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Impact of the Adriatic–Ionian bimodal oscillating system (BiOS) on the biodiversity patterns of the larval fish community in the north-eastern sector of the Strait of Sicily (central Mediterranean, Malta Channel)

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Off the southern coast of Sicily, the frontal region south of Cape Passero (Malta Channel) provides favorable conditions for fish larvae survival and development and hosts a biodiversity hotspot for larval assemblages. In this area, the analysis of ichthyoplankton data collected during 16 oceanographic summer surveys, carried out every year over the period from 2001 to 2016, shows a cyclical pattern in the yearly average larval biodiversity, which appears to be linked to the alternating cyclonic/anticyclonic surface circulation of the North Ionian Gyre (NIG), associated with the Adriatic–Ionian bimodal oscillating system (BiOS). Specifically, the cyclonic mode of NIG, by enhancing the advection of Modified Atlantic Water (MAW) toward the southern Levantine Basin and reducing its deflection toward the Adriatic, is supposed to intensify the frontal thermohaline structure, thus inducing higher retention/survival rates for fish larval stages and, definitively, resulting in higher biodiversity. The association between total fish larval density and biodiversity with available environmental data, namely, satellite-derived sea surface temperature (SST) and *in situ* temperature, salinity, and surface current speed, corroborates this hypothesis. Finally, the observed changes in the biodiversity of the larval fish community would result from increased/reduced retention time for fish larvae (and accordingly, slower/faster larval dispersal) across the frontal area, as induced by the alternating cyclonic–anticyclonic modes of NIG. These results pave the way for future investigations on the role of surface circulation patterns in the dynamics of fish populations,

with special emphasis on the effects of retention processes on fish larval stages.

KEYWORDS

biodiversity, fish larval assemblages, central Mediterranean (southern Italy), Strait of Sicily, surface circulation pattern, north Ionian Sea, Adriatic–Ionian bimodal oscillating system (BiOS)

Introduction

Surface circulation in the Strait of Sicily (SoS) is dominated by the movement of Modified Atlantic Water (MAW), which is known as the "Atlantic Ionian Stream" (AIS) off the southern Sicilian coast; this meandering current flows from the western Mediterranean basin toward the Ionian Sea (Robinson et al., 1999). The path of AIS is characterized by high inter-annual variability, with consequences on the predominant oceanographic phenomena occurring in the region, including the offshore extension of coastal upwelling and the formation of frontal structures, such as the thermohaline front characterizing the eastern border of the Malta Channel off the southernmost tip of Sicily (Cape Passero) (Bonanno et al., 2014).

Although the upwelling events off the southern Sicilian coasts can enrich the typically oligotrophic Mediterranean waters (Piccioni et al., 1988; Patti et al., 2010), the advection of surface waters from coastal areas may be detrimental to the survival of fish larval stages due to food availability constraints characterizing the offshore environment (García-Lafuente et al., 2002; Palatella et al., 2014; Cuttitta et al., 2016; Cuttitta et al., 2018). In general, the AIS path impacts the reproductive ecology of many fish species, as the egg and larval stages are mostly concentrated in the surface layer. Previous studies mainly focusing on the European anchovy (*Engraulis encrasicolus*, Linnaeus, 1758) have shown that the Cape Passero front is an important retention area for fish larval stages, with favorable environmental conditions supporting their survival and development (Basilone et al., 2004; Falcini et al., 2015; Torri et al., 2018). More specifically, it has also been suggested that a longer residence time of larvae in the frontal area may be beneficial for the recruitment success of parental fish populations, and eventually, for short-lived species, it may even play a role in modulating the total fish stock biomass. Notably, for the anchovy stock off the southern Sicilian coast, most of the variance in yearly biomass has been demonstrated to be driven by larval retention processes in the continental shelf area (Patti et al., 2020). In the same area, the analysis of ichthyoplankton survey-based data collected during the summer of the years 2001–2016 has pointed out the role of the Cape Passero thermohaline front in sustaining the biodiversity of larval fish assemblages. Actually, this frontal structure was found to represent an important biodiversity hotspot (Patti et al., 2022).

This study aims to investigate the possible role of local surface circulation patterns in modulating the yearly changes in larval biodiversity across the frontal area south of Cape Passero in relation to the alternating cyclonic–anticyclonic mode of the North Ionian Gyre (NIG) as influenced by the Adriatic–Ionian BiOS (Borzelli et al., 2009; Civitarese et al., 2010; Gačić et al., 2013; Placenti et al., 2022; Civitarese et al., 2023; Placenti et al., 2024). Specifically, we investigated the potential impact of the enhanced MAW advection toward the southern Levantine basin induced by the cyclonic phase of NIG (Schroeder et al., 2017 and internal references) on larval retention and the associated observed increase in biodiversity across the Cape Passero front.

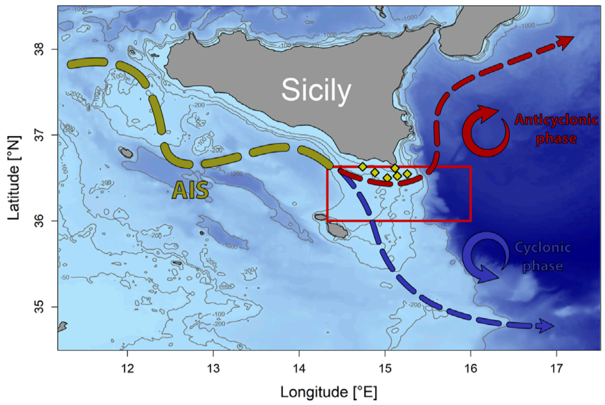

FIGURE 1
Map of the study area. The yellow points indicate the location of the six sampling stations selected for the analysis in this study. They were sampled each year in July from 2011 to 2016, for a total of 96 sampling hauls. The red rectangle delimits the area considered for the analysis of satellite-based SST maps. The dashed green line schematically represents the typical meandering path of the AIS in the Strait of Sicily. Furthermore, a stylized depiction of the relationship between the AIS pathway and the NIG circulation mode is shown in red (anticyclonic phase) and blue (cyclonic phase), respectively, as described in the literature.

Material and methods

Ichthyoplankton data used in this study come from a time series of 16 oceanographic surveys carried out in the SoS during the summer (with July 14th as the central day of the surveys; Patti et al., 2022) from 2001 to 2016; these surveys were conducted using the same systematic spatial coverage and standardized sampling procedures. In particular, as our focus for this study is on the frontal region south of Cape Passero, the analysis was limited to data collected in six sampling sites located in the Malta Channel across the thermohaline front, representing a subset out of 37 stations covering the whole northern sector of the SoS and used in Patti et al. (2022), for a total of 96 sampling hauls (six sampling sites x 16 annual surveys) (Figure 1).

Plankton samples were gathered using a Bongo40 net, which has a 40-cm opening and a 200-µm mesh size. This sampling yielded approximately 3,000 larval specimens, classified into 38 families. To assess the annual total larval density, raw specimen counts for

TABLE 1 Average density (#/10 m^2) and relative abundance (%, percentage) of larval fish families identified in the study area (six selected stations) over the summer surveys during 2001–2016.

Family	Ecological group	#/10 m^2	%
Ammodytidae	B	0.29	0.07
Apogonidae	B	0.26	0.07
Blennidae	B	0.87	0.26
Bothidae	B	6.33	1.57
Callionymidae	B	4.79	1.21
Centracanthidae	B	7.25	1.64
Centriscidae	EP	0.35	0.11
Cepolidae	B	1.18	0.29
Congridae	B	0.19	0.04
Gadidae	B	2.25	0.66
Gobiidae	B	45.63	12.24
Labridae	B	28.86	6.62
Merlucciidae	B	1.00	0.22
Mugilidae	P	0.66	0.18
Ophidiidae	B	0.45	0.11
Phycidae	B	0.13	0.04
Pleuronectidae	B	0.98	0.33
Scophthalmidae	B	0.51	0.07
Scorpaenidae	B	0.40	0.11
Serranidae	B	12.01	2.74
Soleidae	B	0.09	0.04
Sparidae	B	14.30	3.40
Syngnathidae	B	0.13	0.04
Trachinidae	B	0.90	0.18
Triglidae	B	0.52	0.15
Clupeidae	P	70.30	18.68
Engraulidae	P	111.09	29.90
Bramidae	P	0.52	0.15
Caproidae	B	0.12	0.04
Evermannellidae	B	0.27	0.04
Gonostomatidae	M/B	31.73	7.13

(Continued on the following page)

TABLE 1 (*Continued*) Average density (#/10 m^2) and relative abundance (%, percentage) of larval fish families identified in the study area (six selected stations) over the summer surveys during 2001–2016.

Family	Ecological group	#/10 m^2	%
Myctophidae	M	22.79	5.30
Paralepididae	M	1.76	0.40
Phosichthyidae	M	2.74	0.66
Sternoptychidae	M	0.33	0.11
Carangidae	BP	3.40	0.91
Pomacentridae	B	7.13	1.43
Scombridae	EP	12.19	2.89
Total		394.72	100.00

Ecological group: B, benthic; P, pelagic; EP, epipelagic; M, mesopelagic; BP, Bathypelagic (Rodríguez et al., 2017).

all identified taxa were standardized per station to numbers per square meter. This standardization was based on the volume of seawater filtered by the plankton net, measured using mechanical flowmeters (General Oceanics Inc., FL, United States), and the tow depth for each sample. These standardized counts were then averaged annually. The temporal changes in the biodiversity of larval fish assemblages were analyzed by calculating the average yearly Shannon–Wiener diversity index (H′) at the family level, which is defined as follows:

$$H' = -\sum_{i=1}^{n} (p_i * ln\, p_i),$$

where p_i is the proportion of taxon (family) i in the sample and ln p_i is the natural logarithm of this proportion (Shannon and Weaver, 1949; Spellerberg and Fedor, 2003; Magurran, 2004).

Continuous vertical profiles of environmental data were collected at plankton stations to characterize the physical properties of the water column. The (downcast) data used for this study, obtained by a multi-parametric SBE 11plus CTD probe, were quality-checked according to the Mediterranean and Ocean Data Base guidelines (Brankart, 1994) and processed using Seasoft-Win32 software.

From the environmental data collected with CTD casts, the parameters included in the analysis were temperature and salinity. As most fish larvae occur in the surface layer (Palomera, 1991; Mazzola et al., 2000), the 10-m depth was used as a reference for temperature and salinity values at the selected stations. Specifically, the average values from the first 10 m of the water column were used as representative values of surface conditions as the mixed layer depth typically exceeds 10 m during summer.

The surface circulation in the same area was characterized with the zonal (u) component of absolute geostrophic currents using a product delivered by Copernicus Marine Environment Monitoring Service available for download as daily data with a spatial resolution of 0.125 × 0.125° (CMEMS, 2019).

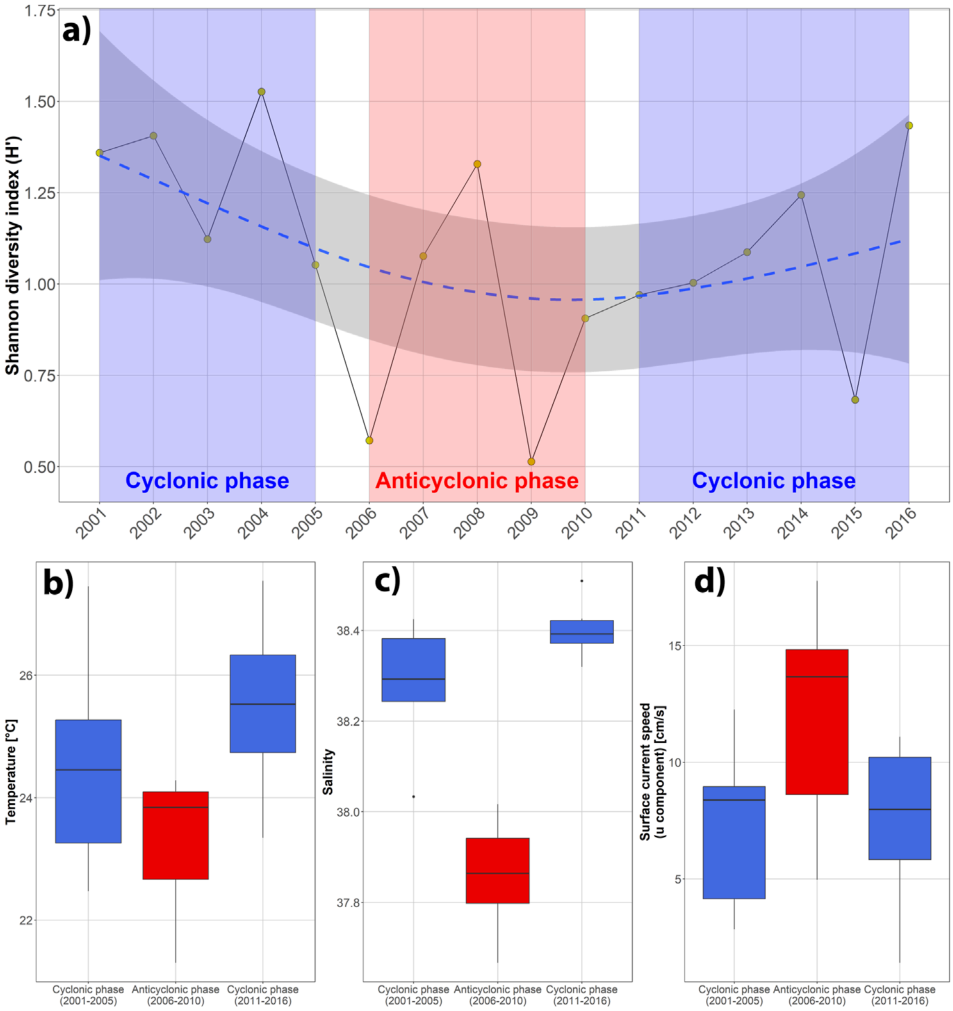

FIGURE 2
(a) Time series of the Shannon diversity index calculated as the average across the six sampling stations. A generalized additive model (GAM; dashed blue line) with its corresponding confidence interval (gray shaded area) was applied to highlight the trend of the index between 2001 and 2016. Additionally, the circulation modes of the NIG are represented as blue areas (cyclonic phase) and red areas (anticyclonic phase) in the graph. **(b, c)** Boxplots of *in situ* surface temperature and salinity, respectively, which were averaged over the first 10 m at each station. Annual observations are grouped according to the NIG circulation mode. **(d)** Boxplot of the zonal (*u*) component of the surface current speed, as derived from remote sensing in correspondence to the sampling stations. Annual observations are grouped according to the NIG circulation mode.

For correlation analysis, the environmental data collected *in situ* (10-m temperature and salinity) and the corresponding satellite-based surface current information were then associated with each one of the plankton stations included in this study based on the locations in space and time of the sampling hauls.

In addition, in order to further characterize the frontal area, satellite-based sea surface temperature (SST) data were also analyzed (CMEMS, 2025). Specifically, The High-Resolution L4 Sea Surface Temperature Reprocessed dataset was used, which consists of daily, optimally interpolated (L4), satellite-based SST estimates and is available for download at a 0.05° resolution grid. Average monthly (July) SST maps from 2001 to 2016 over the region delimited by latitude 36°00′N–36°38′N and longitude 14°20′E–16°00′E, covering the frontal zone in the Malta channel (see the area delimited by the red rectangle in Figure 1), were then derived, and the corresponding ranges in SST were evaluated. The associations between abiotic and biotic parameters were investigated through linear relationships, while the temporal trend of the Shannon diversity index was depicted with a generalized additive model (GAM; Hastie and Tibshirani, 1990) using the R package “mgcv” (Wood, 2011).

Results

The average larval density per unit surface (10 m^2) and the relative abundance (%) aggregated at the family level over the years 2001–2016 are provided in Table 1. The stations included in this study are a subset of the continental shelf stations considered by Patti et al. (2022), specifically those limited to the frontal zone south of Cape Passero. Locally, the estimated mean total larval density (394.72 #/10 m^2; Table 1) is significantly higher than the average

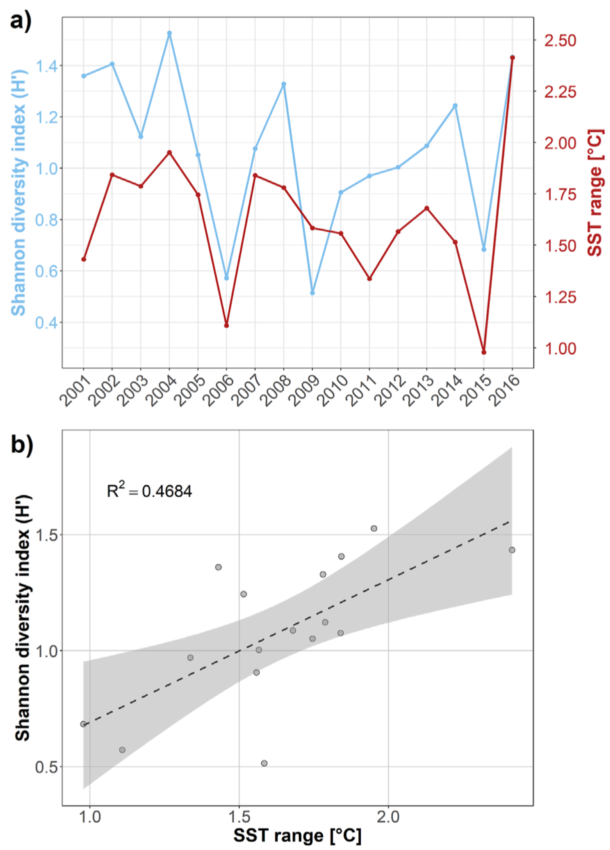

FIGURE 3
(a) Time series of the SST range in the rectangular region over the thermohaline front of Cape Passero displayed in Figure 1A and the average Shannon diversity index calculated from the available ichthyoplankton sampling stations in the same area. **(b)** Linear relationship between the Shannon diversity index and the SST range.

total density value calculated over all the 19 shelf stations included in their study by Patti et al. (2022) (272.02 #/10 m^2), confirming that the study area represents an important retention area for the early life stages of many fish species.

Figure 2A shows the time series of the average yearly Shannon diversity index of larval fish assemblages over the years 2001–2016 across the frontal area south of Cape Passero. Larval biodiversity is characterized by a cyclical pattern, which appears to be associated with the alternating cyclonic–anticyclonic modes of NIG, with higher diversity values during the cyclonic phase of NIG. Particularly, during the years 2001–2016, the NIG presented two cyclonic phases and one anticyclonic phase, with important consequences on the Mediterranean thermohaline circulation. The cyclonic mode of NIG can enhance the advection of the relatively less salty and colder MAW toward the southern Levantine basin and reduce deflection toward the Adriatic (Schroeder et al., 2017). This process favors the flow of saltier and warmer water from the Levantine basin to veer toward the northern Ionian Sea and in the eastern Sicily area, thus potentially enhancing the gradient of the frontal structure south of Cape Passero. This seems to be confirmed by the local higher average salinity and temperature values (Figures 2B,C) and the lower average surface current speed (i.e., the *u* component of the geostrophic velocity) (see Figure 2D) observed during the two cyclonic phases of NIG. This surface circulation pattern, by reducing larval dispersal rates toward the Ionian Sea, is supposed to impact the observed biodiversity levels by enhancing larval retention processes. Actually, during the cyclonic mode of NIG, we observed higher larval density associated with lower values in the zonal component of the surface current speed, and the two series are significantly anti-correlated (R^2 = 0.25; p < 0.005).

The role of the frontal structure in modulating the observed larval biodiversity was further investigated using a different independent approach aimed at estimating the intensity of the front. Since during the summer, the density front south of Cape Passero is typically well identified by surface temperature, we used the range in the values of July SST maps covering the frontal area from 2001 to 2016 as a proxy for the yearly changes in the strength of the front itself. The SST range and Shannon diversity index were found to have similar patterns (Figure 3A), with higher average SST ranges during the cyclonic mode of NIG (Figure 3B), and the two time series are positively correlated (R^2 = 0.47; p < 0.001).

Discussion and conclusion

The results of the present study support the hypothesis that the cyclonic circulation mode of the North Ionian Gyre (NIG), by influencing the characteristics of the thermohaline front, has positive implications for larval biodiversity levels in the area south of Cape Passero *via* enhanced retention processes. Actually, the higher biodiversity levels registered during the cyclonic mode of NIG correspond to an increase in larval retention processes related to physical traits of local surface circulation patterns. In addition, the observed significant positive correlation between the biodiversity index and the SST range further supports the idea that high larval biodiversity is linked to the strengthening of the frontal structure, which reduces the eastward component of the current and enhances larval retention rates within the study area. However, it cannot be excluded that the cyclonic phase, with its counter-clockwise surface circulation, might promote an additional advective mechanism—unaddressed in this study—originating from the northern Ionian Sea, which could synergistically contribute to the observed biodiversity increase. Torri et al. (2023), which was conducted in the same area during a cyclonic phase, showed that this southward advective process may, in some cases, represent the primary larval transport mechanism in the waters off Cape Passero. In this context, the counter-clockwise circulation of the NIG would exert a dual effect on biodiversity in the region. On one hand, it would strengthen the retention mechanism for larvae originating from the northwestern area by reinforcing the frontal structure; on the other hand, it would act as an additional conveyor belt, channeling planktonic stages deposited in the northern Ionian zone into the study area. The opposite occurs during the NIG anticyclonic phase, characterized by lower larval biodiversity. The clockwise circulation mode favors the weakening of the frontal structure, the increase in the zonal component of the surface current velocity, and the subsequent dispersal of larvae in the Ionian Sea. So, the alternating cyclonic/anticyclonic modes of NIG are believed to be able to modulate the changes in the biodiversity of larval fish assemblages in the study area. The results of this study provide new evidence on the potential role of the BiOS as a natural regulator of biodiversity in Mediterranean waters, as recently reported by Civitarese et al. (2023) for the eastern basin, and on the importance of connectivity processes for the reproductive ecology of fish populations and the sustainable exploitation of their stocks (Cowen et al., 2006; Cuttitta et al., 2018; Patti et al., 2018; García-Lafuente et al., 2021).

However, future research is necessary in order to identify the factors that sustain larval retention and survival and the associated biodiversity. This would include the study of the interaction of the observed larval biodiversity patterns with more detailed information on the environmental conditions experienced by fish larvae, which would also involve, e.g., the use of Lagrangian simulations of larval back trajectories (Falcini et al., 2020; Torri et al., 2023), a closer investigation of the main species affecting fish community dynamics, and eventually the adoption of advanced analytical approaches such as hierarchical spatio-temporal Bayesian modeling (Granata et al., 2024). Finally, the role of climate change (i.e. sea warming) as a possible driver of abiotic factors influencing BiOS and the larval fish community needs to be investigated.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

BP: conceptualization, funding acquisition, supervision, writing – original draft, writing – review and editing, data curation, formal analysis, methodology, resources, and software. MT: methodology, writing – review and editing, formal analysis, software, and visualization. FP: formal analysis, software, writing – review and editing, and methodology. AC: methodology, writing – review and editing, data curation, supervision, and validation.

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