longlines in north-west Atlantic suggests that including the discard estimates in the assessments could "substantially change the perception of the population health" (Campana et al., 2006). This sentiment is echoed in the recent stock assessment by the International Commission on Conservation of Atlantic Tunas (ICCAT) that stressed the need to reconstruct discard estimates for a more reliable indication of the stock status (ICCAT, 2015). The known essential function of the wider Azores region as a nursery and juvenile habitat for blue shark (Vandeperre et al., 2014a,b, 2016) further exacerbates the problem, given that demographic analyses show that the productivity of this species is heavily dependent on the survival of juveniles (0–4 years; Aires-da-Silva and Gallucci, 2007). The intersection of these three facts emphasize the need to further examine susceptibility of the species within the EEZ to inform management actions.

Of the other species appearing in the pelagic fishery landings, short-fin mako is ranked second most vulnerable out of the 11 pelagic elasmobranch species in the North Atlantic, suggesting it is at high risk of overexploitation (Cortés et al., 2010). Additionally, both short-fin mako (Morato et al., 2010) and big-eye thresher *A. superciliosus* sharks (Litvinov, 2008) are known to associate with seamounts. The highly probable occurrence of oceanic essential fish habitat for these species and other oceanic sharks (e.g., the adult phase of the smooth hammerhead shark) around the Azores and MAR seamounts demands urgent studies.

Coastal Fisheries

Regional fisheries legislation prohibits the use of any longline gear within a buffer of 6 NM from the coast, but handlines are allowed to operate within buffer limits. This métier seems to opportunistically land elasmobranchs that constitute a regular, though small fraction of their total landings. However, landings from the gillnet fishery, though much smaller in quantity, require special attention. The gillnet fishery in the Azores is regulated by catch limits for both target and non-target species and only operates inshore since it is prohibited below 30 m deep (Portaria n.91, 2005). The "nearshore netting of questionable legality recently observed for tope shark, with small hammerhead sharks also being caught" reported Santos et al. (1995, p. 325) essentially continues with small quantities of tope and hammerhead sharks regularly reported in recent landings. The exclusively coastal nature of the fishery implies that they might overlap with suspected pupping and nursery areas of these sharks. This possibility urgently requires further study, and highlights the need to closely monitor this fishery, including discard practices. Hammerhead and tope sharks were recently assessed as Data Deficient and Vulnerable to extinction risk in the regional Red List, respectively. Both species are highly migratory and seen as having single stocks in the North or north-east Atlantic. This leads us to hypothesize that the putative essential fish habitats for both species in the Azores could have a significant contribution to the larger population.

Future Possibilities and Recommendations

Based on our results we propose three broad areas of further research that can help to further determine the importance of the wider Azores region for elasmobranchs.

The first data-gap that requires closer inspection are errors and omissions in local fishery data. Robust estimates on the extent of unreported/misreported and discarded catch are required to gauge the actual impact of the local fishery on regional stocks of sharks and rays. Since landings cannot provide a holistic overview of local population status, sentinel or fishery-independent surveys are also imperative to monitor the local elasmobranch populations. Some of these could use non-invasive techniques such as, baited remote cameras for coastal nurseries and deepwater sharks on slopes and seamount summits. Additionally, fisheries studies would benefit from an analysis of socio-economic incentives for landing or discarding of different species. This could provide clues regarding future exploitation trends. The second major gap is the lack of region-specific studies focused on the biology and ecology of local elasmobranchs. Finally, and perhaps most importantly, the essential habitat function of the Azores as nursery, mating, migration, feeding needs to be studied in detail, and across species and habitats. Resolving the importance of the Azores in the wider context of the Atlantic will need many more studies on connectivity of shark and ray populations with, or isolation from, other parts of the species distribution ranges. Population dynamics and tagging studies using electronic, genetic or chemical markers, for example, together with the continued monitoring of species occurrence, will further elucidate the importance of the region as an ontogenetic, permanent, or transitionary habitat, and help pinpoint critical habitats for eventual protection as well as future species range shifts in light of current climatic change scenarios.

AUTHOR CONTRIBUTIONS

PA and DD have equally contributed to: conception and design of this study, data acquisition, analysis, and interpretation, drafting the manuscript and revising it critically for important intellectual content, final approval of the version to be published. Both authors agree to be fully accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of this study are appropriately investigated and resolved.

ACKNOWLEDGMENTS

The authors are very grateful to Dr. Gui Menezes (IMAR/DRAM, Azores, Portugal), Dr. Pedro Pascual (IEO, Canaries, Spain) and Dr. Mafalda Freitas (OOM/MARE, Madeira, Portugal) for contributing their time to correct the species list from their respective study areas. The authors would like to thank Ms. Dalia Reis (DOP/IMAR) for her help with obtaining the fisheries data, and Dr. Diana Catarino (DOP/IMAR) for pointing out the taxonomic conflict between *C. monstrosa* and *C. opalescens*. The authors also offer thanks to Dr. Eva Giacomello (DOP/IMAR) for her patience and help with finalizing the species checklist. Finally, we would like to thank the two reviewers who have shared their time and advice to critically improve this manuscript. This study had the support of Fundação para a Ciência e Tecnologia (FCT) through the strategic project UID/MAR/04292/2013 granted to MARE and the contract awarded to PA (SFRH/IF/01640/2015).

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Marine Science

PERSPECTIVE
published: 20 January 2020
doi: 10.3389/fmars.2019.00826

The Azores: A Mid-Atlantic Hotspot for Marine Megafauna Research and Conservation

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Specialty section:
This article was submitted to Deep-Sea Environments and Ecology, a section of the journal Frontiers in Marine Science

Received: 13 April 2019
Accepted: 20 December 2019
Published: 20 January 2020

Citation:
Afonso P, Fontes J, Giacomello E, Magalhães MC, Martins HR, Morato T, Neves V, Prieto R, Santos RS, Silva MA and Vandeperre F (2020) The Azores: A Mid-Atlantic Hotspot for Marine Megafauna Research and Conservation. Front. Mar. Sci. 6:826. doi: 10.3389/fmars.2019.00826

The increasing public perception that marine megafauna is under threat is an outstanding incentive to investigate their essential habitats (EMH), their responses to human and climate change pressures, and to better understand their largely unexplained behaviors and physiology. Yet, this poses serious challenges such as the elusiveness and remoteness of marine megafauna, the growing scrutiny and legal impositions on their study, and difficulties in disentangling environmental drivers from human disturbance. We argue that advancing our knowledge and conservation on marine megafauna can and should be capitalized in regions where exceptional access to multiple species (i.e., megafauna 'hotspots') combines with the adequate legal framework, sustainable practices, and research capacity. The wider Azores region, hosting EMHs of all key groups of vulnerable or endangered vertebrate marine megafauna, is a singular EMH hotspot on a migratory crossroads, linking eastern and western Atlantic margins and productive boreal waters to tropical seas. It benefits from a sustainable development model based on artisanal fisheries with zero or minor megafauna bycatch, and one of the largest marine protected area networks in the Atlantic covering coastal, oceanic and deepsea habitats. Developing this model can largely ensure the future integrity of this EMH hotspot while fostering cutting-edge science and technological development on megafauna behavior, biologging and increased ocean observation, with potential major impacts on the Blue Growth agenda. An action plan is proposed.

Keywords: mid-Atlantic ridge, seamounts, essential habitat, vulnerable species, pelagic predators

INTRODUCTION

Marine megafauna, a broad definition for large marine vertebrates including marine mammals, reptiles, birds and large fishes, has captivated human mind since pre-historic times. The petroglyphs and bone carvings depicting whale hunting, the leviathanic scenes in classical art (many inspired in biblical episodes), the sacred nature of sharks, turtles or whales in many cultures, the profusion of Hollywood movies and TV documentaries featuring fearsome or tender sea giants, all of these are cultural manifestations of a genuine human fascination for these creatures. Today, their iconic role and charismatic nature gained a new momentum, as they embody the contemporary challenge of saving wild animals from mass extinction caused by an unsustainable human development model. The increasing public perception that most marine megafauna species reached a threatened or endangered conservation status, in spite of their great ecological as well as economic value for fisheries and ecotourism, renders them a unique flagship role both for conservation research and citizen science.

This contemporary paradigm represents an unprecedented push to investigate megafauna, including the discovery of the habitats essential for their survival, gauging their individual and population responses to exploitation, shipping, climate change or pollution, or understanding the many behaviors, physiology and motivations behind the migrations, feeding, mating and other vital functions throughout their lives that are still unknown or remain largely unexplained (e.g., Hays et al., 2016). Yet, as obvious as it can be, this strategic scientific move faces serious challenges.

First, the elusiveness and remoteness of many marine megafauna species make them hard and costly to access and to study in detail. The good news here is that the use, performance and sophistication of electronic tagging devices have increased substantially, and appropriate statistical tools to make sense of the wealth of data retrieved from these equipments have now been developed, allowing observation/measuring of behavior of free-ranging organisms with a detail and accuracy that we would only dream of a couple of decades ago (e.g., Hussey et al., 2015; Hays et al., 2016). This change was also accompanied by an increasing capacity to collect and analyze large volumes of oceanographic and remote sensing data at the scales needed to understand the environment in which these animals live in (e.g., Druon et al., 2016; Braun et al., 2019; Chambault et al., 2019). Second, the growing scrutiny and legal rules imposed to the handling and study of threatened megafauna, including the publication of results, requires proven high-standards in research, especially with respect to captivity facilities and at-sea procedures (e.g., tagging and restraining, mitigation of behavioral disruption due to human presence). Third, although the same can be arguably said about other animal groups, it is almost impossible to find situations without some sort of potential human interference on megafauna's individual behavior, given the high sensitivity to human activities (including research) brought about by their general characteristics (large size, high mobility, increased sensory capacities). Thus, it becomes very hard to disentangle the key effects of environmental drivers from human disturbance and, consequently, our capacity to forecast those effects and devise appropriate conservation measures.

There are, however, some areas around the globe where the conditions under which megafauna subsist may be considered less stressful (as opposed to the fable concept of more pristine), as they profit from environmentally sustainable developmental models, adopted rules and cultural behaviors. Arguably, these areas should be broadly favorable from the megafauna conservation biology and research perspectives. Advancing our scientific knowledge and conservation progress on marine megafauna can and should also be capitalized in regions where an exceptional access to multiple species (i.e., megafauna research 'hotspots') combines with the existing adequate legal framework, know-how and research infrastructure. Areas fulfilling the three conditions could, therefore, be targeted for research. In this paper, we argue that the wider Azores region (mid-north Atlantic) is one of such areas, and discuss possible strategies and measures toward achieving that goal.

A MID-ATLANTIC HUB FOR OCEANIC MEGAFAUNA

The Azores (Portugal) is the most remote oceanic archipelago in the north Atlantic, distancing about 1,400 and 2,000 km from continental Europe and north America, respectively. It represents a sub-area of Portugal's Economic Exclusive Zone (EEZ) of around 1 million km^2, one the largest in the European Union. This group of nine volcanic islands and the numerous seamounts surrounding it sits right on the mid-Atlantic ridge at a triple (tectonic plate) junction, and was formed by the high eruptive activity in this region. In climatological-oceanographic terms, the Azores represent an ecotone: its otherwise temperate geographic location is tuned for a subtropical hint by the north Atlantic subtropical gyre via the southeastern branch of the Gulf stream (the Azores current) and its eddies flowing through the southern part of the region (Santos et al., 1995; Caldeira and Reis, 2017). This unique blend of a dynamic oceanography interacting with high seafloor complexity in the middle of the north Atlantic basin is thought to provide the particular conditions which attract oceanic vertebrate megafauna.

The Azores hosts one of the highest cetacean biodiversity in the world, with 24 species of toothed and baleen whales sighted regularly in the region (**Table 1**). It includes a mix of resident species (e.g., bottlenose and Risso's dolphins), species that are present year-round (e.g., sperm whales, common and striped dolphins, pilot whales, *Mesoplodon* beaked whales), and seasonal visitors (baleen whales, Atlantic spotted dolphin, northern bottlenose whale) (Silva et al., 2014). A common trait seems to be the exceptional access to cetacean prey which are available either seasonally (e.g., the krill and baitfish upon which baleen whales and dolphins feed during their spring and summer visits, respectively) or year-round (e.g., the deep-sea squid fed upon by sperm whales – Clarke et al., 1993 – or the mesopelagic prey targeted by dolphins, beaked whales, pelagic sharks or swordfish – Clarke et al., 1995, 1996). Some year-round or seasonal visitors also use the region as a nursery, namely sperm whales, common and spotted dolphins (Silva et al., 2014).

It also represents an important ornithological transition between tropical and temperate regions. Although not ranking as high in number of nesting species than other archipelagic regions such as the Orkneys or Cabo Verde, ten seabird species (six procellariiformes and four charadriiformes) use the Azorean islands and islets as a primary nesting area (**Table 1**). The region holds 100% of the world's breeding population of Monteiro's storm petrel (Bolton et al., 2008), almost 75% of Cory's shearwater, up to 33% of Barolo shearwater and nearly half the European breeding population of roseate tern

TABLE 1 | Resume of the conservation status, pressures and proposed actions for each of the four groups of marine megafauna occurring in the Azores.

	Cetaceans	Seabirds	Sea turtles	Sharks and Large Predatory Fishes
Total no. Species	24	10 (nesting)	5	79
Conservation (no. species)				
IUCN Cr/En/Vu/DD (global assessments)	0/2/2/8	0/0/1/0	2/2/1/0	1/2/20/15
EC Birds/Habitats Directive Annex I or II/IV	1/24	9/0	2/3	
CITES Annexes I/II	8/16	0/0	5/0	6/13
CMS Bonne Annex I/II	5/6	0/2	5/5	18/0
Pressures in the Azores (intensity/actions)				
Target fisheries	Null Maintain legal protection	Null Maintain legal protection	Null Maintain legal protection	Null Maintain legal protection
Fisheries bycatch	Low Maintain fishing regulations and low-impact gears	Low Maintain fishing regulations and low-impact gears	Medium Ban higher-impact gear (pelagic longlines) Use of circle-hooks Implementation of legislation/code of conduct for mandatory release of by-caught animals/avoid hotspots and proper handling	Medium Ban higher-impact gear (pelagic longlines, gillnets) Use of circle-hooks and nylon leader Implementation of legislation/code of conduct for mandatory release of by-caught animals/avoid hotspots and proper handling
Prey depletion	Low R&D on trophic interactions and habitat requirements	Low R&D on trophic interactions and habitat requirements	Low R&D on trophic interactions and habitat requirements	Low R&D on trophic interactions and habitat requirements
Contaminants	Low R&D on contaminant levels and impacts	Low R&D on contaminant levels and impacts	Low R&D on contaminant levels and impacts	Low R&D on contaminant levels and impacts
Litter	Low R&D on litter impact	High Enforce anti-littering legislation Continue education, awareness and clean-up campaigns	High Enforce anti-littering legislation Continue education, awareness and clean-up campaigns	Low R&D on litter impact
Anthropogenic noise	Medium implement stricter permitting processes and stringent regulations for seismic surveying	Not assessed R&D on impacts of noise	Not assessed R&D on impacts of noise	Not assessed R&D on impacts of noise
Light from land	Null	High Implement regulations to reduce disturbance from light sources	Null	Null
Non-indigenous species	Null	High Control/eradication of NIS predators at nesting sites	Null	Not assessed R&D on impacts of NIS (via trophic interactions)
Boat collision	Medium Improved understanding of distribution patterns of large whales and collision risk	Null	Low R&D on distribution patterns of turtles and collision risk	Low R&D on distribution patterns of whale shark and collision risk
Human presence	Medium Tighten and enforce whale-watching legislation	Medium Tighten and enforce non-disturbance legislation	Low R&D on impacts of human presence (whale-watching)	Low Implementation of legislation/code of conduct for shark-diving R&D on impacts of shark-diving

Cetaceans, seabirds, and seaturtle information adapted from Saavedra et al. (2018).

(BirdLife International, 2019), the most oceanic population of this species globally. Studies have also revealed that breeding adults and their reproductive success depend on the epi- and mesopelagic feeding resources around the Azores (Monteiro et al., 1996; Granadeiro et al., 1998; Magalhaes et al., 2008; Amorim et al., 2009; Neves V. et al., 2012; Neves V.C. et al., 2012; Paiva et al., 2018).

Four out of seven species of sea turtles occur in Azorean waters (**Table 1**). The area is used as a prime oceanic juvenile (growth) habitat by the loggerhead turtle population nesting in south-eastern United States (Bolten et al., 1993, 1998) and is along the migratory corridor during oceanic leatherback turtle migrations between feeding and nesting areas (e.g., Fossette et al., 2010). The region's oceanic and ecotonic position favors the blooming along the year of a wide range of gelatinous organisms (Lucas et al., 2014), the main staple of sea turtles in the open ocean (e.g., Frick et al., 2009; Dodge et al., 2011).

Large bony and cartilaginous fishes are another key component of the megafauna ensemble occurring in the region, including six tropical and temperate tuna, five billfishes/spearfishes, five sun/moon fishes, three large groupers (one endemic to Macaronesia) and over 60 species of benthic and pelagic sharks and rays (Porteiro et al., 2010; Das and Afonso, 2017) (**Table 1**). In the case of tuna/billfishes and pelagic/deepsea sharks, this represents a relatively high diversity (e.g., Das and Afonso, 2017). Some are mostly visitors during the warmer season, i.e., June to November (e.g., tropical tuna and billfishes, mobulid rays, whale shark), but others apparently use the area throughout their lives (e.g., groupers, several deepwater sharks, Afonso et al., 2011; Reid et al., 2019) or as a long-term nursery ground for juvenile growth (e.g., blue, smooth hammerhead and tope sharks, Afonso et al., 2014b).

Collectively, these taxa constitute by far the most vulnerable and protected group of animals occurring in the region, including the terrestrial realm (**Table 1**). 80, 29, and 17% of the sea turtles, sharks/fishes and marine mammals that occur in the region are classified as Critically Endangered, Endangered or Vulnerable by the International Union for the Conservation of Nature (IUCN), respectively, and a large number of cetaceans and sharks/fishes are still Data Deficient (**Table 1**). Their catch, trade and use as well as their disturbance and habitat degradation is strictly forbidden by national and international laws and conventions including the EU Common Fisheries Policy (CFP), Natura 2000 and Marine Strategy Framework (MSFD) Directives, the Convention for Biological Diversity (CBD), the Convention on International Trade in Endangered Species of Fauna and Flora (CITES) and the Convention on Migratory Species of Wild Animals (CMS). Nearly all of the large fishes including sharks are of commercial interest worldwide. Large groupers, tuna and most elasmobranchs are IUCN redlisted, protected by international law (e.g., CITES, CBD) and managed tightly by regional marine fisheries organizations, namely the International Council for Exploration of the Sea (ICES) and the International Commission for the Conservation of Atlantic Tunas (ICCAT), in some cases forbidding their catch and trade globally (e.g., mobulid rays, hammerhead and thresher sharks) or in the northeast Atlantic (e.g., most deepwater sharks) (**Table 1**).

In short, the Azores hosts multiple essential megafauna habitats (EMH) for the north Atlantic populations of all four key groups of vulnerable/endangered marine megafauna combined (marine mammals, seabirds, sea turtles, fishes), be them feeding, mating, spawning, pupping, or even resting grounds during their large scale migrations. In addition, documented large-scale migrations, from both Azorean and non-Azorean-based tracking studies, directly connect these EMH in the Azores to the eastern and western north Atlantic and/or to the arctic waters and the tropical/equatorial regions at the individual spatial ecology level of several whales (Silva et al., 2013; Prieto et al., 2014, 2017), seabirds (González-Solís et al., 2007; Neves et al., 2015; Ramos et al., 2015), turtles (Bolten et al., 1998), sharks (Afonso et al., 2014a; Thorrold et al., 2014; Vandeperre et al., 2014) and tuna/billfishes (Druon et al., 2016) (**Figure 1**).

From the broader Atlantic scale perspective, the wider Azores emerge as a singular multispecies oceanic EMH hotspot on a migratory crossroads, linking the eastern to western basin margins as well as the cold productive boreal waters to the tropical and equatorial seas. Yet, we still lack the basic knowledge of the population dynamics, spatial ecology and fine-scale behavior for most of these species, and therefore ignore the full extent of the region's role (and any other region, for that matter) for marine megafauna conservation. Nevertheless, it is clear that the relevance of this Atlantic hotspot results from (1) the diversity of meso- and local scale EMH hotspots located in Azorean island shores, adjacent deepsea and open ocean, some of which are concurrently utilized by multiple species, and (2) the valuable resources (food, shelter, mates, nests) they offer for the survival of the resident and visiting megafauna.

HARNESSING MEGAFAUNA TO SPEARHEAD AN INTEGRATED MARINE CONSERVATION, RESEARCH AND DEVELOPMENT STRATEGY

Marine megafauna populations face rising menaces at the broad scale of their ocean basin distribution and movements including: (1) the targeted or accidental capture by longlining and purse-seining industrial fishing (e.g., Bolten et al., 1998; Ferreira et al., 2001; Amandè et al., 2011; Filmalter et al., 2013); (2) the degradation of their habitat due to chemical, noise and light pollution (Halpern et al., 2008; Fontaine et al., 2011; Peng et al., 2015; Rodríguez et al., 2017; Romagosa et al., 2017), to introduced predators and diseases (e.g., Fontaine et al., 2011; Hermosilla et al., 2016; Neves et al., 2017) or to traffic (Tournadre, 2014); (3) the effects of climate change such as rising sea temperatures (Sundby et al., 2016) and the expansion of oxygen minimum zones (Stramma et al., 2012) which may lead to physiological stress, reduced foraging opportunities or higher parasite loads, and to the subsequent reduction of their physiological condition and reproductive success. These threats are recognized in current European (MSFD and N2000) and global (CBD, Ramsar, Convention for the protection of the marine environment of the northeast Atlantic OSPAR) policies, which tie signatory countries including Portugal to establishing effective protection measures and rigorous scientific monitoring programs.

The global oceans already support few areas of wilderness and even less so in the northern hemisphere and the Atlantic Ocean (Jones et al., 2018). The wider Azores region is one area where those threats, taken together, are less severe and with a slower annual change in the north Atlantic (Halpern et al., 2008, 2019). The region hosts a small (1/4 million) human population and promotes a sustainable development model, with ecotourism now being the fastest growing sector. Fisheries are essentially artisanal and, although the Azores was once an arena for whaling, there is no taking of cetaceans, seabirds or turtles for decades. A moratorium put in place by the European Commission in 2005 as a result of the region's previous policies (independent of the EU CFP) bans all trawling inside the Azores EEZ (Probert et al., 2007). Tuna are an important fishery but caught exclusively using one-by-one line fishing. The bottom hooks-and-lines fishery by-catches very small elasmobranch quantities compared to continental fisheries (Torres et al., 2016; Fauconnet et al., 2019). Industry is very small in scale, and direct sources of human pollution considered to be of minor concern. There are also conservation

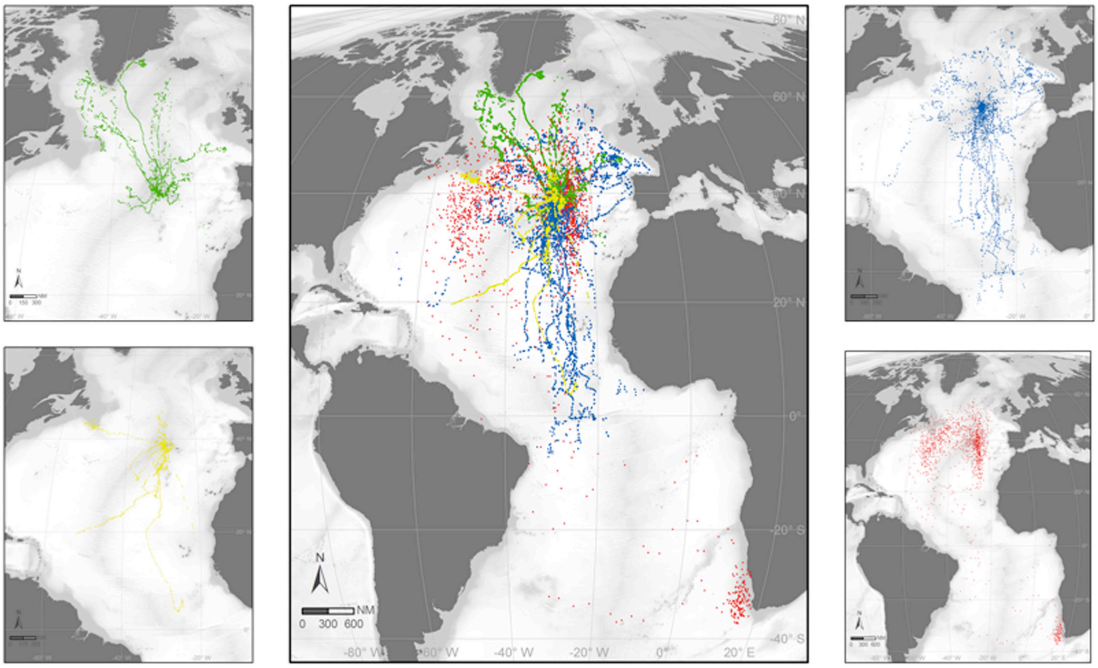

FIGURE 1 | Graphic representation of various megafauna tracks obtained via satellite tagging programs implemented in the Azores archipelago. Dots represent estimated positions from individual baleen whales (green), seabirds (red), and large pelagic teleost (yellow) and cartilaginous (blue) fishes. Redrawn from data in published (see text) and unpublished reconstructed geolocations, GPS-logged or ARGOS positions.

policies and best practice programs implemented by the region that target or benefit megafauna: The Azores has one of the largest and more diverse networks of marine protected areas (MPAs) in Europe and the Atlantic, covering a mix of coastal, oceanic and deep-sea habitats (including several seamounts and pelagic seabird foraging areas), although many still require specific regulations and proper enforcement (Abecassis et al., 2015); whale and shark watching are limited to legally defined carrying capacities and codes of conduct are broadly followed by operators; several public and civil environmental education and impact mitigation programs are now well established, such as the annual rescue campaign of seabird fledglings (Fontaine et al., 2011), the marine litter cleaning events, and the catch-and-release in big-game fishing.

Yet, the region's megafauna also faces some threats locally. The most evident is the high by-catch of pelagic sharks and sea turtles in the EU pelagic longlining occurring within Azorean waters (Pham et al., 2013; Afonso et al., 2014b) (**Table 1**). The increasing marine traffic and noise produced by international cargo vessels, inter-island fast ferries and whale-watching vessels are also a potential problem to cetaceans and other marine megafauna (Romagosa et al., 2017). Documented areas of megafauna aggregation, such as the cetacean ground south of Pico and Faial islands and the of large pelagic fishes aggregations on the summits of the Princess Alice, Condor and Formigas banks, still lack effective protection even when already declared as an MPA (Abecassis et al., 2015; Afonso et al., 2018). Marine litter is, as elsewhere, a growing and pervasive problem all way up to megafauna (Pham et al., 2014).

We argue that the current international-to-local push for an integrated conservation approach and full implementation of a sustainable development model in the Azores, where sustainable harvest levels based on low impact gear and effort may subsist with ecotourism, can support the future integrity of this EMH hotspot. This model could also have major impacts in promoting an innovative Blue Economy agenda leveraged on R&D, where hybrid research programs based on new technological developments could foster cutting edge science on megafauna behavior and biologging, and vice-versa. Some already existing examples demonstrate the feasibility of developing this concept (e.g., Fontes et al., 2018a,b). Importantly, it could promote substantial opportunities for studying and testing the ecosystem approach to the management of marine resources and the understanding of ecosystem-level impacts of climate change. The multispecific nature of this megafauna hotspot also renders it an added opportunity in that it allows the concurrent study of both patterns and processes and the transversal hypothesis testing involving evolutionarily contrasting species, thus partially overcoming the traditional limitation of understanding those mechanisms using single-species approaches.

Thus, the Azores fulfills the three major conditions to qualify as an area of priority for research and development on megafauna conservation biology. The strategic centrality of the region, its exceptional access to multiple megafauna species and hotspots very close to harbor, and its historical low levels of (artisanal) fisheries impact, pollution, and reduced habitat degradation when compared with most other regions, turn it into a realistic opportunity with substantial gains and few, if any, downsides.

AN ACTION PLAN

In order to promote and materialize this vision, we propose an integrated action plan.

Fist, this plan should ensure the long-term survival of effective measures already in place, including an unequivocal political commitment to enforce and periodically reassess current management and conservation measures. On the legal side, these measures include the maintenance of the current legal conservation status of most megafauna species (cetaceans, seabirds, turtles, some elasmobranchs) as well as their associated protection actions (e.g., protection and restoration of seabird nesting sites, mandatory release of listed turtle and shark species), the maintenance of the trawling ban and the prohibition of high impact tuna fishing practices in the region, or the maintenance of the broad protection status of some offshore areas, including seamounts (**Table 1**).

Second, the region should adopt new and expand existing protecting measures when necessary in order to ensure an effective contribution to the conservation of megafauna populations. Among the most obvious are a set of measures to protect pelagic and coastal sharks, which currently have little protection, including the banning of shark landings and gears with higher shark by-catch (i.e., pelagic longlining and coastal gillnetting) and the adoption of best practices to release sharks and turtles in surviving conditions (**Table 1**). Both these fisheries have a minor social-economic impact in the Azores as they contribute a very small fraction to the landings and the number of employments (Carvalho et al., 2011; Pham et al., 2013). Fifteen coastal countries in the Atlantic, Indian, and Pacific Oceans have already opted to ban commercial shark fishing altogether, and have laws that prohibit the possession, trade or sale of sharks and shark products (Ward-Paige and Worm, 2017). Another would be a set of measures targeting cetaceans, such as tightening and effectively enforcing the whale watching codes of conduct and legislation, establishing stringent regulations to reduce noise (including seismic surveying) and the risk of ship strike in areas of high cetacean concentration. Finally, the region should establish no-take MPAs in areas known to serve as multispecific EMHs. The very few currently existing no-take areas in the Azores are all coastal and very small in size (Abecassis et al., 2015; Afonso et al., 2018) and, consequently, have very little, if any, impact on megafauna populations. This measure could be easily achievable by updating the current legislation and zoning of some partially protected MPAs that are known to host multiple megafauna, such as the Condor, D. João Castro, Formigas and Princess Alice seamounts.

Third, this plan requires an ambitious research agenda that can ensure the acquisition of relevant knowledge from local to global scales in support of megafauna conservation while effectively promoting R&D. For example, a thorough multidisciplinary investigation of where those multispecific hotspots are located (patterns) and why they are important (processes) for diverse megafauna is needed in order to better understand what would be the sites of priority for full protection, and what would be the relative contribution of creating a 'megafauna sanctuary' to the populations' health. However, achieving that goal will take several years to decades, even in a relatively well studied area such as the Azores. This agenda should thus focus on ensuring an adequate level of multidisciplinary research infrastructure and funding for the next decade in the region. Essential to the feasibility and broader benefits of this agenda is to be anchored on international collaborations and partnerships that can ensure state-of-the-art scientific and technological developments.

Such an action plan could benefit not only many highly migratory megafauna populations that live and depend on the broader Atlantic Ocean basin, but also leverage the Azores and its marine megafauna as a case study for global environmental awareness of the stakeholders and the wider public about the urgent need for an effective ecosystem approach to marine management. It can serve as a flagship political program to change practices, techniques, policies and options while promoting ocean literacy that help revert the problems menacing marine conservation.

DATA AVAILABILITY STATEMENT

The datasets for this study will not be made publicly available since the data has not yet been published. The data used in the broad mapping presented in **Figure 1** is part of a separate publication and will be available once finalized.

AUTHOR CONTRIBUTIONS

PA designed the study and drafted the manuscript. All other authors improved the draft and critically reviewed the manuscript. PA, MS, and MM provided additional data for **Figure 1**. FV produced the re-analysis and mapped the data on **Figure 1**.

FUNDING

We acknowledge funds provided by the Portuguese Science & Technology Foundation (FCT) through individual contracts/grants to PA (IF/01640/2015), JF (M3.1.a/F/062/201), MS (IF/00943/2013), RP (SFRH/BPD/108007/2015), TM (IF/01194/2013 and IF/01194/2013/CP1199/CT0002), and FV (CEECIND/03469/2017), and to MARE through the strategic project (UID/MAR/04292/2013), the Azorean Science & Technology Fund (FRCT) through individual contracts/grants to TM (PO2020/Acores-01-0145-FEDER-000056) and VN (M3.1.a/F/006/2016/008), the US Fish and Wildlife Service through individual contracts/grants to FV (project COSTA 4, Marine Turtle Conservation Fund F18AP00321), and the EC through individual contracts/grants to PA (H2020 project MEESO, grant agreement no. 817669), MS (project MysticSeas, grant agreement no. 11.0661/2017/750679/Sub/ENV,C2), and TM (H2020 project ATLAS, grant agreement no. 678760).

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