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SYSTEMATIC REVIEW
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Epibiotic Fauna on Cetaceans Worldwide: A Systematic Review of Records and Indicator Potential

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Each individual cetacean is an ecosystem itself, potentially harboring a great variety of animals that travel with it. Despite being often despised or overlooked, many of these epizoites have been proven to be suitable bio-indicators of their cetacean hosts, informing on health status, social interactions, migration patterns, population structure or phylogeography. Moreover, epizoites are advantageous over internal parasites in that many of them can be detected by direct observation (e.g., boat surveys), thus no capture or dissection of cetaceans are necessary. Previous reviews of epizoites of cetaceans have focused on specific geographical areas, cetacean species or epibiotic taxa, but fall short to include the increasing number of records and scientific findings about these animals. Here we present an updated review of all records of associations between cetaceans and their epibiotic fauna (i.e., commensals, ecto- or mesoparasites, and mutualists). We gathered nearly 500 publications and found a total of 58 facultative or obligate epibiotic taxa from 11 orders of arthropods, vertebrates, cnidarians, and a nematode that are associated to the external surface of 66 cetacean species around the globe. We also provide information on the use as an indicator species in the literature, if any, and about other relevant traits, such as geographic range, host specificity, genetic data, and life-cycle. We encourage researchers, not only to provide quantitative data (i.e., prevalence, abundance) on the epizoites they find on cetaceans, but also to inform on their absence. The inferences drawn from epizoites can greatly benefit conservation plans of both cetaceans and their epizoites.

Keywords: epibiotic, fauna, cetacean, indicator, systematic review, checklist

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INTRODUCTION

General Features of Epibiosis in Cetaceans

Cetaceans have developed a number of symbiotic associations (*sensu* Leung and Poulin, 2008) with other organisms, including endo-, meso- and ectoparasitism, commensalism, and mutualism (e.g., Arvy, 1982; Raga, 1994). Some of these organisms, the epibionts (also known as episymbionts or ectosymbionts), are associated to the external surface of cetaceans and can be classified into two basic types. On the one hand, ectoparasites live in/on the skin and cause a variable degree of harm by feeding on hosts' integument (e.g., Smyth, 1962; Geraci and St. Aubin, 1987; Hopla et al., 1994). On the other hand, commensals or phoronts do not trophically depend on the tissues of cetaceans (also named basibionts in this case), thus they are generally harmless but benefit from epibiosis in multiple ways, e.g., *via* an improved feeding performance, reduction of predation, favored intraspecific contacts for reproduction, or offspring dispersion (Anderson, 1994; Seilacher, 2005; Carrillo et al., 2015). Not surprisingly, though, the limits of each type of interaction are not always clear-cut. For instance, whale-lice (fam. Cyamidae) are considered ectoparasites that primarily feed on hosts' skin, but it has been speculated that they may opportunistically feed on plankton, even helping whales to detect plankton blooms, leading to a potentially mutualistic relationship (Rowntree, 1996). Or, high loads of commensal epibionts could increase the swimming drag or damage the skin on the site of settlement, thus producing indirect harm to cetaceans (Tomilin, 1957).

Given the high variety of life cycles of the epibionts of cetaceans, it is perhaps not surprising that their specific interactions are similarly diverse. Some epibionts depend strictly on cetaceans during their whole life (e.g., whale lice; Leung, 1976), whereas others use them only at some stages (e.g., barnacles; Nogata and Matsumura, 2006). Among commensals, many species are obligate epibionts, settling exclusively on cetaceans (e.g., coronulid barnacles; Hayashi et al., 2013), but others can colonize also inanimate substrata such as vessels or floating debris (e.g., *Conchoderma* spp. and *Lepas* spp.; Frick and Pfaller, 2013). The degree of host/basibiont specificity is also variable. For instance, many whale lice are known only from single, or a few, host species (Iwasa-Arai and Serejo, 2018), but other epibionts have a very broad host spectrum (e.g., *Xenobalanus globicitipitis* Steenstrup, 1852 or *Pennella balaenoptera* Koren & Danielssen, 1877; Kane et al., 2008; Fraija-Fernández et al., 2018). Finally, there are examples of hyperepibiosis in which some epibionts, e.g., barnacles, can act as basibionts for other epibionts, e.g., *Conchoderma* spp. or cyamids (Cornwall, 1927; Matthews, 1937; Leung, 1970a).

Susceptibility and Health Impact of Cetacean Epibiosis

As many other symbionts, epibionts must succeed twice to live their associative life. This two-step process is mediated by the so-called encounter and compatibility filters (Combes, 2001). First, spatial and temporal overlap must take place for initial settlement. Second, whether the host is a suitable substratum will determine survival and/or reproduction on it. Epidermis renewal and hydrolytic substances of cetacean skin may prevent fouling, at least to some extent (Hicks 1985; Baum et al., 2000; Baum et al., 2001), but skin regeneration and immune functions are seemingly lower in debilitated dolphins (J. R. Geraci and S. H. Ridgway pers comm. in Aznar et al., 1994). Poor health can also result in slower swimming (Aznar et al., 1994; Lehnert et al., 2021), fostering better conditions for epibiotic settlement (e.g., providing more time for contact with blooms of free-living infective stages, or mild water flow over the host's body, thus reducing drag and facilitating initial colonization). For instance, striped dolphins, *Stenella coeruleoalba* (Meyen, 1833), infected by morbillivirus and in poor nutritional condition harbored high loads of parasitic and commensal epizoites (Aguilar and Raga, 1993; Aznar et al., 1994; Aznar et al., 2005). Also, higher prevalence of cyamids in porpoises could hint a higher incidence of disease-related skin injuries, where they attach (Lehnert et al., 2021). Another example is the massive infestation of cyamids on a stranded humpback whale, *Megaptera novaeangliae* (Borowski, 1781), that suffered from severe discospondylitis and, as a result, reduced mobility (Groch et al., 2018).

Once settled, the impact of epibionts on cetacean health varies among taxa (especially between ectoparasites and commensals; see above). For instance, the mesoparasite *Pennella balaenoptera* penetrates the skin and blubber of its hosts; this process has been related to both macro- and microscopic lesions such as abscesses, inflammation, and dermatitis (Cornaglia et al., 2000; Gomerčić et al., 2006; IJsseldijk et al., 2018). In contrast, no direct damage has been related to whale lice infections (e.g., Migaki, 1987; Lehnert et al., 2021), although it has been speculated that their occurrence may hinder skin healing processes (Lehnert et al., 2021). On the other hand, the possibility that some cetacean epibionts can act as viral or bacterial vectors is an open question, as it has been observed for ectoparasitic crustaceans parasitizing fish (Smit et al., 2019) or lice infecting seals (La Linn et al., 2001). Climate changes have shifted the geographical distribution of arthropod-borne viruses (Gould and Higgs, 2008) and whether these may emerge in cetaceans and even be transmitted by their epibonts (e.g., ectoparasitic lice, see Van Bressem et al., 2009) remains unknown.

Epibionts as Cetacean Indicators

Due to temporal or permanent association with their hosts/basibionts, both endoparasites and epibionts represent a cost-effective tool to study multiple facets of cetacean biology (e.g., Dailey and Vogelbein, 1991; Balbuena et al., 1995; Gomes et al., 2021). However, epibionts are advantageous over endoparasites in that many of them are detectable in the field (e.g., using boat-based photography; see Hermosilla et al., 2015; Siciliano et al., 2020; Flach et al., 2021), and can often be easily found and counted on stranded hosts, be alive or dead, with minimum dissection, if at all (Balbuena et al., 1995). Most studies using epibionts as markers only require basic data to be gathered, i.e. genus- or, preferably, species-level identification, and quantification of population size at host individual or population scales. More elaborated research may require additional information on (1) degree of host specificity, (2) size measurements as an estimate of time since attachment, (3) distribution patterns on hosts' body, (4) geographic range, and/or (5) selected molecular markers (e.g., Bushuev, 1990; Kaliszewska et al., 2005; Ten et al., 2019; Moreno-Colom et al., 2020; Lehnert et al., 2021).

At present, cetacean epibionts have been used, *inter alia*, as 'tags' to trace past (e.g., Collareta et al., 2018a; Taylor et al., 2019) or present-day (e.g., Pearson et al., 2020; Visser et al., 2020) migratory routes and habitat use; shed light on phylogeography, population structure, and ecological stock delimitation (e.g., Bushuev, 1990; Kaliszewska et al., 2005; Iwasa-Arai et al., 2018); give insight into hydrodynamics (e.g., Kasuya and Rice, 1970; Briggs and Morejohn, 1972; Fish and Battle, 1995; Carrillo et al., 2015; Moreno-Colom et al., 2020), assist in individual recognition (e.g., Visser et al., 2020); and act as sentinels of health status (Mackintosh and Wheeler, 1929; Van Waerebeek et al., 1993; Aznar et al., 1994; Aznar et al., 2005; Lehnert et al., 2007; Vecchione and Aznar, 2014; Lehnert et al., 2021; for more references see Results). Nonetheless, there is plently of further opportunities to exploit the full potential of these organisms as biological indicators.

Aims

Studies including information on cetacean epibionts have usually focused on particular geographical areas (e.g., Kane et al., 2008; Lehnert et al., 2019), host species (e.g., Rice, 1978; Stimmelmayr and Gulland, 2020) or epibiotic taxa (e.g., Kane et al., 2008; Iwasa-Arai and Serejo, 2018). Furthermore, in the last decades a number of nomenclatural changes, new associations, and geographical records have been accumulating, thus we think that the available comprehensive reviews and checklists on this subject (Beneden, 1870; Dailey and Brownell, 1972; Arvy, 1977; Arvy, 1982; Raga, 1994) should be updated. On the other hand, few articles have reviewed the use of marine mammal parasites as biological tags (Balbuena et al., 1995; Mackenzie, 2002), and none gathered information about the whole epibiotic fauna of cetaceans.

The present systematic review aims to compile and update all records of cetacean epibiotic fauna (= epizoites) to date as a thorough, handy catalogue for researchers. Other organisms, i.e. diatoms and cookie-cutter shark, *Isistius brasiliensis* (Quoy & Gaimard, 1824) are also included in a specific section of this review to provide a complete picture of other externally-associated organisms that have been proven to be valuable biological indicators for cetaceans. Finally, we identify information gaps and future research directions and highlight the value of cetacean epibionts as indicator tools, encouraging their application in cetacean research.

METHODS

Literature Search

A systematic literature review was performed following PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (Moher et al., 2015; **Figure 1**). We conducted a thorough bibliographic search in the following databases: Google Scholar (https://scholar.google.com), Scopus (https://www.scopus.com), ScienceDirect (https://www.sciencedirect.com), Web of Science (https://www.webofscience.com), and Sage (https://journals.sagepub.com). The following search string was used for Scopus, ScienceDirect, Web of Science, and Sage: (*epibiont* OR *epibiotic* OR *epibiosis* OR *epizoite* OR *epizoic* OR *barnacle* OR *ectoparasite* OR *mesoparasite*) AND (*balaena* OR *eubalaena* OR *balaenoptera* OR *megaptera* OR *eschrichtius* OR *caperea* OR *cephalorhynchus* OR *delphinus* OR *feresa* OR *globicephala* OR *grampus* OR *lagenodelphis* OR *lagenorhynchus* OR *lissodelphis* OR *orcaella* OR *orcinus* OR *peponocephala* OR *pseudorca* OR *sotalia* OR "*Sousa chinensis*" OR "*Sousa plumbea*" OR "*Sousa sahulensis*" OR "*Sousa teuszii*" OR *stenella* OR "*Steno bredanensis*" OR *tursiops* OR "*Inia geoffrensis*" OR *kogia* OR *delphinapterus* OR "*Monodon monoceros*" OR *neophocaena* OR *phocoena* OR *phocoenoides* OR *physeter* OR *platanista* OR *pontoporia* OR *berardius* OR *hyperoodon* OR *mesoplodon* OR *tasmacetus* OR *ziphius* OR *indopacetus*)

Note that the use of genus name in some cetacean genera, i.e., *Monodon* Linnaeus, 1758, *Sousa* Gray, 1866, and *Steno* Gray, 1846 yielded many records of unrelated taxa, thus full species name was included in these cases. The output was exported and checked for duplicates and non-relevant papers with the open-source reference management software Zotero.

In the case of Google Scholar, only the first 100 result pages are available, thus we used the search strings "(*epibiont* OR *epibiotic* OR *epibiosis* OR *epizoite* OR *epizoic* OR *barnacle* OR *ectoparasite* OR *mesoparasite*) AND *i*", where *i* stands for a cetacean genus, to maximize the number of obtainable records. The output of each search was checked manually. In addition, we searched each epibiotic species in GBIF.org and included those associations and geographic locations that had not been reported in scientific publications. For all publications obtained, we looked up their references to search for potential missing records.

The final list includes the literature published until December 2021 that provides information on cetacean-epibiont(s) associations (**Figure 1**). These results are listed according to the epibiotic (see the Results) and the cetacean taxa (**Supplementary Table 1**). For each selected record, we extracted the following information, when available: cetacean species, epibiotic species, geographic area(s), prevalence (i.e., percent occurrence of the epibiont in each cetacean species of the sample), location on the cetacean, and any information related to indicator potential. Current species nomenclature and synonyms were checked in WoRMS (https://www.marinespecies.org/) and recent literature. Geographical locations were also classified at the scale of Large Marine Ecosystem (LME) (see e.g., Brotz et al., 2012).

For comparative purposes, we investigated research effort on each cetacean species using the number of results in Google Scholar as a proxy. For each species, we used the scientific name in quotation marks as search string. For the 6 species that previously constituted the *Lagenorynchus* genus (see Vollmer et al., 2019), we used the former nomenclature for the search to avoid understimation (i.e., "*Lagenorynchus*" followed by species name).

RESULTS

General Patterns

A total of 492 published documents, including 7 unpublished manuscripts, and 9 GBIF records were found. Three additional reliable records were serendipitously found in internet photo-catalogues and were also included in the final list (**Supplementary Table 1**). A roughly exponential trend in the

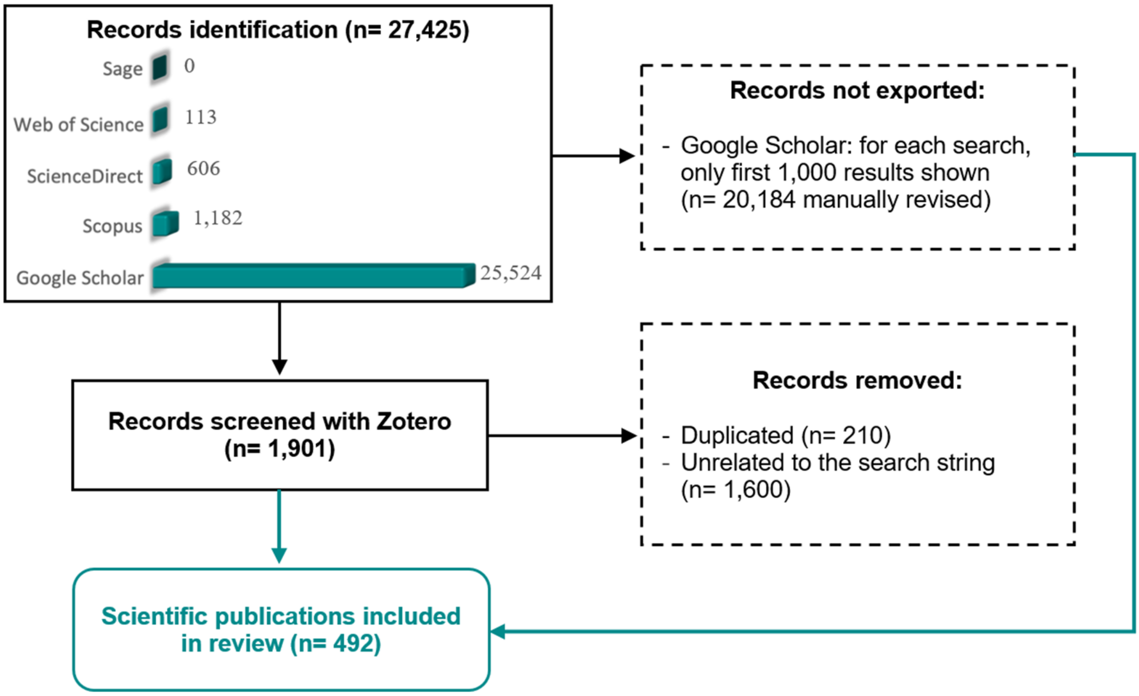

FIGURE 1 | Flow diagram of the methodology used in the literature search performed in this systematic review. Adaptation from PRISMA (Preferred Reporting Items for Systematic Reviews) template (Page et al., 2021).

number of publications was found throughout the period covered (1655-2021), with a peak in the 2010s decade (**Figure 2**); 2020 was the most productive year with 21 publications.

Baleen whales, and particularly *Megaptera novaeangliae* (Borowski, 1781), show the highest diversity of epibionts, followed by *Tursiops* spp. (**Figure 3**). However, it is difficult to ascertain the extent to which this pattern is affected by sampling effort (**Figure 3**). Likewise, 26 cetacean species from four genera have no published records of epibiotic fauna to date (**Supplementary Table 1**), but these hosts have also been generally little studied (< 4,000 publications in Google Scholar, **Figure 3**). Research effort varies also among geographic regions (**Figure 4**). The Mediterranean Sea and Antarctica are, by far, the geographic areas with the highest number of publications of cetacean epizoites, and some areas still lack such studies.

Systematic List

A systematic list of the 58 epizoic taxa (53 at species level) found to date on cetaceans follows. For each one, we provide information on (i) taxonomic synonyms; (ii) a subset of selected references that provide a complete overview of the species morphology; (iii) molecular sequences available on GenBank (https://www.ncbi.nlm.nih.gov/genbank/), with references or with Accession Number whenever no published manuscript was available; (iv) primary type of association, including parasitic (34 spp.), obligate commensal (8-9 spp.), facultative commensal (8 spp.), mutualistic (possibly 1 sp.), or unknown (2 spp.); (v) a list of cetacean hosts/basibionts; (vi) geographic range; (vii) life-cycle; and (viii) microhabitat, i.e., the location(s) on the cetacean body, with references; and (ix) indicator use or potential, with references. Any other relevant data are reported in the 'Remarks' section, and all records of association between epizoites and cetaceans are cited in the 'References' section.

Phylum Arthropoda von Siebold, 1848
Class Malacostraca Latreille, 1802
Subclass Eumalacostraca, Grobben, 1892
Order Amphipoda Latreille, 1816
Family Cyamidae Rafinesque, 1815

The Cyamidae ('whale lice') comprises a group of amphipods that are found exclusively on marine cetaceans (see, e.g., Iwasa-Arai and Serejo, 2018). These 3-30 mm creatures use their pereopods to cling to areas of reduced water flow (e.g., ventral grooves, blowhole, genital slit), where they spend their whole life feeding primarily on cetacean skin (Rowntree, 1983; Rowntree, 1996; Schell et al., 2000); thus, they are all considered ectoparasites. However, evidence that they cause any harm is rather scarce, so some authors support the use of the term 'ectocommensals' for them (Leung, 1976; Kenney, 2009). Rowntree (1996) discussed the possibility that some cyamids from whales may also feed on plankton, having perhaps developed mutualistic associations with their hosts. In particular, the cyamid species covering the

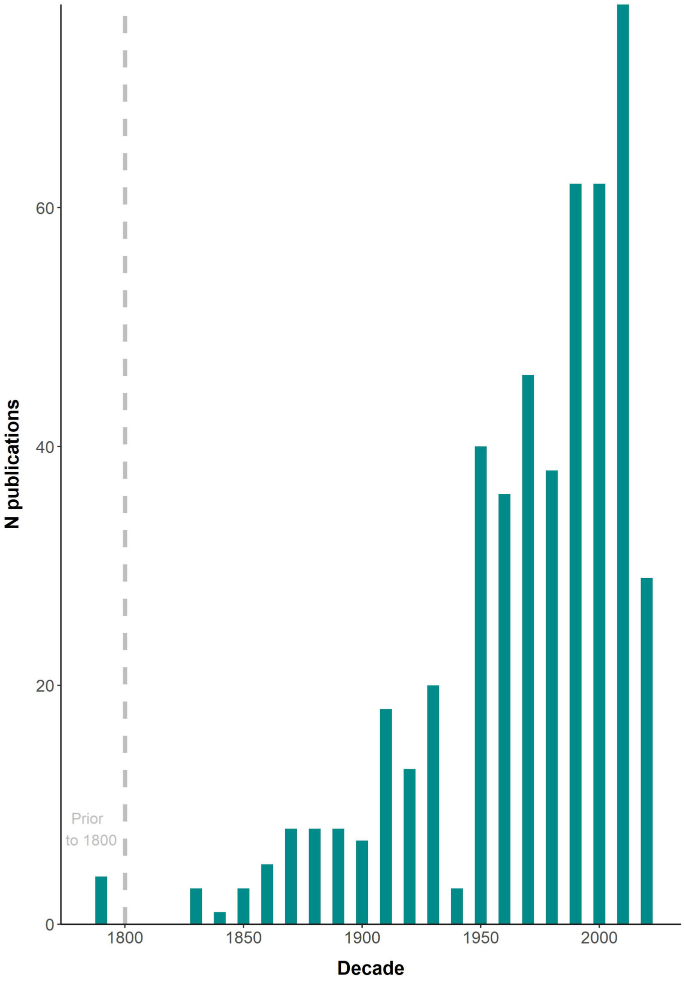

FIGURE 2 | Number (N) of publications including data on cetacean epibiotic fauna at a decadal scale from 1655 to 2021.

sensory hairs of whales could increase their activity during plankton blooms, amplifying the signal for prey detection by whales. In addition, it has also been suggested that cyamids could feed on cetaceans' dead skin and epibiotic algae, thus cleaning up wounds and speeding up healing (Williams and Bunkley-Williams, 2019). Lehnert et al. (2021), on the contrary, hypothesized that cyamids' feeding activity could actually hinder the healing of skin injuries, and some authors have suggested that heavy cyamid infections may contribute to the death of their hosts (Mignucci-Giannoni et al., 1998).

Since cyamids lack swimming stages, transmission must occur through bodily contacts (Fransen and Smeenk, 1991; Pfeiffer, 2009). Males are typically larger than females (but see Fraija-Fernández et al., 2017) and, at least in some species, have been observed to perfom pre-copulatory mate guarding (Rowntree, 1996; Oliver and Trilles, 2000). Females mate after molting (Conlan, 1991) and incubate eggs and protect the hatchling in a ventral brood pouch (Leung, 1976; Williams and Bunkley-Williams, 2019).

Balaenocyamus balaenopterae (Barnard K.H. 1931)

Synonyms

Cyamus balaenopterae Barnard K.H. 1931

Morphological Description

Barnard, 1932; Margolis, 1959; Leung, 1967; Iwasa-Arai and Serejo, 2018

Molecular Sequences

18S rRNA (Ito et al., 2011)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Balaenoptera acutorostrata Lacépède, 1804, *B. bonaerensis* Burmeister, 1867, *B. musculus* (Linnaeus, 1758), *B. physalus* (Linnaeus, 1758)

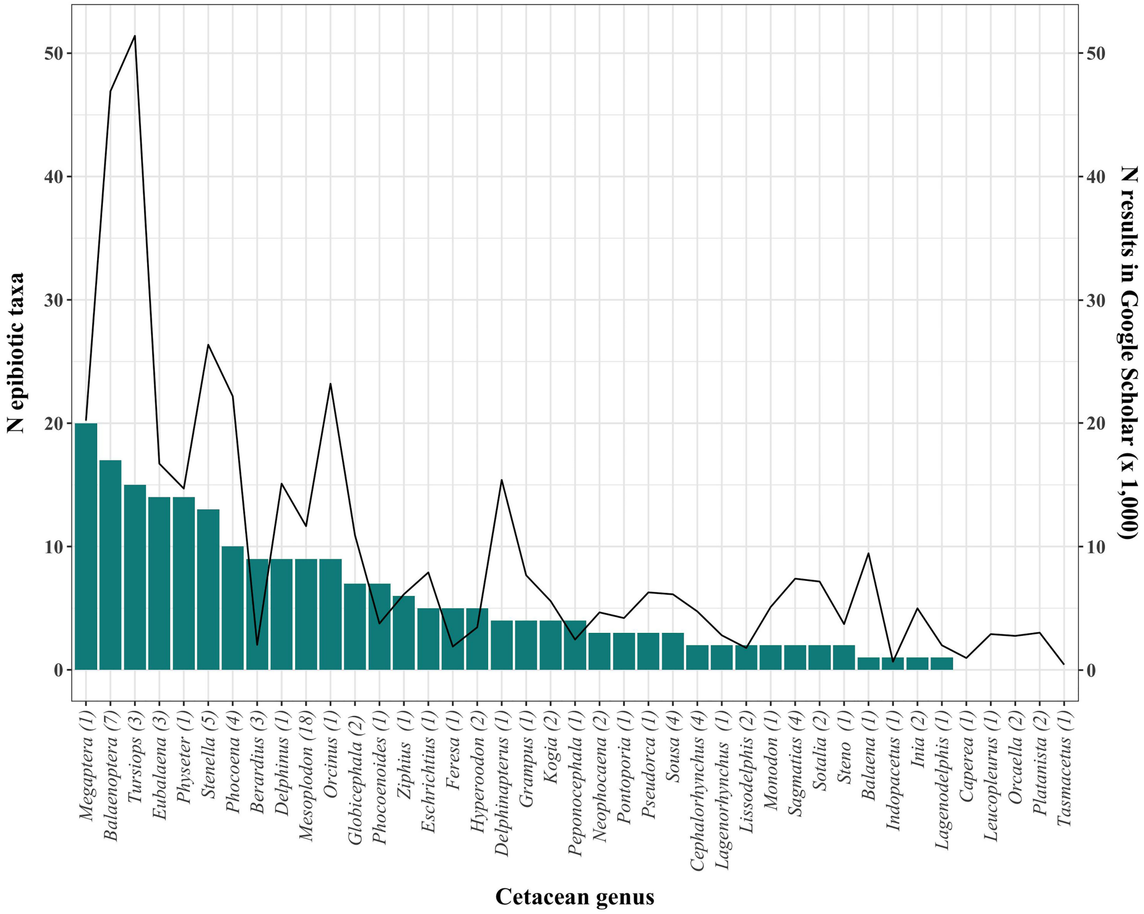

FIGURE 3 | Number of epibiotic species (bars, left y-axis) and total number of general results in Google Scholar (line, right y-axis) of each cetacean genus. The number of cetacean species in each genus is shown in parentheses.

Geographic Range

Atlantic, Pacific, Mediterranean, Indian Ocean, Antarctica

Life Cycle

In common minke whales, *Balaenoptera acutorostrata*, captured off Iceland, a one-year long life cycle is assumed; similar to other whale lice, hatching occurs in autumn, juveniles are released from the females' pouch in mid-winter, and they reach sexual maturity in spring or summer (Ólafsdóttir and Shinn, 2013). This life cycle may be synchronized with whales' seasonal migration (Raga and Sanpera, 1986).

Microhabitat

Natural orifices, i.e., ventral grooves, eyes, umbilicus, mammary slits, anus, and genital slit (Ohsumi et al., 1970; Ivashin, 1975; Raga and Sanpera, 1986)

Use as Indicator

Used to delineate ecological stocks and detect sex segregation in migrating cetaceans (Kawamura, 1969; Bushuev, 1990; Ólafsdóttir and Shinn, 2013).

Remarks

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References

Mackintosh and Wheeler, 1929; Barnard, 1931; Barnard, 1932; Margolis, 1959; Leung, 1965; Kawamura, 1969; Ohsumi et al., 1970; Lincoln and Hurley, 1974a; Ivashin, 1975; Rice, 1978; Berzin and Vlasova, 1982; Best, 1982; Raga and Sanpera, 1986; Avdeev, 1989; Bushuev, 1990; Sedlak-Weinstein, 1990 (unpubl.); Dailey and Vogelbein, 1991; Kuramochi et al., 1996; Araki et al., 1997; Uchida, 1998; Kuramochi et al., 2000; Margolis et al., 2000; Uchida and Araki, 2000; Ólafsdóttir and Shinn, 2013; Iwasa-Arai and Serejo, 2018; Ten et al., unpubl.

Cyamus boopis (Lütken, 1870)

Synonyms

Cyamus elongatus Hiro, 1938, *C. pacificus* Lütken, 1873, *C. suffuses* Dall, 1872, *Paracyamus boopis* (Lütken, 1870)

Morphological Description

Sars, 1895; Barnard, 1932; Leung, 1967; Margolis et al., 2000; Iwasa-Arai et al., 2016

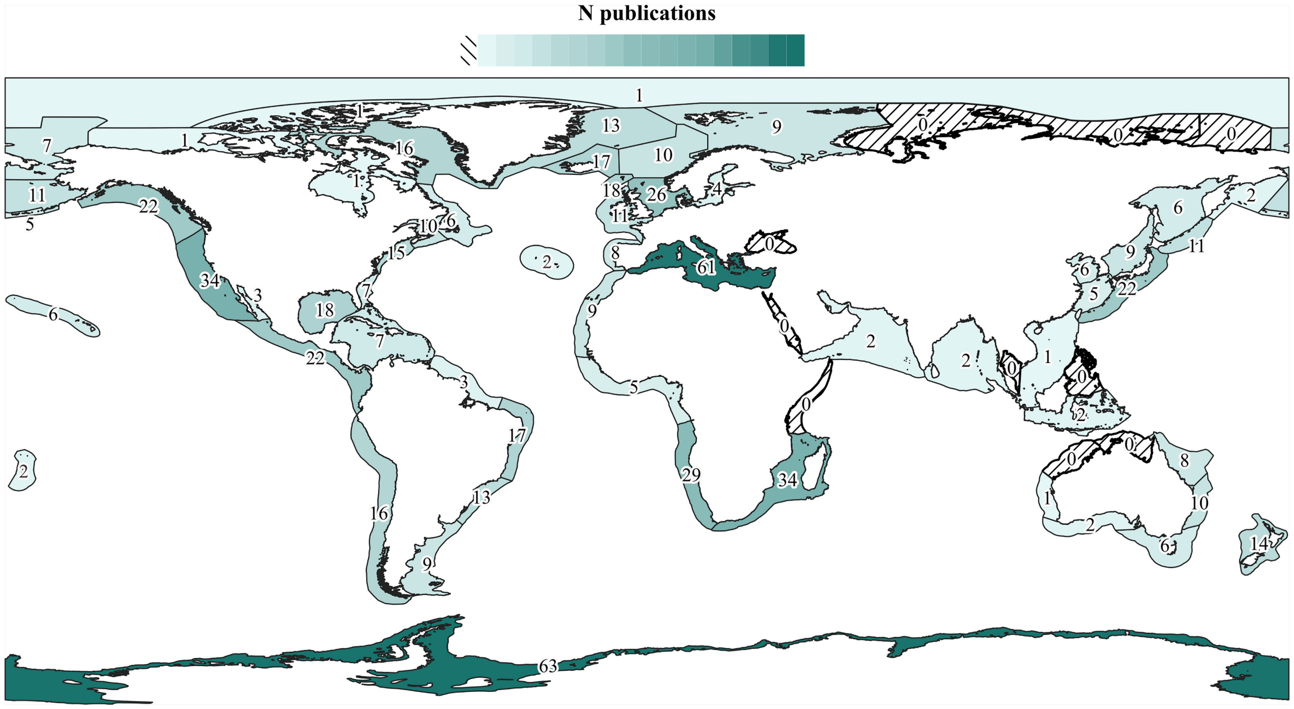

FIGURE 4 | Number of publications (indicated by numbers and color gradient) on cetaceans that contain data on their epibiotic fauna at least to genus level grouped by Large Marine Ecosystems (LME). When the same publication includes data for several LMEs, it is counted separately for each one. Azores (NE Atlantic) and Tonga (SW Pacific) are not in the LME system but were included as additional areas.

Molecular Sequences

COI (Iwasa-Arai et al., 2017a, Iwasa-Arai et al., 2018; GenBank FJ751158; FJ751159; MT551876; OK562816-OK562832), COII, COIII, ATP6, ATP8, ND3 (Kaliszewska et al., 2005) and the complete mitochondrial genome (GenBank MT458501)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Typically on *Megaptera novaeangliae*, but once reported on *Berardius bairdii* Duvernoy, 1851, *Eubalaena australis* (Desmoulins, 1822), and *Tursiops truncatus* (Montagu, 1821)

Geographic Range

Arctic, Atlantic, Pacific, Mediterranean, Indian Ocean, Antarctica

Life Cycle

Transmission may regularly occur during contacts between migrating hosts or at the feeding areas (Iwasa-Arai et al., 2018).

Microhabitat

Ubiquitous, i.e., head tubercles, eye, jaw, ventral grooves, genital slit, fins (Matthews, 1937; Cockrill, 1960; Ivashin, 1965; Rowntree, 1996). Sometimes attached to the epibiotic cirripedes *Coronula diadema* (Linnaeus, 1767) and *Conchoderma* spp. (Dall, 1872; Matthews, 1937; Stephensen, 1942; Angot, 1951; Cockrill, 1960).

Use as Indicator

Haplotype and nucleotide diversities have been used to assess inter-mixing between different breeding populations of humpback whales (Iwasa-Arai et al., 2018). Also, its presence on a southern right whale suggests an interspecific interaction with humpback whales in Brazilian waters (Iwasa-Arai et al., 2017a). The presence of an alive unidentified cyamid (likely *C. boopis*) on a humpback whale was used to infer that the stranding occurred less than three days before (Bortolotto et al., 2016).

Remarks

Some records of *C. boopis* on sperm whales (e.g., Barnard, 1932) were re-classified as *C. catodontis* by Margolis (1955) and later authors (e.g., Stock, 1973a; Iwasa-Arai and Serejo, 2018).

References

Lütken, 1870; Dall, 1872; Scammon, 1874; Pouchet, 1888; Pouchet, 1892; Sars, 1895; Collet, 1912; Chevreux, 1913a; Liouville, 1913; Ishi, 1915; Cornwall, 1928; Barnard, 1932; Matthews, 1937; Hiro, 1938; Scheffer, 1939; Angot, 1951; Hurley, 1952; Rees, 1953; Margolis, 1954a; Cockrill, 1960; Rice, 1963; Ivashin, 1965; Leung, 1965; Leung, 1970b; Lincoln and Hurley, 1974a; Berzin and Vlasova, 1982; Sedlak-Weinstein, 1991; Rowntree, 1996; Abollo et al., 1998; Osmond and Kaufman, 1998; Margolis et al., 2000; Alonso de Pina and Giuffra, 2003; Carvalho et al., 2010; Iwasa-Arai et al., 2016; Iwasa-Arai et al., 2017b; Iwasa-Arai et al., 2018; Groch et al., 2018; Iwasa-Arai et al., 2021; Iwasa-Arai et al., 2018; Qiao et al., 2020

Cyamus catodontis (Margolis, 1954)

Synonyms

Cyamus bahamondei Buzeta, 1963

Morphological Description

Margolis, 1954a; Margolis, 1955; Buzeta, 1963; Leung, 1967; Stock, 1973a; Margolis et al., 2000

Molecular Sequences

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Association

Ectoparasite

Cetacean Hosts/Basibionts

Typically on *Physeter macrocephalus* Linnaeus, 1758, but once reported on *Balaenoptera acutorostrata*, *B. bonaerensis*, *B. musculus*, *B. physalus*, and *Berardius bairdii*

Geographic Range

Eastern Atlantic, Pacific, Indian Ocean, Antarctica

Life Cycle

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Microhabitat

One record on a sperm whale's deformed jaw (Buzeta, 1963)

Use as Indicator

Used to detect social segregation in sperm whales; large males, but not females nor male bachelors, were infected with *C. catodontis*, suggesting that the former leave their natal pods at puberty (Best, 1969a; Best, 1979).

Remarks

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References

Barnard, 1932; Margolis, 1954a; Clarke, 1956; Buzeta, 1963; Rice, 1963; Leung, 1965; Best, 1969a; Best, 1969b; Best, 1979; Stock, 1973b; Lincoln and Hurley, 1974a; Berzin and Vlasova, 1982; Fransen and Smeenk, 1991; Iwasa-Arai and Serejo, 2018

Cyamus ceti (Linnaeus, 1758)

Synonyms

Oniscus ceti Linnaeus, 1758

Morphological Description

Krøyer, 1843; Leung, 1967; Margolis et al., 2000; Iwasa-Arai and Serejo, 2018

Molecular Sequences

COI (GenBank FJ751160-FJ751180)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Typically on *Balaena mysticetus* Linnaeus, 1758, but once reported on *Eschrichtius robustus* (Lilljeborg, 1861) and *Eubalaena japonica* (Lacépède, 1818)

Geographic Range

Artic, North Pacific

Life Cycle

Similar to *C. scammoni* (see below), but juveniles reach maturity before whales' northern migration to summer grounds (Leung, 1976). Females carry 150-240 eggs in the brood pouch, of which about 75% are fertilized (Leung, 1976).

Microhabitat

Creases of the lips, flippers, flukes, and thin areas, e.g., armpit and genital slit (Stephensen, 1942; Leung, 1976)

Use as Indicator

-

Remarks

-

References

Linnaeus, 1758; Lütken, 1870; Dall, 1872; Scammon, 1874; Margolis, 1955; Omura, 1958; Rice, 1963; Lincoln and Hurley, 1974a; Leung, 1976; Berzin and Vlasova, 1982; Heckmann et al., 1987; Margolis et al., 2000; Kaliszewska et al., 2005; Von Duyke et al., 2016; Chernova et al., 2017; Iwasa-Arai and Serejo, 2018

Cyamus erraticus (Roussel de Vauzème, 1834)

Synonyms

Paracyamus erraticus Roussel de Vauzème, 1834

Morphological Description

Barnard, 1932; Iwasa, 1934; Margolis, 1955; Leung, 1967

Molecular Sequences

COI, COII, COIII, ATP6, ATP8, ND3 (Kaliszewska et al., 2005), EF1a (Seger et al., 2010)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Typically on *Eubalaena australis*, *E. glacialis* (Müller, 1776), and *E. japonica*; also found on *Megaptera novaeangliae*

Geographic Range

Atlantic, Pacific, Indian Ocean, Antarctica

Life Cycle

-

Microhabitat

Genital, mammary, and anal slits, armpits, and opportunistically on wounds (Stephensen, 1942; Rowntree, 1996; see Remarks)

Use as Indicator

Sequence variation in mitochondrial DNA was used to investigate associations among right whale individuals and subpopulations, to estimate the time of past divergence of right whale populations, and to infer possible changes in their population sizes (Kaliszewska et al., 2005).

Remarks

Transmission probably occurs from mothers's genital slit to calves' head at birth. As callosity tissue develops, calves are colonized by the putative competitor *Cyamus ovalis* Roussel de Vauzème, 1834, likely by head-to-head contact with the mother; the distribution of *C. erraticus* is then restricted to skin folds and wounds (Rowntree, 1996).

References

Rossel de Vauzème, 1834; Lütken, 1873; Collet, 1912; Chevreux, 1913a; Liouville, 1913; Barnard, 1932; Iwasa, 1934; Margolis, 1955; Lincoln and Hurle7y, 1974a; Berzin and Vlasova, 1982; Rowntree, 1996; Margolis et al., 2000; Iwasa-Arai and Serejo, 2018

Cyamus eschrichtii (Margolis, McDonald & Bousfield, 2000)

Synonyms

-

Morphological Description

Margolis et al., 2000

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Eschrichtius robustus

Geographic Range

California (eastern North Pacific)

Life Cycle

-

Microhabitat

-

Use as Indicator

-

Remarks

-

References

Margolis et al., 2000

Cyamus gracilis (Roussel de Vauzème, 1834)

Synonyms

Paracyamus gracilis (Roussel de Vauzème, 1834)

Morphological Description

Barnard, 1932; Leung, 1967; Iwasa-Arai and Serejo, 2018

Molecular Sequences

COI, COII, COIII, ATP6, ATP8, ND3 (Kaliszewska et al., 2005), EF1a (Seger et al., 2010)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Eubalaena australis, *E. glacialis*, *E. japonica*

Geographic Range

Atlantic, Pacific, Antarctica

Life Cycle

-

Microhabitat

Head callosities (Barnard, 1932; Rowntree, 1996)

Use as Indicator

See *C. erraticus.*

Remarks

In a South African sample, *C. gracilis* co-occurred with *C. ovalis* Roussel de Vauzème, 1834 (Barnard, 1932).

References

Rossel de Vauzème, 1834; Lütken, 1873; Barnard, 1932; Margolis, 1955; Leung, 1965, Leung 1967; Lincoln and Hurley, 1974a; Berzin and Vlasova, 1982; Rowntree, 1996; Alonso de Pina and Giuffra, 2003; Iwasa-Arai and Serejo, 2018

Cyamus kessleri (A. Brandt, 1873)

Synonyms

-

Morphological Description

Brandt, 1872; Leung, 1967; Margolis et al., 2000; Iwasa-Arai and Serejo, 2018

Molecular Sequences

COI (GenBank FJ751215-FJ751224)

Association
Ectoparasite

Cetacean Hosts/Basibionts
Eschrichtius robustus

Geographic Range
From Chukchi Sea to California (eastern North Pacific)

Life Cycle
Similar to *C. scammoni* (see below), but juveniles reach maturity before whales' northern migration to summer grounds (Leung, 1976). Females carry up to 300 eggs in the brood pouch, of which 75-80% are fertilized (Leung, 1976).

Microhabitat
Umbilicus, genital slit, and anal aperture (Leung, 1976)

Use as Indicator
-

Remarks
-

References
Hurley and Mohr, 1957; Leung, 1976; Berzin and Vlasova, 1982; Margolis et al., 2000; Kaliszewska et al., 2005; Iwasa-Arai and Serejo, 2018

Cyamus mesorubraedon (Margolis, McDonald & Bousfield, 2000)

Synonyms
-

Morphological Description
Margolis et al., 2000

Molecular Sequences
-

Association
Ectoparasite

Cetacean Hosts/Basibionts
Physeter macrocephalus

Geographic Range
Vancouver Island (eastern North Pacific)

Life Cycle
-

Microhabitat
-

Use as Indicator
-

Remarks
-

References
Margolis et al., 2000

Cyamus monodontis (Lütken, 1870)

Synonyms
-

Morphological Description
Leung, 1967; Margolis et al., 2000; Iwasa-Arai et al., 2017b; Iwasa-Arai and Serejo, 2018

Molecular Sequences
-

Association
Ectoparasite

Cetacean Hosts/Basibionts
Delphinapterus leucas (Pallas, 1776), *Monodon monoceros* Linnaeus, 1758, *Ziphius cavirostris* Cuvier, 1823

Geographic Range
Arctic, western North Atlantic, eastern North Pacific

Life Cycle
-

Microhabitat
Tusk base, caudal fin along with *C. nodosus*, skin injuries (Porsild, 1922; Stephensen, 1942)

Use as Indicator
-

Remarks
-

References
Lütken, 1870; Porsild, 1922; Lincoln and Hurley, 1974a; Heyning and Dahlheim, 1988; Mignucci-Giannoni et al., 1998; Margolis et al., 2000; Iwasa-Arai et al., 2017a

Cyamus nodosus (Lütken, 1861)

Synonyms
Paracyamus nodosus (Lütken, 1861)

Morphological Description
Leung, 1967; Iwasa-Arai et al., 2017b; Iwasa-Arai and Serejo, 2018

Molecular Sequences
-

Association
Ectoparasite

Cetacean Hosts/Basibionts

Delphinapterus leucas, *Monodon monoceros*

Geographic Range

Greenland (Arctic, western North Atlantic)

Life Cycle

-

Microhabitat

Tusk base, caudal fin along with *C. monodontis*, skin injuries (Porsild, 1922; Stephensen, 1942)

Use as Indicator

-

Remarks

-

References

Lütken, 1870; Porsild, 1922; Margolis, 1954b; Margolis, 1955; Lincoln and Hurley, 1974a; Iwasa-Arai et al., 2017a

Cyamus orubraedon (Waller, 1989)

Synonyms

-

Morphological Description

Margolis et al., 2000

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Berardius bairdii

Geographic Range

North Pacific

Life Cycle

-

Microhabitat

Lower jaw (Waller, 1989)

Use as Indicator

-

Remarks

-

References

Waller, 1989; Margolis et al., 2000; Iwasa-Arai and Serejo, 2018

Cyamus ovalis (Roussel de Vauzème, 1834)

Synonyms

-

Morphological Description

Roussel de Vauzème, 1834; Iwasa, 1934; Leung, 1967; Margolis et al., 2000; Iwasa-Arai and Serejo, 2018

Molecular Sequences

COI (Kaliszewska et al., 2005; Seger et al., 2010), COII, COIII, ATP6, ATP8, ND3 (Kaliszewska et al., 2005), EF1a (Seger et al., 2010)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Eubalaena australis, *E. glacialis*, *E. japonica*, *Physeter macrocephalus*; once reported on *Megaptera novaeangliae*

Geographic Range

Atlantic, Pacific, Antarctica

Life Cycle

-

Microhabitat

Head callosities, sometimes with *C. erraticus* (Stephensen, 1942; Rowntree, 1996; see *C. erraticus*, above)

Use as Indicator

See *C. erraticus*.

Remarks

Once misidentified as *Cyamus rhytinae* (J. F. Brandt, 1846), ectoparasitic on the extinct Steller's sea cow, *Hydrodamalis gigas* (Zimmermann, 1780) Palmer, 1895 (see Leung, 1967; O'Clair and O'Clair, 1998).

References

Roussel de Vauzème 1834; Lütken, 1873; Collet, 1912; Liouville, 1913; Barnard, 1932; Iwasa, 1934; Margolis, 1955; Leung, 1967; Lincoln and Hurley, 1974a; Berzin and Vlasova, 1982; Rowntree, 1996; Margolis et al., 2000; Pettis et al., 2004; Iwasa-Arai and Serejo, 2018

Cyamus scammoni (Dall, 1872)

Synonyms

-

Morphological Description

Lütken, 1887; Leung, 1967; Margolis et al., 2000; Iwasa-Arai and Serejo, 2018

Molecular Sequences

COI (GenBank FJ751214), hemocyanin mRNA (Terwilliger and Ryan, 2006)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Eschrichtius robustus

Geographic Range

North Pacific

Life Cycle

Females can carry about 1,000 eggs in the brood pouch, although only about a 60% are fertilized (Leung, 1976). Eggs hatch in autumn, when gray whales arrive in California, and the young remain in the female's pouch for 2-3 months and then find shelter in host's crevices (Leung, 1976). Juveniles reach maturity during the winter northward migration of whales, and have full-grown brood upon arrival to summer grounds. The whole cycle takes 8-9 months to complete and there is probably some overlap in the life cycle of different individuals, given that juveniles are present throughout the year (Leung, 1976). The number of instars is presumed to be at least 7 or 8, but the number of ecdysis was untraceable (Leung, 1976).

Microhabitat

Ventral grooves, i.e., jaw and belly; flukes; on the cirriped *Cryptolepas rachianecti* Dall, 1872 (Leung, 1976; Dailey et al., 2000)

Use as Indicator

-

Remarks

Chonotrichous ciliates can infest its ventral surface (Leung, 1976).

References

Dall, 1872; Scammon, 1874; Lütken, 1887; Margolis, 1954a; Rice, 1963; Leung, 1965; Lincoln and Hurley, 1974a; Leung, 1976; Sullivan and Houck, 1979; Berzin and Vlasova, 1982; Dailey et al., 2000; Margolis et al., 2000; Kaliszewska et al., 2005; Takeda and Ogino, 2005; Murase et al., 2014; Iwasa-Arai and Serejo, 2018

Isocyamus antarcticensis (Vlasova in Berzin & Vlasova, 1982)

Synonyms

Cyamus antarcticensis Vlasova in Berzin & Vlasova, 1982

Morphological Description

Berzin and Vlasova, 1982

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Orcinus orca (Linnaeus, 1758)

Geographic Range

Antarctica

Life Cycle

-

Microhabitat

Pectoral fins, umbilicus (Berzin and Vlasova, 1982)

Use as Indicator

-

Remarks

-

References

Berzin and Vlasova, 1982

Isocyamus delphinii (Guérin-Méneville, 1836)

Synonyms

Cyamus delphinii Guérin-Méneville, 1836, *C. globicipitis* Lütken, 1870

Morphological Description

Barnard, 1932; Leung, 1967; Stock, 1973a; Stock, 1973b; Stock, 1977; Sedlak-Weinstein, 1991; Margolis et al., 2000; Lehnert et al., 2007; Lehnert et al., 2021

Molecular Sequences

COI (Lehnert et al., 2021)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Typically found on *Globicephala melas* (Traill, 1809); some records on *Delphinus delphis* Linnaeus, 1758, *Grampus griseus* (G. Cuvier, 1812), *Lagenorhynchus albirostris* (Gray, 1846), *Phocoena phocoena* (Linnaeus, 1758), and *Pseudorca crassidens* (Owen, 1846); once reported on *Globicephala macrorhynchus* Gray, 1846, *Megaptera novaeangliae*, *Mesoplodon europaeus* (Gervais, 1855), *Peponocephala electra* (Gray, 1846), *Phocoena dioptrica* Lahille, 1912, *Steno bredanensis* (G. Cuvier in Lesson, 1828), and *Tursiops truncatus*

Geographic Range

Arctic, Atlantic, Pacific, Mediterranean, Indian Ocean

Life Cycle

-

Microhabitat

Ubiquitous; i.e., blowhole, eyes, jaw, insertion of pectoral fin, wounds (Stock, 1973a; Stock, 1977; Greenwood et al., 1979; Raga et al., 1988; Balbuena et al., 1989; Balbuena and Raga, 1991; Raga and Balbuena, 1993; Jauniaux et al., 2002; Lehnert et al., 2007; Batista et al., 2012; Lehnert et al., 2021)

Use as Indicator

The higher prevalence and intensity of *I. delphinii* on mature long-finned pilot whale males (*vs.* females and immature males) may identify the males that are dominant in sexual fights, given that the resulting wounds serve as shelter for this cyamid species (Balbuena and Raga, 1991; Raga and Balbuena, 1993).

Remarks

Lehnert et al. (2021) pose that some records around the 1970-90s misidentified this species and refer to *Isocyamus deltobranchium* Sedlak-Weinstein, 1992, which has triangular accessory gills (*vs.* cylindrical in *I. delphinii*).

References

Lütken, 1870; Lütken, 1893; Collet, 1912; Chevreux, 1913b; Hiro, 1938; Bowman, 1955; Sergeant, 1962; Leung, 1965; Stock, 1973a; Stock, 1973b; Lincoln and Hurley, 1974a; Stock, 1977; Van Bree and Smeenk, 1978; Greenwood et al., 1979; Berzin and Vlasova, 1982; Raga et al., 1983a; Rappé, 1985; Raga et al., 1988; Balbuena et al., 1989; Mead, 1989; Rappé, 1991; Balbuena and Raga, 1991; Fransen and Smeenk, 1991; Sedlak-Weinstein, 1991; Raga and Balbuena, 1993; Abollo et al., 1998; Gibson et al., 1998; Margolis et al., 2000; Wardle et al., 2000; Haelters, 2001; Jauniaux et al., 2002; Haney et al., 2004; Lehnert et al., 2007; Batista et al., 2012; Lehnert et al., 2021; Iwasa-Arai and Serejo, 2018

Isocyamus deltobranchium (Sedlak-Weinstein, 1992)

Synonyms

-

Morphological Description

Sedlak-Weinstein, 1992a; Martínez et al., 2008; Lehnert et al., 2021

Molecular Sequences

COI (Lehnert et al., 2021)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Phocoena phocoena; once reported on *Delphinus delphis*, *Globicephala macrorhynchus*, *G. melas*, *Mesoplodon mirus* True, 1913, and *Orcinus orca*

Geographic Range

Eastern North Atlantic, western north Pacific, Indian Ocean

Life Cycle

-

Microhabitat

Skin wounds (Sedlak-Weinstein, 1992a; Martínez et al., 2008; Lehnert et al., 2021)

Use as Indicator

Higher prevalence in some harbor porpoise populations may reveal more interspecific contacts than in other areas (Lehnert et al., 2021). Also, temporal changes in prevalence could trace trends in the health status of cetacean hosts, given that it has been suggested that poor nutritional status may increase the susceptibility of porpoises to whale lice infections (Lehnert et al., 2021).

Remarks

Diatoms have been reported between *I. deltobranchium* forearms (Lehnert et al., 2021).

References

Sedlak-Weinstein, 1992a; Martínez et al., 2008; Iwasa-Arai and Serejo, 2018; Lehnert et al., 2021

Isocyamus indopacetus (Iwasa-Arai & Serejo, 2017)

Synonyms

-

Morphological Description

Iwasa-Arai et al., 2017b; Iwasa-Arai and Serejo, 2018; Kobayashi et al., 2021

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Indopacetus pacificus (Longman, 1926)

Geographic Range

Japan, New Caledonia (western Pacific)

Life Cycle

-

Microhabitat

Mouth, mammary slits, and scars provoked by *Isistius* sp. (Kobayashi et al., 2021)

Use as Indicator

-

Remarks

-

References

Iwasa-Arai et al., 2017a; Kobayashi et al., 2021

Isocyamus kogiae (Sedlak-Weinstein, 1992)

Synonyms

-

Morphological Description

Sedlak-Weinstein, 1992b

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Kogia breviceps (de Blainville, 1838)

Geographic Range

Australia (western South Pacific)

Life Cycle

-

Microhabitat

Skin wounds (Sedlak-Weinstein, 1992b)

Use as Indicator

-

Remarks

-

References

Sedlak-Weinstein, 1992b

Neocyamus physeteris (Pouchet, 1888)

Synonyms

Cyamus fascicularis Verrill, 1901, *C. physeteris* Pouchet, 1888, *Paracyamus physeteris* (Pouchet, 1888)

Morphological Description

Pouchet, 1892; Leung, 1967; Margolis et al., 2000; Iwasa-Arai and Serejo, 2018

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Typically on *Physeter macrocephalus*; single record on *Phocoenoides dalli* (True, 1885)

Geographic Range

Eastern Pacific, Atlantic

Life Cycle

-

Microhabitat

-

Use as Indicator

Used to detect social segregation in sperm whales: females and male bachelors, but not large males, harbour *N. physeteris*, suggesting that the later leave their natal pods at puberty (Best, 1969a; Best, 1979).

Remarks

-

References

Pouchet, 1888; Pouchet, 1892; Verrill, 1902; Clarke, 1956; Margolis, 1959; Buzeta, 1963; Leung, 1965; Leung, 1967; Best, 1969a; Lincoln and Hurley, 1974a; Best, 1979; Berzin and Vlasova, 1982; Mignucci-Giannoni et al., 1998; Margolis et al., 2000; Iwasa-Arai and Serejo, 2018

Orcinocyamus orcini (Leung, 1970)

Synonyms

Cyamus orcini Leung, 1970b

Morphological Description

Leung, 1970b; Margolis et al., 2000

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Orcinus orca

Geographic Range

Senegal (eastern South Atlantic)

Microhabitat

-

Use as Indicator

-

Remarks

-

References

Leung, 1970b

Platycyamus flaviscutatus (Waller, 1989)

Synonyms

-

Morphological Description

Margolis et al., 2000

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Berardius bairdii

Geographic Range

North Pacific

Life Cycle

-

Microhabitat

Head, back, flanks, flukes (Waller, 1989)

Use as Indicator

-

Remarks

-

References

Waller, 1989; Margolis et al., 2000

Platycyamus thompsoni (Gosse, 1855)

Synonyms

Cyamus thompsoni Gosse, 1855

Morphological Description

Gosse, 1855; Lütken, 1873; Wolff, 1958; Leung, 1967; Sedlak-Weinstein, 1991; Iwasa-Arai and Serejo, 2018

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Typically on *Hyperoodon ampullatus* (Forster, 1770); once reported on *H. planifrons* Flower, 1882 and *Mesoplodon grayi* von Haast, 1876

Geographic Range

North Atlantic, Pacific, Antarctica

Life Cycle

At least four instars have been distinguished in females (Wolff, 1958). Males are more difficult to classify by morphological features and could die and fall off the whale after copulation (Wolff, 1958).

Microhabitat

Ubiquitous on skin, i.e., eyes, beak, corners of the mouth (Tomilin, 1957; Wolff, 1958; Lincoln and Hurley, 1974a; Sedlak-Weinstein, 1991)

Use as Indicator

-

Remarks

-

References

Gosse, 1855; Lütken, 1870; Vosseler, 1889; Collet, 1912; Liouville, 1913; Tomilin, 1957; Wolff, 1958; Stock, 1973b; Lincoln and Hurley, 1974a; Berzin and Vlasova, 1982; Fransen and Smeenk, 1991; Sedlak-Weinstein, 1991; Iwasa-Arai and Serejo, 2018

Scutocyamus antipodensis (Lincoln & Hurley, 1980)

Synonyms

-

Morphological Description

Lincoln and Hurley, 1980

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Cephalorhynchus hectori (Lacépède, 1804), *Phocoena dioptrica*, *Sagmatias obscurus* (Gray, 1828)

Geographic Range

Off Namibia (eastern South Atlantic) and New Zealand (western South Pacific)

Life Cycle

-

Microhabitat

Ubiquitous on skin (Lincoln and Hurley, 1980; Best and Meÿer, 2010; Lehnert et al., 2017)

Use as Indicator

-

Remarks

-

References
Lincoln and Hurley, 1980; Best and Meÿer, 2010; Lehnert et al., 2017

Scutocyamus parvus (Lincoln & Hurley, 1974)
Synonyms
-

Morphological Description
Lincoln and Hurley, 1974b

Molecular Sequences
-

Association
Ectoparasite

Cetacean Hosts/Basibionts
Lagenorhynchus albirostris

Geographic Range
North Sea

Life Cycle
-

Microhabitat
-

Use as Indicator
-

Remarks
-

References
Lincoln and Hurley, 1974a, Lincoln and Hurley, 1974b; Stock, 1977; Fransen and Smeenk, 1991

Syncyamus aequus (Lincoln & Hurley, 1981)
Synonyms
See Remarks.

Morphological Description
Lincoln and Hurley, 1981; Raga, 1988; Sedlak-Weinstein, 1991

Molecular Sequences
-

Association
Ectoparasite

Cetacean Hosts/Basibionts
Delphinus delphis, *Stenella coeruleoalba*; once reported on *Sousa chinensis* (Osbeck, 1765), *Stenella longirostris* (Gray, 1828), *Tursiops aduncus* (Ehrenberg, 1832 [1833]), and *T. truncatus*

Geographic Range
Mediterranean, western South Pacific, Indian Ocean

Life Cycle
-

Microhabitat
Blowhole, eyes, corner of mouth, snout, jaw, axilla (Lincoln and Hurley, 1981; Raga and Raduan, 1982; Aznar et al., 1994; Cerioni and Mariniello, 1996; Haney, 1999; Haney et al., 2004; Fraija-Fernández et al., 2017)

Use as Indicator
-

Remarks
On the one hand, Mediterranean striped dolphins, *Stenella coeruleoalba*, harbored low prevalence and intensity of *S. aequus* (27% and 3 ind./host, respectively; Fraija-Fernández et al., 2017). Since striped dolphins are highly social animals (Carlucci et al., 2015), transmission success would be hardly hampered by the scarcity of contacts, but rather by the low sizes of source populations. These small populations may result from the extreme limitation of suitable microhabitats to shelter on these fast-swimming dolphins (Fraija-Fernández et al., 2017). This phenomenon seems also to impact the reproductive strategy of this species (Fraija-Fernández et al., 2017). On the other hand, the species *Cyamus chelipes* was first described by Costa (1866) and later re-classified in the genus *Syncyamus* by Bowman (1958). It is considered a nomen dubium (Haney, 1999), the type series is lost (Bowman, 1958), and it was not included in later reviews of the Cyamidae (Leung, 1965; Iwasa-Arai and Serejo, 2018|). Thus, it is possible that *S. chelipes* is a synonym of *S. aequus*, later described and common in the Mediterranean Sea (see above, **Supplementary Table 1**).

References
Lincoln and Hurley, 1981; Raga and Raduan, 1982; Raga et al., 1983; Raga and Carbonell, 1985; Raga, 1988; Sedlak-Weinstein, 1991; Aznar et al., 1994; Mariniello et al., 1994; Ross et al., 1994; Cerioni and Mariniello, 1996; Margolis et al., 2000; Fraija-Fernández et al., 2017

Syncyamus ilheusensis (Haney, de Almeida & Reid, 2004)
Synonyms
-

Morphological Description
Haney et al., 2004; Iwasa-Arai et al., 2017b; Iwasa-Arai and Serejo, 2018

Molecular Sequences
-

Association
Ectoparasite

Cetacean Hosts/Basibionts
Globicephala macrorhynchus, *Peponocephala electra*, *Stenella clymene* (Gray, 1850)

Geographic Range
Brazil (western South Atlantic)

Life Cycle
-

Microhabitat
Eyes, blowhole (Haney et al., 2004; Batista et al., 2012)

Use as Indicator
-

Remarks
-

References
Haney et al., 2004; Batista et al., 2012; Iwasa-Arai et al., 2017a; Iwasa-Arai et al., 2018

Syncyamus pseudorcae (Bowman, 1955)
Synonyms
-

Morphological Description
Bowman, 1955; Leung, 1967

Molecular Sequences
-

Association
Ectoparasite

Cetacean Hosts/Basibionts
Delphinus delphis, *Pseudorca crassidens*, *Stenella clymene*

Geographic Range
North Atlantic, Pacific

Life Cycle
-

Microhabitat
Blowhole, mouth, snout, jaw (Carvalho et al., 2010)

Use as Indicator
-

Remarks
-

References
Bowman, 1955; Leung, 1970a; Sedlak-Weinstein, 1991; Jefferson et al., 1995; Carvalho et al., 2010

Order Isopoda Latreille, 1817
Family Cymothoidae Leach, 1818

Representatives from the family Cymothoidae are obligate parasites of mainly marine but also freshwater fish (Smit et al., 2014). Identification of cymothoid isopods is often difficult because species often show high morphological variation (Trilles et al., 2013). Many species of *Nerocila* Leach, 1818 require taxonomic revision (Aneesh et al., 2019).

Nerocila sp.
Synonyms
-

Morphological Description
A general account of the genus *Nerocila* and of some of its species can be found Hai-yan and Xin-zheng (2002) and Trilles et al. (2013).

Molecular Sequences
COI, LSU rRNA, 16S rRNA, and 18S rRNA of nine *Nerocila* spp. (see GenBank)

Association
Unknown

Cetacean Hosts/Basibionts
Pontoporia blainvillei (Gervais & d'Orbigny, 1844)

Geographic Range
-

Life Cycle
See Brusca (1978) and Smit et al. (2014) for a description of the cymothoid cycle.

Microhabitat
Neck region (Brownell, 1975)

Use as Indicator
-

Remarks
Brownell (1975) reported this ectoparasite on some La Plata dolphins that had been captured accidentally in gillnets, and interpreted that it could have been transmitted from sharks or other fish while all were trapped in the gillnet. Thus, the association with cetaceans should be viewed as accidental.

References
Brownell, 1975

Class Thecostraca Gruvel, 1905
Subclass Copepoda Milne Edwards, 1840
Order Harpacticoida Sars G.O., 1903
Family Balaenophilidae Sars G.O., 1910

The genus *Balaenophilus* Aurivillius P.O.C., 1879 contains two species that live in close association with marine vertebrates. *B. unisetus* Aurivillius P.O.C., 1879 is considered an obligate commensal of baleen whales that feeds on algae and/or baleen tissue (Vervoort and Tranter, 1961; Fernandez-Leborans, 2001; Badillo et al., 2007), causing no harm to hosts (Ogawa et al., 1997; Badillo et al., 2007). In contrast, *B. manatorum* (Ortiz et al., 1992) infects manatees and sea turtles; in the latter they can feed on healthy skin (Badillo et al., 2007; Domènech et al., 2017), sometimes producing extensive lesions (Crespo-Picazo et al., 2017). Thus, this species is considered an ectoparasite.

Balaenophilus unisetus (Aurivillius P.O.C., 1879)

Synonyms

-

Morphological Description

Aurivillius, 1879; Vervoort and Tranter, 1961; Bannister and Grindley, 1966

Molecular Sequences

-

Association

Obligate commensal

Cetacean Hosts/Basibionts

Balaenoptera borealis Lesson, 1828, *B. edeni* Anderson, 1878, *B. musculus*, *B. physalus*

Geographic Range

Arctic, Atlantic, eastern Pacific, Indian Ocean, Antarctica

Life Cycle

Aurivillius (1879) describes a nauplius and five copepodite stages preceding the adult phase. In the allied species *B. manatorum* nauplii and early copepodite stages are unable to swim, and copepodite V and adults can perform only short swimming excursions (Domènech et al., 2017). Thus, host bodily contact or closeness is likely necessary for transmission in both species.

Microhabitat

Baleen plates (Aurivillius, 1879; Cocks, 1885; Lillie, 1910; Scharff, 1913; Matthews, 1938b; Vervoort and Tranter, 1961; Rice, 1963; Gambell, 1964; Bannister and Grindley, 1966; Ichihara, 1966; Ichihara, 1978; Collet, 1986; Raga and Sanpera, 1986; Dalla Rosa and Secchi, 1997; Esteves et al., 2020), corner of the mouth (Raga and Sanpera, 1986)

Use as Indicator

-

Remarks

The presence of this species is likely underestimated since it can be easily overlooked without exhaustive inspection of baleen plates (Aurivillius, 1879; Vervoort and Tranter, 1961). It can sometimes be colonized by chonotrichous ciliates, acting as basibiont (Fernandez-Leborans, 2001).

References

Cocks, 1885; Aurivillius, 1879; Lillie, 1910; Collet, 1912; Scharff, 1913; Allen, 1916; Cornwall, 1927; Cornwall, 1928; Matthews, 1938b; Vervoort and Tranter, 1961; Rice, 1963; Gambell, 1964; Bannister and Grindley, 1966; Ichihara, 1966; Kawamura, 1969; Rice, 1977; Ichihara, 1978; Collet, 1986; Raga and Sanpera, 1986; Dalla Rosa and Secchi, 1997; Esteves et al., 2020

Family Harpacticidae Dana, 1846

Members of this family are mostly marine or brackishwater macroalgal associates, with a few freshwater species (Joon and Young, 1993).

Harpacticus pulex (Humes, 1964)

Synonyms

-

Morphological Description

Humes, 1964

Molecular Sequences

-

Association

Unknown

Cetacean Hosts/Basibionts

Tursiops truncatus

Geographic Range

-

Life Cycle

Unknown for this species, but naupliar and copepodite stages have been described for other *Harpacticus* spp. (e.g., Itô, 1976; Walker, 1981; Choi and Kim, 1994). Harpacticoids generally lack planktonic larval stages, but adults are active swimmers (e.g., Hicks, 1985; Palmer, 1988). It is thus plausible that transmission to bottlenose dolphin occurred during the adult phase.

Microhabitat

On ulcerated and sloughed skin (Humes, 1964)

Use as Indicator

-

Remarks

This species was described by Humes (1964) on captive marine mammals and has never been reported again. Species of *Harpacticus* Milne Edwards H., 1840 typically colonize seagrass, algal clumps or sandy and muddy bottoms (Ólafsson, 2001 and references therein), thus the occurrence of *H. pulex* on cetaceans is intriguing and perhaps forced by confinement conditions (Humes, 1964). Future re-examination of the taxonomic status of *H. pulex* is advisable.

References

Humes, 1964

Order Siphonostomatoida Burmeister, 1835
Family Caligidae Burmeister, 1835

The family Caligidae ("sea lice") contains 30 genera (Walter and Boxshall, 2020); species of *Caligus* Müller O. F., 1785 and *Lepeophtheirus* Nordmann, 1832 have great economic relevance due to their impact on salmonid fish mariculture (Costello, 2006; Hemmingsen et al., 2020). Caligids use their siphon and a pair of mandibles to feed on fish skin (Kabata, 1974), causing ulcerations and even death to their hosts (Tørud and Håstein, 2008), but their impact on cetaceans has not yet been reported.

Caligus elongatus (Nordmann, 1832)

Synonyms

Caligus arcticus Brandes, 1956, *C. kroyeri* Milne Edwards, 1840, *C. latifrons* Wilson C.B., 1905, *C. leptochilus* Leuckart in Frey & Leuckart, 1847, *C. lumpi* Krøyer, 1863, *C. rabidus* Leigh-Sharpe, 1936, *C. rissoanus* Milne Edwards, 1840, *C. trachypteri* Krøyer, 1863

Morphological Description

Hemmingsen et al., 2020 and references therein

Molecular Sequences

COI (Øines and Heuch, 2005; Raupach et al., 2015; GenBank AY386272; AY386273; EF452647), 16S rRNA (Øines and Schram, 2008; GenBank AY660020), 18S rRNA (Huys et al., 2006; Øines and Schram, 2008; Mohrbeck et al., 2015; Khodami et al., 2017; GenBank JX845119-JX845131), 28S rRNA (Khodami et al., 2017; GenBank DQ180336; DQ180337; EU118301; EU118302)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Balaenoptera acutorostrata, *Hyperodoon ampullatus*

Geographic Range

North Atlantic (Hemmingsen et al., 2020)

Life Cycle

Two free-living planktonic nauplius stages, one free-swimming infective copepodid stage, and four chalimus stages and one adult stage attached to the host (Maran et al., 2013).

Microhabitat

Skin (O'Reilly, 1998; Ólafsdóttir and Shinn, 2013)

Use as Indicator

-

Remarks

This is a typical fish ectoparasite that has been reported on more than 80 species (Kabata, 1979; Agusti-Ridaura et al., 2019). Infections in cetaceans are exceptional and likely related to their occurrence close to cage farms (Ólafsdóttir and Shinn, 2013). The hyperparasitic monogenean *Udonella caligorum* Johnston, 1835, which typically attaches to fish copepods (Freeman and Ogawa, 2010), has been found on *C. elongatus* infecting common minke whales (Ólafsdóttir and Shinn, 2013).

References

O'Reilly, 1998; Ólafsdóttir and Shinn, 2013

Caligus rufimaculatus (Wilson C.B., 1905)

Synonyms

-

Morphological Description

Wilson, 1905; Takemoto and Luque, 2002; Kim et al., 2019

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Tursiops truncatus

Geographic Range

Western Atlantic (Benz et al., 2011)

Life Cycle

See *C. elongatus* (above).

Microhabitat

Skin (Benz et al., 2011)

Use as Indicator

-

Remarks

This species typically infects fish, but there is an exceptional record of adult individuals, including ovigerous females, on a carcass of bottlenose dolphin (Benz et al., 2011).

References

Benz et al., 2011

Lepeophtheirus crassus (Wilson & Bere, 1936)

Synonyms

Gloiopotes crassus Wilson & Bere, 1936

Morphological Description

Lewis, 1967

Molecular Sequences

-

Association

Ectoparasite

Cetacean Hosts/Basibionts

Delphinus delphis

Geographic Range

Western Atlantic, North Pacific, Indian Ocean (Lewis, 1967)

Life Cycle

Species of *Lepeophtheirus* have 2-4 chalimus stages and two preadult stages. The latter can be distinguished by their ability to detach and move over the surface of the host (Krøyer, 1834; see Hamre et al., 2013).

Microhabitat

Hyperparasitic on *Remora australis* (Bennett, 1840; Radford and Klawe, 1965)

Use as Indicator

-

Remarks

-

References

Radford and Klawe, 1965

Family Pennellidae Burmeister, 1835

Unlike other families of the order Siphonostomatoida, members of the family Pennellidae do have intermediate hosts, usually a fish or invertebrate (Kabata, 1979; Nagasawa et al., 1985; Suyama et al., 2021a and references therein). Mating seemingly occurs in the intermediate host and fertilized females attach to the final host in which they produce and release the eggs (Arroyo et al., 2002).

Pennella balaenoptera (Koren & Danielssen, 1877)

Synonyms

Pennella antarctica Quidor, 1913, *P. anthonyi* Quidor, 1913, *P. balaenopterae* Koren & Danielssen, 1877, *P. cettei* Quidor, 1913, *P. charcoti* Quidor, 1913

Morphological Description

Koren and Danielssen, 1877; Turner, 1905; Hogans, 1987, Hogans, 2017; Abaunza et al., 2001; Vecchione and Aznar, 2014; Suyama et al., 2021b

Molecular Sequences

COI (Fraija-Fernández et al., 2018)

Association

Mesoparasite. The head penetrates the blubber and musculature to feed on blood and expands as 2-3 cephalic horns in host's tissue to enable attachment, whereas the trunk, genital complex, and abdominal plumes protrude and hang on the host body (Hogans, 1987; Abaunza et al., 2001; Schmidt and Roberts, 2009; Hogans, 2017).

Cetacean Hosts/Basibionts

Balaenoptera acutorostrata, *B. bonaerensis*, *B. borealis*, *B. edeni*, *B. musculus*, *B. physalus*, *Delphinus delphis*, *Eubalaena australis*, *Feresa attenuata* Gray, 1874, *Globicephala melas*, *Grampus griseus*, *Hyperoodon ampullatus*, *Kogia breviceps*, *Lissodelphis borealis* (Peale, 1848), *Megaptera novaeangliae*, *Mesoplodon bidens* (Sowerby, 1804), *M. carlhubbsi* Moore, 1963, *M. mirus*, *Orcinus orca*, *Phocoena phocoena*, *Physeter macrocephalus*, *Stenella coeruleoalba*, *Tursiops truncatus*, *Ziphius cavirostris*

Geographic Range

Atlantic, Pacific, Mediterranean, Indian Ocean, Antarctica

Life Cycle

Based on information from other penellids, its life cycle is believed to include a pelagic naupliar stage and several copepodid and chalimus instars on the intermediate (squid) hosts; females are fertilized as late chalimi and undergo a pelagic phase to search out the definitive host, where they metamorphose into the adult stage (Schmidt and Roberts, 2009). In the case of *P. balaenoptera*, only adult females and the first naupliar stage are known (Arroyo et al., 2002). However, the copepodid and chalimus stages have been described for *P. filosa* (Linnaeus, 1758) collected from squids (Rose and Hamon, 1953; see also Arroyo et al., 2002), and *P. filosa* is now considered conspecific with *P. balaenoptera* (Fraija-Fernández et al., 2018; see also the Discussion). The life cycle of *P. balaenoptera* could be primarily oceanic because this species is more prevalent on pelagic versus coastal cetaceans (Fraija-Fernández et al., 2018).

Microhabitat

Commonly on the flanks (Raga and Sanpera, 1986; Aznar et al., 1994; Gomerčić et al., 2006; Souza et al., 2005; Ciçek et al., 2007; Foskolos et al., 2017), but occasionally reported on the head (Pouchet and Beauregard, 1889; Foskolos et al., 2017) and flukes (Foskolos et al., 2017). A single record on a whale sucker, *Remora australis* (Bennett, 1840) attached to a dolphin (Radford and Klawe, 1965).

Use as Indicator

It may be an indicator of compromised health in cetacean hosts (Mackintosh and Wheeler, 1929; Aznar et al., 2005; Vecchione and Aznar, 2014).

Remarks

Since *P. balaenoptera* is the only recognized species of *Pennella* Oken, 1815 parasitizing cetaceans, we consider that the published records of *Pennella* sp. in cetaceans could be assigned to this species, unless proven otherwise. Dailey et al. (2002) reported *P. balaenoptera* in one northern elephant seal, *Mirounga angustirostris* (Gill, 1866). Recently, molecular analyses revealed that specimens of *P. balaenoptera* collected from several cetaceans in western Mediterranean could be conspecific with *P. filosa* from swordfish, *Xiphias gladius* Linnaeus, 1758, collected in the same area (Fraija-Fernández et al., 2018). This finding begs further attention (see the Discussion).

References

Steenstrup and Lütken, 1861; Sars, 1866; Pouchet and Beauregard, 1889; Anthony and Calvet, 1905; Turner, 1905; Bouvier, 1910; Japha, 1910; Mörch, 1911; Collet, 1912; Quidor, 1912; Liouville, 1913; Olsen, 1913; Scharff, 1913; Cornwall, 1927; Cornwall, 1928; Mackintosh and Wheeler, 1929; Van Oorde-de Lint and Schuurmans-Stekhoven, 1936; Matthews, 1938b; Allen, 1941; Stephensen, 1942; Mizue, 1950; Nishiwaki and Hayashi, 1950; Mizue and Murata, 1951; Nishiwaki and Oye, 1951; Ohno and Fujino, 1952; Kakuwa et al., 1953; Barnard, 1955; Chapman and Santler, 1955; Clarke, 1956; Zenkovich, 1956; Tomilin, 1957; Rice, 1963; Radford and Klawe, 1965; Kawamura, 1969; Berzin, 1972; Rice, 1977; Rice, 1978; Dailey and Stroud, 1978; Dailey and Walker, 1978; Ivashin and Golubovsky, 1978; Greenwood et al., 1979; Best, 1982; Raga and Carbonell, 1985; Raga and Sanpera, 1986; Smiddy, 1986; Mead, 1989; Bushuev, 1990; Dorsey et al., 1990; Sedlak-Weinstein, 1990 (unpubl.); Dailey and Vogelbein, 1991; Raga and Balbuena, 1993; Aznar et al., 1994; Aznar et al., 2005, unpubl.; Raga, 1994; Vecchione, 1994; Cerioni and Mariniello, 1996; Kuramochi et al., 1996; Araki et al., 1997; Kuramochi et al., 2000; McAlpine et al., 1997; Terasawa et al., 1997; Uchida, 1998; Walker and Hanson, 1999; Cornaglia et al., 2000; Uchida and Araki, 2000; Abaunza et al., 2001; Arroyo et al., 2002; Brzica, 2004; Gomerčić et al., 2006; Souza et al., 2005; Ciçek et al., 2007; Kautek et al., 2008; Martín et al., 2011; Rosso et al., 2011; Bertulli et al., 2012; Ólafsdóttir and Shinn, 2013; Tonay and Dede, 2013; Danyer et al., 2014; Öztürk et al., 2015; Delaney et al., 2016; Birincioğlu et al., 2017; Foskolos et al., 2017; Hogans, 2017; Fraija-Fernández et al., 2018; IJsseldijk et al., 2018; Marcer et al., 2019; Methion and Díaz López, 2019; Herr et al., 2020; Orrell, 2020; Ten et al., unpubl.

Subclass Cirripedia Burmeister, 1834
Order Balanomorpha Pilsbry, 1916
Family Balanidae Leach, 1817

Thoracic barnacles (Infraclass Thoracica) are sessile, hermaphroditic crustaceans that attach to diverse substrata and have specialized cirri to filter organic particles from water for feeding (Anderson, 1994). The life cycle typically includes a free-swimming nauplius larva that undergoes several (usually 6) moults, and a non-feeding cypris larva that searchs out, and attaches to, an appropriate substratum. Subsequent metamorphosis leads to a juvenile filter-feeding version of the adult (Darwin, 1854; Cornwall, 1955; Maruzzo et al., 2012). The cyprid stage is unique to barnacles and shows little morphological variability across species, even though they can attach to strikingly different substrata (Maruzzo et al., 2012; Dreyer et al., 2020).

This family originally encompassed all sessile barnacles (Leach, 1817), but whale barnacles and most sea turtles were later re-classified (Pitombo, 2004; see below). Most members of Balanidae are intertidal, although some species are facultative epibionts, e.g., those found on sea turtles, such as *Balanus trigonus* (Ten et al., 2019).

Balanus trigonus (Darwin, 1854)

Synonyms

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Morphological Description

Darwin, 1854

Molecular Sequences

COI (Chen et al., 2013; Ashton et al., 2016; GenBank JQ035523; JQ035524; MF974362; MK308152; MK308163; MK308322; MK496572; MT258956; MW277718; MW277822), EF1a (Chan et al., 2017), RPII (Chan et al., 2017), 12S rRNA (Endo et al., 2010; Kamiya et al., 2012; Pérez-Losada et al., 2014; Chan et al., 2017; GenBank GU983669; GU983670), 16S rRNA (Chan et al., 2017; GenBank JQ035491; JQ035492), 18S rRNA (Pérez-Losada et al., 2014; Chan et al., 2017), 28S rRNA (Pérez-Losada et al., 2014), and the complete mitochondrial genome (GenBank MW646099; MZ049958; NC_056392)

Association

Facultative commensal

Cetacean Hosts/Basibionts

Megaptera novaeangliae

Geographic Range

Cosmopolitan (Werner, 1967)

Life Cycle

Metamorphosis from nauplius to cyprid stage is speeded up at higher water temperature, i.e., 4-11 days (Thiyagarajan et al., 2003). Recruitment is seasonal and takes place at approximately 24°C (Lam, 2000).

Microhabitat

As a hyperepibiont on the barnacle *Coronula diadema* (Cornwall, 1928)

Use as Indicator

-

Remarks

-

References

Cornwall, 1928

Balanus spp.

Synonyms

-

Morphological Description

A general account of *Balanus* spp. can be found in Darwin (1854); Newman and Ross (1976), and Pitombo (2004).

Molecular Sequences

> 5,000 results in GenBank

Association

Presumably facultative commensal

Cetacean Hosts/Basibionts

Megaptera novaeangliae

Geographic Range

-

Life Cycle

Information for *Balanus* spp. is available from Brown and Roughgarden (1985) and Maruzzo et al. (2012).

Microhabitat

As a hyperepibiont on the barnacle *Coronula* spp. (Rice, 1963)

Use as Indicator

-

Remarks

Balanus spp., as in Rice (1963), may correspond to a single or several species.

References

Rice, 1963

Megabalanus tintinnabulum (Linnaeus, 1758)

Synonyms

Balanus tintinnabulum (Linnaeus, 1758), *Lepas tintinnabulum* Linnaeus, 1758

Morphological Description

Darwin, 1854; Barnard, 1924

Molecular Sequences

COI (Chen et al., 2013; Ashton et al., 2016; GenBank JQ035525-JQ035527), H3 (Pérez-Losada et al., 2004), 12S rRNA (Pérez-Losada et al., 2004), 16S rRNA (Pérez-Losada et al., 2004; GenBank JQ035505-JQ035508), 18S rRNA, 28S rRNA (Pérez-Losada et al., 2004), and the complete mitochondrial genome (Che et al., 2019; GenBank MW281857; NC_056162)

Association

Facultative commensal

Cetacean Hosts/Basibionts

Unidentified whale

Geographic Range

Tropical or sub-tropical to warm temperate waters (Otani et al., 2007)

Life Cycle

In the Arabian Sea, barnacles breed at lower temperatures, i.e., less than 24 °C in winter *vs.* > 28 °C in summer; and grow at a rate of 0.44-0.63 mm/year (Ali and Ayub, 2021).

Microhabitat

As a hyperepibiont on the barnacle *Coronula diadema* (Barnard, 1924)

Use as Indicator

-

Remarks

-

References

Barnard, 1924

Family Coronulidae Leach, 1817

Coronulids are typically obligate epibionts of sea turtles, sirenians or cetaceans (Marlow, 1962; Hayashi et al., 2013). One species, *Chelonibia testudinaria* (Linnaeus, 1758), can also be found on crustaceans and sea snakes, and even on inanimate substrata (Frazier and Margaritoulis, 1990; Cheang et al., 2013).

Cetopirus complanatus (Mörch, 1852)

Synonyms

Coronula balaenaris (Gmelin, 1791), *C. complanata* (Mörch, 1852)

Morphological Description

Darwin, 1854; Pilsbry, 1916; Scarff, 1986; Pastorino and Griffin, 1996; Seilacher, 2005

Molecular Sequences

-

Association

Obligate commensal

Cetacean Hosts/Basibionts

Eubalaena australis, *E. glacialis*

Geographic Range

Arctic, Atlantic, eastern North Pacific, Antarctica

Life Cycle

-

Microhabitat

Lips, fins (Guiler, 1956; Best, 1991)

Use as Indicator

Shell plate remains of *C. complanatus* in Nerja Cave (Málaga, southern Spain) were used as indirect evidence of whale consumption by humans in the Upper Magdalenian (Álvarez-Fernández et al., 2013) and of the presence and migration of right whales (Balaenidae) in the Mediterranean during the Early Pleistocene (Collareta et al., 2016; Bosselaers et al., 2017).

Remarks

There is a single record on *Megaptera novaeangliae* (Guiler, 1956), but it was probably confused with *Coronula reginae* (Holthuis et al., 1998).

References

Chemnitz, 1785; Chemnitz and Martini, 1790; Darwin, 1854; Gruvel, 1903; Pilsbry, 1916; Nilsson-Cantell, 1931; Best, 1991

Coronula diadema (Linnaeus, 1767)

Synonyms

-

Morphological Description

Darwin, 1854; Dall, 1872; Cornwall, 1955; Scarff, 1986; Anderson, 1994

Molecular Sequences

H3, 12S rRNA, 16S rRNA, 18S rRNA, 28S rRNA (Hayashi et al., 2013)

Association

Obligate commensal

Cetacean Hosts/Basibionts

Typical from *Megaptera novaeangliae* but some records on *Balaenoptera bonaerensis*, *B. borealis*, *B. musculus*, *B. physalus*, *Eubalaena glacialis*, *Hyperoodon ampullatus* and *Physeter macrocephalus*

Geographic Range

Atlantic, Pacific, Indian Ocean, Antarctica

Life Cycle

A one-year life cycle has been proposed (Angot, 1951; Newman and Abbott, 1980). Larval release and settlement seem to occur in warm waters (20-25°C in September-October off Madagascar), whereas adult development may take place during whale migration to the poles (Angot, 1951). Details of development from the embryo to the juvenile stage have been studied *in vitro* (Nogata and Matsumura, 2006). Larval settlement is likely induced by chemical cues from whale skin, such as alpha-2-macroglobulin (Nogata and Matsumura, 2006).

Microhabitat

Rostrum, lips, lower jaw, fins (Dall, 1872; Pilsbry, 1916; Nilsson-Cantell, 1930a, Nilsson-Cantell, 1930c; Stephensen, 1938; Scheffer, 1939; Tomilin, 1957; Scarff, 1986)

Use as Indicator

Isotope analyses ($\delta^{18}O$) of shells of *C. diadema* and its direct ancestor *C. bifida* (Dominici et al., 2011) accurately trace current and Pleistocene-Miocene whale migration routes (Buckeridge et al., 2018; Collareta et al., 2018a; Collareta et al., 2018b; Buckeridge et al., 2019; Taylor et al., 2019). Fossil remains have also been used to infer humpback whale migration routes and breeding areas in the Late Pliocene-Pleistocene (Bianucci et al., 2006a; Bianucci et al., 2006b). Present-day observations of *Coronula* sp. (Olsen, 1913; Angot, 1951) helped to elucidate right whales' migration from warmer waters (Best, 1991). The co-occurrence of *C. bifida* with *Cetopirus complanatus* may indicate that whales belonging to Balaenopteridae and Balaenidae shared breeding grounds during the Early Pleistocene (Collareta et al., 2016). Interestingly, the presence of *C. diadema* on cetaceans other than humpback whales could also indicate some geographical overlap between species (see the Discussion). *Coronula* spp. have been suggested as natural marks for individual photo-identification (Franklin et al., 2020). The pattern of attachment of barnacles (presumably *C. diadema*) indicates non-uniform water flow over humpback whale flippers and has shed light on the function of leading-edge tubercles (Fish and Battle, 1995). Rubbing against rocks and the sea bottom has been observed in humpback whales, which may be an attempt to remove these barnacles (Tomilin, 1957) and could limit its application as an indicator.

Remarks

This species serves as a basibiont of the facultative epibionts *Balanus* spp., *Conchoderma auritum* (Linnaeus, 1767), and *Megabalanus tintinnabulum*, and of the hydroid *Obelia dichotoma* (Linnaeus, 1758) (Liouville, 1913; Barnard, 1924; Cornwall, 1928; Stephensen, 1938; Rice, 1963; Kim et al., 2020).

References

Dall, 1872; Scammon, 1874; Fischer, 1884; Sars, 1890-1895; Borradaile, 1903; Liouville, 1913; Pilsbry, 1916; Cornwall, 1924; Cornwall, 1927; Cornwall, 1928; Nilsson-Cantell, 1930a; Nilsson-Cantell, 1930c, Hiro, 1935; Hiro, 1938; Stephensen, 1938; Nilsson-Cantell, 1939; Scheffer, 1939; Mizue and Murata, 1951; Rees, 1953; Tomilin, 1957; Nishiwaki, 1959; Cockrill, 1960; Wolff, 1960; Rice, 1963; Nilsson-Cantell, 1978; O'Riordan, 1979; Scarff, 1986; Paterson and Van Dyck, 1991; Young, 1991; Holthuis and Fransen, 2004; Félix et al., 2006; Nogata and Matsumura, 2006; Wirtz et al., 2006; Jones, 2010; Ávila et al., 2011; Jiménez et al., 2011; Hayashi, 2012; Angeletti et al., 2014; Kim et al., 2020; Minton et al., 2020 (*in press.*); Tasmanian Museum and Art Gallery, 2020; Ueda, 2020; Ten et al., unpubl.

Coronula reginae (Darwin, 1854)

Synonyms

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Morphological Description

Darwin, 1854; Scarff, 1986

Molecular Sequences

-

Association

Obligate commensal

Cetacean Hosts/Basibionts

Balaenoptera bonaerensis, *B. borealis*, *B. musculus*, *B. physalus*, *Eubalaena glacialis, Megaptera novaeangliae*; single report on *Delphinapterus leucas* and *Physeter macrocephalus*

Geographic Range

Arctic, Atlantic, North Pacific, Indian Ocean, Antarctica

Life Cycle

-

Microhabitat

Lower jaw, flukes (Cockrill, 1960; Scarff, 1986)

Use as Indicator

See *Coronula diadema* (above).

Remarks

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References

Collet, 1912; Pilsbry, 1916; Cornwall, 1927; Cornwall, 1928; Mackintosh and Wheeler, 1929; Nilsson-Cantell, 1930a; Nilsson-Cantell, 1930b; Hiro, 1938; Stephensen, 1938; Scheffer, 1939; Rees, 1953; Guiler, 1956; Tomilin, 1957; Cockrill, 1960; Rice, 1963; Klinkhart, 1966; Kawamura, 1969; Rice, 1977; Nilsson-Cantell, 1978; Silva-Brum, 1985; Scarff, 1986; Bushuev, 1990; Smiddy and Berrow, 1992; Holthuis and Fransen, 2004; Ten et al., unpubl.

Cryptolepas rhachianecti **(Dall, 1872)**

Synonyms

-

Morphological Description

Dall, 1872; Cornwall, 1955; Achituv, 1998; Seilacher, 2005

Molecular Sequences

H3, 12S rRNA, 16S rRNA, 18S rRNA, 28S rRNA (Hayashi et al., 2013)

Association

Obligate commensal, although Tomilin (1957) considered this species to be potentially harmful because it can impede whales' movement and damage their skin.

Cetacean Hosts/Basibionts

Eschrichtius robustus; once reported on *Delphinapterus leucas* and *Orcinus orca*

Geographic Range

North Pacific; one record in the Gulf of Mexico (eastern North Atlantic)

Life Cycle

Gray whales wintering in waters off California and Mexico bear large and small specimens of *C. rhachianecti* when migrating northward, but only large barnacles when sighted during the southbound migration (Rice and Wolman, 1971). This would suggest that larval settlement occurs in wintering areas. This interpretation is supported by the observation that belugas held captive in San Diego Bay have *C. rhachianecti* in synchrony with gray whale northward migration (Rice and Wolman, 1971; Ridgway et al., 1997). Vertical shell growth is 0.12 mm/day (Killingley, 1980).

Microhabitat

Rostrum, lips, throat, peduncle, fins (Kasuya and Rice, 1970; Briggs and Morejohn, 1972)

Use as Indicator

Isotope analysis ($\delta^{18}O$) and geographical patterns of occurrence of fossilized remains have helped to reveal gray whale migration routes (Killingley, 1980; Bosselaers and Collareta, 2016; Taylor et al., 2019). Small size of barnacles and other features (appearance and associated scarring) have been used to identify calves of gray whale in photo-identification studies (Bradford et al., 2011). Barnacle orientation reflects waterflow patterns on gray whales (Kasuya and Rice, 1970; Briggs and Morejohn, 1972). Greater abundance of *C. rachianecti* on the left side of the head of gray whales may indicate that the right side is used predominantly for benthic feeding (Kasuya and Rice, 1970). In fact, right-sided feeding bias has been observed in some cetaceans (e.g., Clapham et al., 1995; Marino and Stowe, 1997; Karenina et al., 2016), including gray whales (e.g., Woodward and Winn, 2006).

Remarks

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References

Dall, 1872; Pilsbry, 1916; Rice, 1963; Roest, 1970; Rice and Wolman, 1971; Briggs and Morejohn, 1972; Leung, 1976; Wellington and Anderson, 1978; Sullivan and Houck, 1979; Achituv, 1998; Weller et al., 1999; Takeda and Ogino, 2005; Sokolov and Arsen'ev, 2006; Murase et al., 2014; Scordino et al., 2017; Kasuya and Rice, 1970; Killingley, 1980; Swartz, 1981; Samaras, 1989; Ridgway et al., 1997; Findley and Vidal, 2002

Tubicinella major **(Lamarck, 1802)**

Synonyms

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Morphological Description

Darwin, 1854; Seilacher, 2005

Molecular Sequences

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Association

Obligate commensal, although Tomilin (1957) considered this species to be potentially harmful because it can impede whales' movement and damage their skin.

Cetacean Hosts/Basibionts

Eubalaena australis; once reported on *Balaenoptera borealis* and *E. glacialis*

Geographic Range

Atlantic, western South Pacific, Antarctica

Life Cycle

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Microhabitat

Upper jaw, callosities, forehead, over the eye (Pilsbry, 1916; Scarff, 1986)

Use as Indicator

Shell plate remains of *T. major* found in Nerja Cave (Málaga, southern Spain) were used as indirect evidence of whale consumption by humans in the Upper Magdalenian (Álvarez-Fernández et al., 2013).

Remarks

Reported as a basibiont of facultative epibionts of the genus *Conchoderma* (Liouville, 1913).

References

Worm, 1655; Marloth, 1900; Gruvel, 1903; Liouville, 1913; Pilsbry, 1916; Reeb et al., 2007

Xenobalanus globicipitis (Steenstrup, 1852)

Synonyms

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Morphological Description

Darwin, 1854; Cornwall, 1955; Rajaguru and Shantha, 1992; Anderson, 1994; Seilacher, 2005

Molecular Sequences

COI (Pérez-Losada et al., 2014), H3, 12S rRNA, 16S rRNA, 18S rRNA, 28S rRNA (Hayashi et al., 2013)

Association

Obligate commensal

Cetacean Hosts/Basibionts

Balaenoptera acutorostrata, *B. bonaerensis*, *B. borealis*, *B. edeni*, *B. musculus*, *B. physalus*, *Delphinus delphis*, *Feresa attenuata*, *Globicephala macrorhynchus*, *G. melas*, *Grampus griseus*, *Kogia* sp., *Lagenodelphis hosei* Fraser, 1956, *Lissodelphis borealis*, *Megaptera novaeangliae*, *Mesoplodon bidens*, *M. mirus*, *Neophocaena asiaeorientalis* Pilleri & Gihr, 1972, *N. phocaenoides* (Cuvier, 1829), *Orcinus orca*, *Peponocephala electra*, *Phocoena phocoena*, *P. sinus* Norris & McFarland, 1958, *P. spinnipinnis* (Burmeister, 1865), *Physeter macrocephalus*, *Pontoporia blainvillei*, *Pseudorca crassidens*, *Sagmatias obliquidens* (Gill, 1865), *S. obscurus*, *Sotalia fluviatilis* (Gervais & Deville in Gervais, 1853), *S. guianensis* (Van Beneden, 1864), *Sousa plumbea* (G. Cuvier, 1829), *Stenella attenuata*, *S. clymene*, *S. coeruleoalba*, *S. frontalis* (Cuvier, 1829), *S. longirostris*, *Steno bredanensis*, *Tursiops aduncus*, *T. truncatus*, *Ziphius cavirostris*

Geographic Range

Cosmopolitan (Arctic, Atlantic, Pacific, Mediterranean, South China Sea, Indian Ocean, Antarctica)

Life Cycle

Under experimental conditions at 28°C, the nauplii develop into cyprids in c. 8 days of hatching (Dreyer et al., 2020). Cyprids are similar to those of other barnacles but show variation in the structures that contact the substratum (Dreyer et al., 2020). In Guiana dolphins, *Sotalia fluviatilis*, off southern Brazil, field observations suggest that barnacle growth rate is initially fast and slows down after c. 30 days; sexual maturity seems to be reached in 40-45 days, and life span does not exceed one year (Flach et al., 2021).

Microhabitat

Trailing edge of dorsal fin, pectoral flippers, and mostly tail flukes (Calman, 1920; Barnard, 1924; Cornwall, 1927; Cornwall, 1928; Pope, 1958; Caldwell et al., 1971; Devaraj and Bennet, 1974; Bryden, 1976; Rice, 1978; Greenwood et al., 1979; Bane and Zullo, 1980; Spivey, 1980; Raga et al., 1983b; Ross, 1984; Raga and Sanpera, 1986; Brownell et al., 1987; Mead and Potter, 1990; Rajaguru and Shantha, 1992; Van Waerebeek et al., 1993; Watson et al., 1994; Jefferson et al., 1995; Reyes and Van Waerebeek, 1995; Araki et al., 1997; Orams and Schuetze, 1998; Rittmaster et al., 1999; Vidal et al., 1999; Barros and Stolen, 2001; Parsons et al., 2001; Resendes et al., 2002; Berland et al., 2003; Di Beneditto and Ramos, 2004; Palacios et al., 2004; Kane et al., 2008; Bearzi and Patonai, 2010; Best and Meÿer, 2010; Carvalho et al., 2010; Ribeiro et al., 2010; Foote et al., 2011; Karaa et al., 2011; Martín et al., 2011; Oliveira et al., 2011; Rosso et al., 2011; Díaz-Aguirre et al., 2012; González et al., 2012; Ólafsdóttir and Shinn, 2013; Towers et al., 2013; Whitehead et al., 2014; Díaz-Gamboa, 2015; Kim and Sohn, 2016; Methion and Díaz López, 2019; Pacheco et al., 2019; Herr et al., 2020; Matthews et al., 2020; Siciliano et al., 2020; Visser et al., 2020; Flach et al., 2021); also reported on the head (Samaras, 1989; Engel, 1994) and on a facial lesion (Alves-Motta et al., 2020).

Use as Indicator

The high detectability of *X. globicipitis* from visual surveys makes it applicable for individual marking of cetaceans (Visser et al., 2020) and as a multifaceted indicator. First, differences in its prevalence have been used to trace cetacean long-distance migrations (Best, 1982; Bushuev, 1990; Matthews et al., 2020; Ten et al., unpubl.) and to discriminate ecological stocks (Kawamura, 1969; Bushuev, 1990; Toth et al., 2012; Towers et al., 2013; Urian et al., 2019; Silva et al., 2020) and climate change-derived shifts in cetacean distribution (Visser et al., 2020). Second, its settlement patterns on hosts, which seem mainly driven by water flow, have been used to investigate cetacean swimming and hydrodynamics (Carrillo et al., 2015; Moreno-Colom et al., 2020). Lastly, the higher prevalence on immunosuppressed hosts highlights its potential as an indicator of health status in cetacean populations (Aznar et al., 1994; Aznar et al., 2005).

Remarks

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References

Steenstrup, 1852; Darwin, 1854; Hoek, 1883; True, 1890; Richard and Neuville, 1897; Weltner, 1897; Gruvel, 1905; Gruvel, 1912; Collet, 1912; Liouville, 1913; Gruvel, 1920; Calman, 1920; Nilsson-Cantell, 1921; Barnard, 1924; Broch, 1924; Cornwall, 1927; Cornwall, 1928; Mackintosh and Wheeler, 1929; Nilsson-Cantell, 1930a; Richard, 1936; Matthews, 1938b; Heldt, 1950; Cornwall, 1955; Pope, 1958; Rice, 1963; Zullo, 1963; Stubbings, 1965; Pilleri, 1967; Dollfus, 1968; Kawamura, 1969; Pilleri and Gihr, 1969; Pilleri and Knuckey, 1969; Pilleri, 1970; Rice, 1977; Rice, 1978; Caldwell et al., 1971a; Devaraj and Bennet, 1974; Brownell, 1975; Mead, 1975; Bryden, 1976; Spivey, 1977; Dailey and Walker, 1978; Greenwood et al., 1979; Bane and Zullo, 1980; Spivey, 1980; Raga et al., 1982; Raga et al., 1983b; Ross, 1984; Raga and Carbonell, 1985; Gittings et al., 1986; Raga and Sanpera, 1986; Brownell et al., 1987; Rappé, 1988; Rappé and Van Waerebeek, 1988; Pinedo et al., 1989; Samaras, 1989; Bushuev, 1990; Mead and Potter, 1990; Van Waerebeek et al., 1990; Young, 1991; Duignan et al., 1992; Rajaguru and Shantha, 1992; Aguilar and Raga, 1993; Raga and Balbuena, 1993; Van Waerebeek et al., 1993; Aznar et al., 1994; Aznar et al., 2005; Aznar et al., 2016, unpubl.; Engel, 1994; Fertl, 1994; Watson et al., 1994; Jefferson et al., 1995; Reyes and Van Waerebeek, 1995; Azevedo et al., 1996; Fertl et al., 1996; Araki et al., 1997; Orams and Schuetze, 1998; Uchida, 1998; Rittmaster et al., 1999; Vidal et al., 1999; Di Beneditto and Ramos, 2001; Guerrero-Ruiz and Urbán, 2000; Kuramochi et al., 2000; Uchida and Araki, 2000; Addink and Smeenk, 2001; Barros and Stolen, 2001; Parsons et al., 2001; Danilewicz et al., 2002; Louella and Dolar, 2002; Resendes et al., 2002; Berland et al., 2003; Di Beneditto and Ramos, 2004; Karuppiah et al., 2004; Palacios et al., 2004; Watson and Gee, 2005; Bellido et al., 2006; Sakai et al., 2006; Best, 2007; Pitman et al., 2007; Toth-Brown and Hohn, 2007; Kane et al., 2008; Kautek et al., 2008; Rotstein et al., 2009; Sakai et al., 2009; Bearzi and Patonai, 2010; Best and Meÿer, 2010; Carvalho et al., 2010; Ribeiro et al., 2010; Weir, 2010; Foote et al., 2011; Karaa et al., 2011; Martín et al., 2011; Oliveira et al., 2011; Rosso et al., 2011; Bertulli et al., 2012; Díaz-Aguirre et al., 2012; González et al., 2012; Hayashi, 2012; Pugliese et al., 2012; Toth et al., 2012; Ólafsdóttir and Shinn, 2013; Towers et al., 2013; Lane et al., 2014; Whitehead et al., 2014; Díaz-Gamboa, 2015; Carrillo et al., 2015; Blum and Fong, 2016; Prestridge, 2016; Kim and Sohn, 2016; Denkinger and Alarcon, 2017; Donnelly et al., 2018; Ronje et al., 2018; Cortés-Peña, 2019; Methion and Díaz López, 2019; Pacheco et al., 2019; Urian et al., 2019; Alves-Motta et al., 2020; Gagnon and Torgersen, 2020; Gómez-Hernández et al., 2020; Herr et al., 2020; Matthews et al., 2020; Minton et al., 2020 (in press); Minussi, 2020; Moreno-Colom et al., 2020; Natural History Museum, 2020; Orrell, 2020; Siciliano et al., 2020; Silva et al., 2020; Ueda, 2020; Vargas-Bravo et al., 2020; Visser et al., 2020; CW Azores, 2021; Flach et al., 2021; iNaturalist, 2021; Ten et al., unpubl.

Order Scalpellomorpha Buckeridge & Newman, 2006
Family Lepadidae Darwin, 1852

Lepadids are oceanic fugitive species with relatively rapid growth and require a hard substratum to settle (e.g., Skerman, 1958; Patel, 1959; Southward, 1987; Harper, 1995; Hinojosa et al., 2006; Fraser et al., 2011; Wegner and Cartamil, 2012; Frick and Pfaller, 2013; Schiffer and Herbig, 2016). Overall, they are generalistic settlers on floating objects, be living or inanimate. This feature makes it often difficult to ascertain whether settlement on putative basibionts is *pre-* or *postmortem* (e.g., Magni et al., 2015; Ten et al., 2019). However, some degree of specialization for living cetaceans seems to be apparent especially for *Conchoderma auritum* (see below). Apart from cetaceans, other basibionts for species of *Lepas* and *Conchoderma* are, *inter alia*, bull kelps (Fraser et al., 2011; López et al., 2017), sea turtles (Ten et al., 2019), and even human corpses (Magni et al., 2015). Extensive description of the metamorphosis for species of this family is provided by Darwin (1854).

Conchoderma auritum (Linnaeus, 1767)

Synonyms

Conchoderma leporinum Olfers, 1814, *Lepas aurita* Linnaeus, 1767, *Otion stimpsoni* Dall, 1872

Morphological Description

Darwin, 1854; Dall, 1872; Monod, 1938; Cornwall, 1955

Molecular Sequences

COI (Ashton et al., 2016; GenBank MT563423; MT563438; MT563441), H3 (Pérez-Losada et al., 2008), 12S rRNA (Endo et al., 2010), 16S rRNA (Tomioka et al., 2020), 18S rRNA, 28S rRNA (Pérez-Losada et al., 2008)

Association

Facultative commensal. However, Newman and Abbott (1980) considered that this species might actually be an obligate commensal on cetaceans because most records of this species involve, as substrata, the shells of coronulid barnacles and/or on exposed hard surfaces of these mammals, e.g., baleens or tusks of ziphids. Rasmussen (1980) postulated that *C. auritum* prefers hard substrates in motion, although this species has also been reported on animate objects (see below).

Cetacean Hosts/Basibionts

Balaenoptera acutorostrata, *B. bonaerensis*, *B. borealis*, *B. musculus*, *B. physalus*, *Berardius bairdii*, *Eschrichtius robustus*, *Eubalaena glacialis*, *Feresa attenuata*, *Globicephala macrorhynchus*, *G. melas*, *Hiperoodon ampullatus*, *H. planifrons*, *Megaptera novaeangliae*, *Mesoplodon bidens*, *M. densirostris* (de Blainville, 1817), *M. europaeus*, *M. hectori* (Gray, 1871), *M. layardii* (Gray, 1865), *M. mirus*, *M. stejnegeri* True, 1885, *Neophocaena phocaenoides*, *Peponocephala electra*, *Physeter macrocephalus*, *Pontoporia blainvillei*, *Stenella attenuata*, *S. frontalis*, *S. longirostris*, *Tursiops aduncus*, *T. truncatus*, *Ziphius cavirostris*

Geographic Range

Cosmopolitan

Life Cycle

Growth rate of metamorphosed individuals are available only from inanimate substrata (0.1-1.0 mm/day; Il'in et al., 1978; Rasmussen, 1980; Dalley and Crisp, 1981). At a mean temperature of 23°C, the capitulum of newly recruited individuals can reach 1 mm long in just two days, and 6 mm in 9 days; in older individuals, growth rate estabilizes at 0.55 mm/day (Dalley and Crisp, 1981). Cyprids of *C. auritum* sampled along the Atlantic Ocean were found in low concentration between 25° N and 34 °S (Dalley and Crisp, 1981).

Microhabitat

On baleen plates (Nilsson-Cantell, 1930a; Nilsson-Cantell, 1939; Omura, 1950a; Christensen, 1985; Raga and Sanpera, 1986; Ólafsdóttir and Shinn, 2013); odontocete teeth (Beneden, 1870; Ohlin, 1893; Lillie, 1910; Hamilton, 1914; Broch, 1924; Nansen, 1925; Nilsson-Cantell, 1930a; Nilsson-Cantell, 1930c; Gauthier, 1938; Monod, 1938; Nilsson-Cantell, 1939; Scheffer, 1939; Fabian, 1950; Mizue, 1950; Omura, 1950a; Omura et al., 1955; Sergeant and Fisher, 1957; Tomilin, 1957; Wolff, 1960; Marlow, 1963; Rice, 1963; Morris and Mowbray, 1966; Pilleri, 1969a; Pilleri, 1969b; Caldwell et al., 1971b; Van Bree, 1971; Fordyce et al., 1979; Dixon, 1980; Baker, 1983; Pastene et al., 1990; Balbuena, 1991; Debrot, 1992; Rodríguez-López and Mignucci-Giannoni, 1999; Soto, 2001; O'Connor and Franco, 2003; Bermúdez-Villapol et al., 2006; Van Waerebeek et al., 2008; Holmes and Franco, 2010; Martín et al., 2011; Bachara and Gullan, 2016; Foskolos et al., 2017; Tomioka et al., 2020), and on the coronulid barnacles *C. diadema* (Beneden, 1870; Dall, 1872; Sars, 1880; Gruvel, 1911; Mörch, 1911; Liouville, 1913; Borradaile, 1916; Pilsbry, 1916; Broch, 1924; Cornwall, 1924; Cornwall, 1927; Cornwall, 1928; Nilsson-Cantell, 1930a; Nilsson-Cantell, 1930c; Hiro, 1935; Stephensen, 1938; Nilsson-Cantell, 1939; Scheffer, 1939; Tomilin, 1957; Rice, 1963; Clarke, 1966; Newman and Ross, 1971; Holthuis and Fransen, 2004; Kim et al., 2020), *C. reginae* (Nilsson-Cantell, 1930a; Nilsson-Cantell, 1939; Wolff, 1960; Rice, 1963; Clarke, 1966; Newman and Ross, 1971), and *X. globicipitis* (Ten et al., unpubl.). Also, on deformed or injured jaws that leave the teeth exposed (Davis, 1874; Mörch, 1911; Matthews, 1938c; Chapman and Santler, 1955; Clarke, 1956; Nasu, 1958; Cockrill, 1960; Wolff, 1960; Slijper, 1962; Spaul, 1964; Clarke, 1966; Pilleri, 1969b; Beach, 2015). Once recorded as an hyperepibiont on *P. balaenoptera* (Nilsson-Cantell, 1930a).

Use as Indicator

Holmes and Franco (2010) observed several individuals of *C. auritum* on the left tooth of Sowerby's beaked whale, *Mesoplodon bidens*, but none on the right tooth. These authors speculated that the barnacles could indicate some type of chirality during feeding, which may hinder barnacle development on the right side (see *Cryptolepas rachianecti* above). On the other hand, the presence of *C. auritum* has been suggested as an indicator of previous interaction of cetaceans with fisheries since these barnacles can attach on scarred mouth injuries (Beach, 2015; Welch, 2017). Finally, knowledge of growth rates of *C. auritum* makes this species potentially suitable to make temporal calibrations of time since settlement. This could inform on basibiont movements or interaction with fisheries (see, e.g., Dalley and Crisp, 1981; Wegner and Cartamil, 2012; Zettler, 2021), although this application has not been used yet in cetaceans.

Remarks

Also recorded on inanimate substrata (e.g., ship hulls, moorings, ropes; Foster and Willan, 1979; Rasmussen, 1980; Farrapeira et al., 2007) and elephant seals, *Mirounga* spp. (Best, 1971; Joseph et al., 1986).

References

Bennet, 1837; Bennett, 1840; Hallas, 1868; Beneden, 1870; Dall, 1872; Davis, 1874; Sars, 1880; Ohlin, 1893; Lillie, 1910; Gruvel, 1911; Mörch, 1911; Collet, 1912; Liouville, 1913; Hamilton, 1914; Allen, 1916; Borradaile, 1916; Pilsbry, 1916; Broch, 1924; Cornwall, 1924; Hinton, 1925; Nansen, 1925; Cornwall, 1927; Cornwall, 1928; Mackintosh and Wheeler, 1929; Nilsson-Cantell, 1930a; Nilsson-Cantell, 1930c; Matthews, 1937; Matthews, 1938c; Gauthier, 1938; Hiro, 1938; Monod, 1938; Stephensen, 1938; Nilsson-Cantell, 1939; Scheffer, 1939; Fabian, 1950; Mizue, 1950; Omura, 1950a; Omura, et al., 1955; Angot, 1951; Ohno and Fujino, 1952; Kakuwa et al., 1953; Rees, 1953; Chapman and Santler, 1955; Clarke, 1956; Sergeant and Fisher, 1957; Tomilin, 1957; Nasu, 1958; Symons and Weston, 1958; Cockrill, 1960; Wolff, 1960; Sergeant, 1962; Slijper, 1962; Marlow, 1963; Rice, 1963; Spaul, 1964; Clarke, 1966; Morris and Mowbray, 1966; Perrin, 1969; Pilleri, 1969b; Newman and Ross, 1971; Van Bree, 1971; Monod and Serene, 1976; Fordyce et al., 1979; Dixon, 1980; Baker, 1983; Christensen, 1985; Raga and Sanpera, 1986; Mead, 1989; Bushuev, 1990; Pastene et al., 1990; Bordino and González, 1992; Debrot, 1992; García-Godos, 1992; Raga and Balbuena, 1993; Mignucci-Giannoni et al., 1998; Rodríguez-López and Mignucci-Giannoni, 1999; Huang et al., 2000; Soto, 2001; O'Connor and Franco, 2003; Holthuis and Fransen, 2004; Bermúdez-Villapol et al., 2006; Van Waerebeek et al., 2008; Holmes and Franco, 2010; Ávila et al., 2011; Martín et al., 2011; Ólafsdóttir and Shinn, 2013; Angeletti et al., 2014; Insacco et al., 2014; Beach, 2015; Elorriaga-Verplancken et al., 2015; Bachara and Gullan, 2016; Foskolos et al., 2017; Iwasa-Arai et al., 2017b; Wheeler and McIntosh, 2018; Kim et al., 2020; Natural History Museum, 2020; Tomioka et al., 2020; Ueda, 2020; Ten et al., unpubl.

Conchoderma virgatum (Spengler, 1789)

Synonyms

Conchoderma virgata (Spengler, 1790), *Lepas virgata* Spengler, 1790

Morphological Description

Darwin, 1854; Nilsson-Cantell, 1928

Molecular Sequences

COI (Chen et al., 2013), H3 (Pérez-Losada et al., 2008), 12S rRNA (Endo et al., 2010), 18S rRNA (Pérez-Losada et al., 2008; Yusa et al., 2012), 28S rRNA (Pérez-Losada et al., 2008)

Association

Facultative commensal

Cetacean Hosts/Basibionts

Balaenoptera acutorostrata, *B. bonaerensis*, *B. borealis*, *B. musculus*, *B. physalus*, *Delphinus delphis*, *Feresa attenuata*, *Megaptera novaeangliae*, *Neophocaena phocaenoides*, *Physeter macrocephalus*, *Stenella coeruleoalba*

Geographic Range

Cosmopolitan

Life Cycle

Most growth rate estimates of this species have been studied on inanimate substrata (0.1-1.5 mm/day; Darwin, 1851; Annandale, 1909; MacIntyre, 1966; Tsikhon-Lukanina et al., 1977; Il'in et al., 1978; Dalley and Crisp, 1981). For instance, at a mean temperature of 23°C and 14 days after metamorphosis, individuals grew 0.66 mm/day on an experimental torpedo (Dalley and Crisp, 1981). Eckert and Eckert (1987) provide a von Bertalanffy's growth equation obtained from *C. virgatum* measurements on nesting sea turtles, which shows an asymptotic trend comparable to that of previous studies. Differences in growth rate estimates and maximum size between studies suggest an effect of the ecological conditions (Eckert and Eckert, 1987).

Microhabitat

Mostly as a hyperepibiont of *Pennella balaenoptera* (Sars, 1866; Koren and Danielssen, 1877; Turner, 1905; Nilsson-Cantell, 1930a; Clarke, 1956; Clarke, 1966; Raga and Sanpera, 1986; Araki et al., 1997; Terasawa et al., 1997; Uchida, 1998; Ólafsdóttir and Shinn, 2013), but it can also attach directly to odontocete teeth (Lillie, 1910; Aznar et al., 1994). Once reported on *C. auritum* (Clarke, 1966), *Neocyamus physeteris* (Oliver and Trilles, 2000), and on the shell of *Xenobalanus globicipitis* (Ten et al., unpubl.).

Use as Indicator

Knowledge of growth rates of *C. virgatum* makes this species potentially suitable to make temporal calibrations of time since settlement (see *C. auritum*). Indeed, unusual attachment of *C. virgatum* and *Lepas* spp. on dolphin teeth may have occurred after dolphin death, when teeth remain exposed (Aznar et al., 1994). This provides the opportunity to infer the approximate time of death, as it has been done in sea turtles (Ten et al., 2019). The finding of *Conchoderma* sp. (presumably *C. virgatum*) attached to a marlin spear that was inserted into the jaw of an Antarctic minke whale suggested that spearing occurred a few months before the finding (Ohsumi, 1973). Lastly, its presence and size has been used as an indicator of oceanic habitat use by sea turtles (Casale et al., 2004; Casale et al., 2012; Ten et al., 2019) and of interaction with pelagic fisheries (Wegner and Cartamil, 2012; Ten et al., 2019).

Remarks

It is typical settler of inanimate substrata, e.g., ship vessels, buoys (Foster and Willan, 1979; Farrapeira et al., 2007; González et al., 2012; Wegner and Cartamil, 2012), but also attaches to multiple marine animals, including fish (e.g., Crozier, 1916; Hastings, 1972; Ohsumi, 1973), sea turtles (e.g., Eckert and Eckert, 1987; Alonso et al., 2010), elephant seals (Joseph et al., 1986), sea snakes (Annandale, 1909; Yamato et al., 1996), and pelagic crabs (Jerde, 1967; Moazzam and Rizvi, 1979). It has also been reported as a hyperepibiont of fish copepods (e.g., Williams, 1978; Williams and Williams, 1986).

References

Sars, 1866; Koren and Danielssen, 1877; Turner, 1905; Lillie, 1910; Collet, 1912; Liouville, 1913; Mackintosh and Wheeler, 1929; Nilsson-Cantell, 1930a; Clarke, 1956; Clarke, 1966; Kawamura, 1969; Berzin, 1972; Rice, 1977; Greenwood et al., 1979; Raga and Carbonell, 1985; Raga and Sanpera, 1986; Bushuev, 1990; Aguilar and Raga, 1993; Aznar et al., 1994, unpubl.; Araki et al., 1997; Terasawa et al., 1997; Uchida, 1998; Huang et al., 2000; Kuramochi et al., 2000; Oliver and Trilles, 2000; Uchida and Araki, 2000; Ólafsdóttir and Shinn, 2013; Ten et al., unpubl.

Lepas (Anatifa) hillii (Leach, 1818)

Synonyms

Lepas hillii (Leach, 1818)

Morphological Description

Darwin, 1854; Cornwall, 1955

Molecular Sequences

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Association

Facultative commensal

Cetacean Hosts/Basibionts

Once reported on *Stenella coeruleoalba*

Geographic Range

Pantropical (González et al., 2012)

Life Cycle

At temperatures *ca.* 25 °C, individuals attached to a ship in central Atlantic Ocean reached maturity after 30-43 days for a capitulum 13-17 mm long (i.e., a growth rate of 0.5 mm/day; Evans, 1958). Similarly as in *Conchoderma* spp. (see above), growth was asymptotic and fell to 0.03 mm/day after maturity (Evans, 1958).

Microhabitat

Teeth (Aznar et al., 1994)

Use as Indicator

Deeper knowledge of growth rates of *L. hillii* would refine estimates of time since settlement (see *C. virgatum*). Some applications include the estimation of the time of death of basibionts (Aznar et al., 1994; Ten et al., 2019), interaction with fisheries (Wegner and Cartamil, 2012; Ten et al., 2019), and oceanic habitat use (Casale et al., 2004; Casale et al., 2012; Ten et al., 2019).

Remarks

On inanimate substrata, e.g., buoys, ship hulls, a rope (Il'in et al., 1978; Dalley and Crisp, 1981; Farrapeira et al., 2007; Wegner and Cartamil, 2012) and on marine vertebrates, including fish (Dulčić et al., 2015), sea turtles (Domènech et al., 2015; Ten et al., 2019), and elephant seals (Joseph et al., 1986).

References

Aznar et al., 1994

Lepas (Anatifa) pectinata (Spengler, 1793)

Synonyms

Lepas pectinata Spengler, 1793

Morphological Description

Darwin, 1854; Cornwall, 1955

Molecular Sequences

COI (Chen et al., 2013; Schiffer and Herbig, 2016; Aguilar et al., 2018; Rech et al., 2018; GenBank KY639421-KY639424; MF974366-MF974369), H3 (Pérez-Losada et al., 2008), 18S rRNA (Pérez-Losada et al., 2008; Schiffer and Herbig, 2016), 28S rRNA (Pérez-Losada et al., 2008)

Association

Facultative commensal

Cetacean Hosts/Basibionts

Stenella coeruleoalba

Geographic Range

Cosmopolitan (González et al., 2012)

Life Cycle

This is the most abundant lepadid in the Northeast Atlantic, where its development has been studied (Ellis et al., 1983; Conway et al., 1990). Interestingly, *L. pectinata* presumably performs ontogenetic depth migrations, i.e., nauplii feed in the upper 150 m and the non-feeding cyprids distribute at 300-400 m (Conway et al., 1990). Nauplii show similar feeding and swimming features as other barnacle larvae (Moyse, 1984).

Microhabitat

Teeth (Aznar et al., 1994)

Use as Indicator

See *L. hillii* (above).

Remarks

Closely associated to *Sargassum* spp. weed (Fine, 1970; Conway et al., 1990); also found on inanimate substrata (e.g., floating crude oil, plastic debris; Horn et al., 1970; Minchin, 1996; Bergami et al., 2021) and on sea turtles (Domènech et al., 2015; Ten et al., 2019).

References

Aguilar and Raga, 1993; Aznar et al., 1994

Phylum Chordata Haeckel, 1874
Class Actinopteri Cope, 1871
Subclass Teleostei Müller, 1846
Order Carangiformes Jordan, 1963
Family Echeneidae Rafinesque, 1810

Remoras or diskfishes include 8 species of specialized teleosts that use their dorsal fin as an adhesive disc to attach to a great variety of marine vertebrates from which they benefit through, e.g., ventilation, protection from predators, and increased contact with conspecifics (Fertl and Landry, 1999a; Fertl and Landry, 1999b). The fact that remoras live in association with elasmobranchs, teleosts, sea turtles, and cetaceans (Cressey and Lachner, 1970) has hampered research on basic biological features such as growth and reproduction for most species (Battaglia et al., 2016).

Echeneis naucrates (Linnaeus, 1758)

Synonyms

Echeneis chiromacer Duméril, 1858, *E. fasciata* Gronow, 1854, *E. fusca* Gronow, 1854, *E. guaican* Poey, 1860, *E. lunata* Bancroft, 1831, *E. metallica* Poey, 1860, *E. naucratus* Linnaeus, 1758, *E. neucrates* Linnaeus, 1758, *E. scaphecrates* Duméril, 1858, *E. vittate* Rüppell, 1838, *Echensis naucrates* Linnaeus, 1758, *Echneis naucrates* Linnaeus, 1758, *Leptecheneis flaviventris* Seale, 1906, *L. naucrates* (Linnaeus, 1758)

Morphological Description

Collette, 2003; Skaramuca et al., 2009

Molecular Sequences

> 40,000 results in GenBank

Association

Facultative commensal

Cetacean Hosts/Basibionts

Sotalia guianensis, *Tursiops truncatus*

Geographic Range

Cosmopolitan (Collette et al., 2015)

Life Cycle

In the eastern Gulf of Mexico females show slower growth but achieve larger size than males; spawning takes place in August (Bachman et al., 2018).

Microhabitat

Flanks and both dorsal and ventral sides

Use as Indicator

-

Remarks

It can free swim in the water column while feeding on small fishes and plankton (O'Toole, 2002), but also attach to a broad spectrum of basibionts, including reef teleosts, sharks, and sea turtles (O'Toole, 2002; Sazima and Grossman, 2006; Gray et al., 2009), nearshore dolphins (above), and even to conspecifics (Brunnschweiler and Sazima, 2006). It is considered a sister-species of *E. neucratoides* (O'Toole, 2002).

References

Fertl and Landry, 1999b; Fertl et al., 2002; Noke, 2004; Santos and Sazima, 2005

Echeneis neucratoides (Zuiew, 1789)

Synonyms

-

Morphological Description

-

Molecular Sequences

COI (GenBank KF461171), EGR1, EGR2B, EGR3 (Campbell et al., 2013), ITS1 (Gray et al., 2009), ND2 (Gray et al., 2009), RAG1, RH1 (Campbell et al., 2013), VCPIP, ZIC1 (Betancur et al., 2013), 5.8S rRNA, 12S rRNA, 16S rRNA, 18S rRNA (Gray et al., 2009)

Association

Presumably facultative commensal

Cetacean Hosts/Basibionts

Two unidentified cetaceans

Geographic Range

Western Atlantic Ocean (Fertl and Landry, 1999a; Fertl and Landry, 1999b)

Life Cycle

-

Microhabitat

-

Use as Indicator

-

Remarks

Typical commensal of sharks and once observed on a West Indian manatee captured in Puerto Rico (Mignucci-Giannoni et al., 1999).

References

O'Toole, 2002

Remora australis (Bennett, 1840)

Synonyms

Echeneis australis Bennett, 1840, *E. scutata* Günther, 1860, *Remilegia australis* (Bennett, 1840), *Remora australia* (Bennett, 1840), *R. scutata* (Günther, 1860)

Morphological Description

Rice and Caldwell, 1961

Molecular Sequences

COI (GenBank GU440495; OK030822), CYTB (Sanciangco et al., 2016), ITS1, ND2 (Gray et al., 2009), RAG1 (GenBank EU167871), 5.8S rRNA, 12S rRNA, 16S rRNA, 18S rRNA (Gray et al., 2009)

Association

Obligate commensal/mutualist. Although previously considered as an obligate commensal (Rice and Caldwell, 1961), later evidence has shown that this species can feed on host's ectoparasites (O'Toole, 2002). However, remoras may potentially disrupt the flow over cetaceans' body, increasing drag, and their sucking disk may produce irritation (Fish et al., 2006).

Cetacean Hosts/Basibionts

Balaenoptera borealis, *B. edeni*, *B. musculus*, *Delphinus delphis*, *Orcinus orca*, *Physeter macrocephalus*, *Stenella attenuata*, *S. frontalis*, *S. longirostris*, *Tursiops truncatus*

Geographic Range

eastern Pacific, Atlantic, Indian Ocean, Indonesian Sea

Life Cycle

Off Brazil, remoras of the smallest size class (i.e., < 10 cm) were the most abundant size class in May and their frequency fell until none were reported in October (Wingert et al., 2021).

Microhabitat

Ubiquitous on skin (Wingert et al., 2021)

Use as Indicator

Remoras on blue whales preferentially attach to regions with reduced drag. Therefore, they could evince patterns of water flow over swimming whales, which could optimize tag deployment for extended ecological monitoring (Flammang et al., 2020).

Remarks

The records from *B. edeni, O. orca, S. attenuata*, and *T. truncatus* above provide only identification to genus level, but are here assigned to *R. australis* since it is the only species of *Remora* associated to cetaceans (O'Toole, 2002). Individuals of *R. australis* appear to disengage from whales during whaling (Pike, 1951; Rice and Caldwell, 1961), which might result in gross underestimations of actual prevalence in nature. Prior to towing, the prevalence of *R. australis* on blue whales, *Balaenoptera musculus*, captured in California and Peru was close to 100 percent (Rice and Caldwell, 1961). Attachment marks of this species on the host's epidermis are superficial, and scarring is not typically observed (Rice and Caldwell, 1961; Visser, pers. obs.). There is a single record of two copepod hyperparasites on *R. australis*, namely *Pennella balaenoptera* and *Lepeophtheirus crassus* (Radford and Klawe, 1965).

References

Carl and Wilby, 1945; Cadenat, 1953; Krefft, 1953; Follet and Dempster, 1960; Mahnken and Gilmore, 1960; Rice and Caldwell, 1961; Rice, 1963; Radford and Klawe, 1965; Rice, 1977; Rice, 1978; Notarbartolo di Sciara and Watkins, 1979; Fertl and Landry, 1999a; Fertl and Landry, 1999b; Wingert et al., 2021

Order Siluriformes -
Family Trichomycteridae Bleeker, 1858

Catfishes (Siluriformes) are widely distributed in freshwater, estuarine, and marine habitats of continental shelves (de Pinna, 1998). Members of the family Trichomycteridae, known as pencil or parasitic catfishes (de Pinna and Wosiacki, 2003), inhabit continental freshwaters from Costa Rica to Patagonia (de Pinna and Wosiacki, 2003; Eschmeyer et al., 2017).

Ochmacanthus sp.

Synonyms

-

Morphological Description

Araújo-Wang et al., 2019

Molecular Sequences

COI, CYTB, H3, ND4, MYH6, RAG1, RAG2, 12S rRNA, and 16S rRNA of three *Ochmacanthus* spp. (see GenBank)

Association

Presumably obligate commensal

Cetacean Hosts/Basibionts

Inia geoffrensis (Blainville, 1817)

Geographic Range

South American rivers (Koch, 2002)

Life Cycle

-

Microhabitat

On lateral and ventral surfaces (Araújo-Wang et al., 2019)

Use as Indicator

-

Remarks

Candirus are generally commensal on various freshwater fishes (Adriaens et al., 2010), but Araújo-Wang et al. (2019) reported year-round observations on *Inia geoffrensis*.

References

Araújo-Wang et al., 2019

Class Hyperoartia Müller, 1844
Order Petromyzontiformes Berg, 1940
Family Petromyzontidae Bonaparte, 1831

Anadromous lampreys (Petromyzontiformes) are jawless fishes distributed antitropically around the world. They develop in estuaries and oceans, where they parasitize large vertebrates consuming their blood, fluids, and flesh, and then migrate into freshwater streams to spawn and die (Renaud, 2011; Johnson et al., 2015; Clemens et al., 2019). Species of Petromyzontidae are exclusively found in the Northern Hemisphere (Renaud, 2019; Miller et al., 2021). The family Petromyzontidae is described in Renaud (2019).

Entosphenus tridentatus (Richardson, 1836)

Synonyms

Entosphenus epihexodon Gill, 1862, *E. tridentatus tridentatus* (Richardson, 1836), *Lampetra tridentatus* (Richardson, 1836), *Petromyzon astori* Girard, 1858, *P. ciliatus* Ayres, 1855, *P. epihexodon* (Gill, 1862), *P. lividus* Girard, 1858, *P. tridentatus* Richardson, 1836

Morphological Description

Creaser and Hubbs, 1922

Molecular Sequences

COI (Yamazaki et al., 2006; April et al., 2011; Carim et al., 2017; GenBank GU440367; KF918874; KF918875; KF929845; KY570333), CR (GenBank AY205567), CYTB (Docker et al., 1999; Lorion et al., 2000; Yamazaki et al., 2006; Boguski et al., 2012; GenBank DW022992; GQ206157; KR422618; KR422619; KU672473-KU672485), ETR-1, ETR-2, ETR-3, ETR-4, ETR-5, ETR-6 (Spice et al., 2011), GnRH-III (Silver et al., 2004), ND1, ND2, ND4, ND5 (Docker et al., 2007), RT (GenBank AJ244558), 12S rRNA (GenBank LC091545; LC091546), 16S rRNA (GenBank KJ010762), and the whole genome (Hess et al., 2020)

Association

Ectoparasite

Cetacean Hosts/Basibionts

Balaenoptera borealis, *B. musculus*, *B. physalus*, *Berardius bairdii*, *Megaptera novaeangliae*, *Physeter macrocephalus*

Geographic Range

North Pacific, from Baja California north to the Bering and Chukchi seas and westward into Russia and Japan, showing the greatest latitudinal range of any lamprey (Renaud, 2011)

Life Cycle

Laboratory observations hypothesized that the time of residence in the ocean is ≤ 3.5 years (Beamish, 1980). Movements in the ocean are poorly understood, but they are typically caught between the surface and 500 m (see Clemens et al., 2019).

Microhabitat

-

Use as Indicator

Based on the degree of healing of the marks of Pacific lampreys on several species of whales, Pike (1951) inferred that lamprey attacks took place during the northward migration in the North Pacific. Therefore, marks could be used to trace whale's migration.

Remarks

Typically parasitizes fish (Clemens et al., 2019).

References

Carl, 1950; Pike, 1951; Nemoto, 1955; Rice, 1963; Rice, 1977; Rice, 1978

Petromyzon marinus (Linnaeus, 1758)

Synonyms

Ammocoetes bicolor Lesueur, 1818, *Batymyzon bairdii* (Gill, 1883), *Lampetra marina* (Linnaeus, 1758), *Oceanomyzon wilsoni* Fowler, 1908, *Petromyzon adriaticus* Nardo, 1847, *P. americanus* Lesueur, 1818, *P. bairdii* Gill, 1883, *P. concolor* Wright, 1892, *P. lampetra* Pallas, 1814, *P. maculosus* Gronow, 1854, *P. marinus dorsatus* Wilder, 1883, *P. marinus unicolor* Gage, 1928, *P. maximus* Cuvier, 1816, *P. nigricans* Lesueur, 1818, *P. ruber* Lacepède, 1800

Morphological Description

Creaser and Hubbs, 1922

Molecular Sequences

> 193,000 results in GenBank

Association

Ectoparasite, inferred from resulting wounds and scars (Silva et al., 2014)

Cetacean Hosts/Basibionts

Balaenoptera acutorostrata, *B. borealis*, *B. physalus*, *Eubalaena glacialis*, *Grampus griseus*, *Megaptera novaeangliae*, *Mesoplodon bidens*, *Orcinus orca*, *Physeter macrocephalus*, *Tursiops truncatus*, *Ziphius cavirostris*

Geographic Range

Atlantic coast of North America and Europe, including the central Mediterranean Sea (Holčík et al., 2004; Kottelat and Freyhof, 2007)

Life Cycle

This hematophagous species grows to adult size in 1 year; the complete metamorphosis and reproduction takes 1.5 years (Silva et al., 2013).

Microhabitat

Flanks of middle and posterior body areas (Bertulli et al., 2012; Ólafsdóttir and Shinn, 2013)

Use as Indicator

In some cases, the individuals are still attached to the host when found, being easier to detect (Nichols and Hamilton, 2004; Nichols and Tscherter, 2011; Samarra et al., 2012; Miočić-Stošić et al., 2020). In others, however, only the remaining marks are visible. The applicability of these marks is still to be determined. Samarra et al. (2012) stated that they apparently disappear within 1 year, whereas Miočić-Stošić et al. (2020) claim that they are seemingly short-lived, thus not being suitable markings in photo-identification. In the past years, it has been more commonly found in Icelandic waters, and this change in distribution seems to be due to a gradual increase in water temperatures around Iceland (Astthorsson and Palsson, 2006).

Remarks

This species is often found on freshwater and marine fishes (Collette and Klein-MacPhee, 2002).

References

Japha, 1910; Collet, 1912; Nichols and Hamilton, 2004; Nichols and Tscherter, 2011; Rosso et al., 2011; Bertulli et al., 2012; Samarra et al., 2012; Ólafsdóttir and Shinn, 2013; Silva et al., 2014; Bertulli et al., 2016; Miočić-Stošić et al., 2020

Phylum Cnidaria Hatschek, 1888
Class Hydrozoa Owen, 1843
Subclass Hydroidolina Collins, 2000
Order Leptothecata Cornelius, 1992
Family Campanulariidae Johnston, 1836

Members of this family of thecate hydroids are ubiquitous in marine benthic communities. Given that the morphology of colonies and polips are highly variable within species, it is difficult to find diagnostic morphological characters to separate congeneric species (Cunha et al., 2015), which may hinder correct identification to species level.

Obelia dichotoma (Linnaeus, 1758)

Synonyms

Multiple; see Schuchert (2021).

Morphological Description

Orejas et al., 2012

Molecular Sequences

COI (Govindarajan et al., 2006; Cunha et al., 2015; Cunha et al., 2017; GenBank MG791815; MW277711; MW277730;

MZ580517; MZ580890), calmodulin (Govindarajan et al., 2006), LSU rRNA (Pruski and Miglietta, 2019; Penney and Rawlings, 2021; GenBank MG786561; MG786562), SSU rRNA (MG792325), 5.8S rRNA (Cunha et al., 2015), 16S rRNA (Bridge et al., 1995; Govindarajan et al., 2006; Cunha et al., 2015; Cunha et al., 2017; Rech et al., 2018), 18S rRNA, 28S rRNA (Bridge et al., 1995; Govindarajan et al., 2006; Cunha et al., 2015; Maronna et al., 2016; Cunha et al., 2017)

Association
Unknown, although a commensalist or even mutualistic association cannot be ruled out since newly released medusae of this species are bacteriophagous (Boero et al., 2007).

Cetacean Hosts/Basibionts
Once reported on *Megaptera novaeangliae*

Geographic Range
Nearly cosmopolitan (Orejas et al., 2012)

Life Cycle
Kubota (1999) reported the complete life cycle of *O. dichotoma* in Northern Japan.

Microhabitat
As a hyperepibiont on the barnacle *Coronula diadema* (Cornwall, 1928)

Use as Indicator
-

Remarks
It can be found on hard substrata, such as floats, pilings, rocks, and shells (Orejas et al., 2012).

References
Cornwall, 1928

Obelia sp.
Synonyms
-

Morphological Description
Cornelius (1990) provides extensive descriptions of European *Obelia* spp.

Molecular Sequences
> 400 results in GenBank

Association
Unknown

Cetacean Hosts/Basibionts
Once reported on *Megaptera novaeangliae*

Geographic Range
-

Life Cycle
See Cornelius (1990).

Microhabitat
As a hyperepibiont on *Coronula* spp. (Rice, 1963)

Use as Indicator
-

Remarks
-

References
Rice, 1963

Phylum Nematoda Cobb, 1932
Class Chromadorea Inglis, 1983
Subclass Chromadoria Pearse, 1942
Order Monhysterida Filipjev, 1929
Family Monhysteridae de Man, 1876

This family is composed of terrestrial, freshwater, and marine forms. Some species are free-living in the sediment (e.g., Fonseca and Decraemer, 2008), bacterivorous on plants (Alkemade et al., 1992), associated to pack ice (Blome and Riemann, 1999) or living epibiotically on crustaceans in marine, limnetic, and terrestrial habitats (Lorenzen, 1986).

Odontobius ceti (Roussel de Vauzème, 1834)
Synonyms
-

Morphological Description
Roussel de Vauzème, 1834; Baylis, 1923; Lorenzen, 1986

Molecular Sequences
-

Association
Obligate commensal; it probably feeds primarily on organic particles from whales' diet (Baylis, 1923).

Cetacean Hosts/Basibionts
Balaenoptera borealis, *B. musculus*, *B. physalus*, *Eubalaena australis*, *Megaptera novaeangliae*

Geographic Range
Atlantic, North Pacific, Antarctica

Life Cycle
Eggs are laid on the baleen plates but, since no larval stages have been found on cetaceans, further development may take place in the sea (Baylis, 1923).

Microhabitat
Baleen plates (Roussel de Vauzème, 1834; Baylis, 1923; Skrjabin, 1959; Rice, 1963; Lorenzen, 1986), in association with the ciliated

protozoon *Haematophagus megaptere* Woodcock & Lodge, 1921 (Baylis, 1923).

Use as Indicator

-

Remarks

Considered a taxon inquirendum (WoRMS, 2021).

References

Roussel de Vauzème, 1834; Baylis, 1923; Skrjabin, 1959; Rice, 1963; Lorenzen, 1986

Other Taxa With Indicator Value

Some organisms have been reported on cetaceans but cannot be considered epibiotic animals (i.e., they belong to another kingdom or are not intimately associated to cetaceans). For instance, the cirolanid isopods *Natatolana* spp. or the hagfish *Myxine glutinosa* Linnaeus, 1758 are scavengers (Hale, 1926; Bowman, 1971; Pinedo et al., 1989; Martini, 1998; Keable, 2006; Zintzen et al., 2011) and records on living cetaceans are unusual (Pace et al., 2016). The following taxa, despite not being intimate associates or not belonging to the animal kingdom, can provide valuable information on cetacean biology.

At least 14 genera of diatoms (Chromista: Bacillariophyceae) have been recorded on over a dozen cetacean species (e.g., Hart, 1935; Matthews, 1938b; Hustedt, 1952; Nemoto, 1958; Nemoto et al., 1977; Heckman et al., 1987; Ferrario et al., 2018). Several species belonging to genera such as *Bennettella* Holmes, 1985, *Epipellis* Holmes, 1985, *Epiphalaina* Holmes, Nagasawa & Takano, 1993, *Plumosigma* Nemoto, 1956, and *Tursiocola* Holmes, Nagasawa & Takano, 1993 are believed to be exclusive to cetaceans. It has been proposed that these animal-specific diatoms settle on cetaceans in polar waters and take approximately one month to develop into a yellowish-brown film visible to the naked eye (Omura, 1950b). Therefore, it can be inferred that whales in polar areas that are covered by diatom films are at least one-month visitors, whereas those at lower latitudes and still showing skin colouration returned recently from polar regions (Hart, 1935; Matthews, 1938b; Omura, 1950b; Cockrill, 1960; Bannister, 1968; Sekiguchi et al., 1993). In South Africa, diatom films were detected more frequently as the Antarctic whaling season advanced (Cockrill, 1960) *vs.* at the beginning of the season (Best, 1969b). Diatom films have also been used to investigate population segregation, i.e., they were almost absent on sperm whale females and young males, which coincides with inferences of social segregation based in cyamid infections (see *C. catodontis* and *N. physeteris*; Best, 1969a; Best, 1969b).

The cookie-cutter shark *Isistius brasiliensis* (Quoy & Gaimard, 1824) preys on multiple marine organisms, including finfish (Papastamatiou et al., 2010), elasmobranchs (Yamaguchi and Nakaya, 1997), pinnipeds (Gallo-Reynoso and Figueroa-Carranza, 1992; Hiruki et al., 1993), sirenians (Reddacliff, 1988), and cetaceans (Dwyer and Visser, 2011). About 25% of stomach content consists of marine mammal remains, i.e., tissue plugs, skin, blubber (Carlisle et al., 2021), thus being considered a cetacean (micro)predator (Barros and Stolen, 2001). It has been hypothesized that cookie-cutter sharks use an ambush style of hunting; when potential preys are close enough, they latch and remove large plugs of tissue (Widder, 1998). This feeding mode has been catalogued as ectoparasitic (Carlisle et al., 2021). Despite its widespread distribution (Dwyer and Visser, 2011), its common range lies within equatorial and tropical waters (Nakano and Tabuchi, 1990; Yamaguchi and Nakaya, 1997). Accordingly, marks of *I. brasiliensis* on cetaceans at higher latitudes have been used as a migration tag (Tomilin, 1957 -who refers to them as 'light spots'; Renner and Bell 2009; Foote et al., 2011; Bertulli et al., 2016). Interestingly, this species has not been reported on the southern right whale, *Eubalaena australis* (Matthews, 1938a), which is found only further south than 13°S (Peters and Barendse, 2016). Also, due to the long duration of the marks it leaves on cetaceans, it has been suggested as a tool for individual recognition and marking (Dorsey et al., 1990; Visser, 1999; Gill et al., 2000; McSweeney et al., 2007; Visser et al., 2010; Rosso et al., 2011; Bertulli et al., 2016; Visser et al., 2020; Franklin et al., 2020). Other applications of this biological tag include distinguishing cetacean age classes (McSweeney et al., 2007), populations (Sherchenko, 1970; Best, 1977; Moore et al., 2003), and orca ecotypes (Dwyer and Visser, 2011; Visser et al., 2020); characterizing whale wintering grounds (Bushuev, 1990); and as an indicator of swimming in deep waters (Baird et al., 2006) and of emaciation (Gasparini and Sazima, 1996). Its congeneric member, the largetooth cookiecutter shark, *Isistius plutodus* Garrick & Springer, 1964, once observed on a Cuvier's beaked whale, *Ziphius cavirostris* (Pérez-Zayas et al., 2002), has a poorly known distribution (Moore et al., 2003). It leaves larger flesh "plugs" different from the wounds produced by *I. brasiliensis* (Compagno, 1984). Scars of *Isistius* spp. can harbor high loads of cyamids (Kobayashi et al., 2021).

As a final anecdotal remark, Ohsumi (1973) found the broken spear of a marlin, *Makaira* sp., stuck in the jaw of an Antarctic minke whale, *Balaenoptera bonaerensis*, which this author used to infer migration of this whale from tropical and sub-tropical waters, where marlins are distributed.

DISCUSSION

Gaps and Biases

The present review includes records covering over three and a half centuries, a fact that attests to the curiosity that cetacean epibionts have sparked among naturalists, probably due to their often bizarre appearance and conspicuousness. As a result, a reasonable account of the associations between cetaceans and their metazoan epibionts has been achieved. However, important biases and gaps still remain. First of all, the vast majority of studies has not primarily focused on epibiosis and thus provides little quantitative information on these associations. For instance, less than a quarter (110 out of 493) of the publications in this review include data on prevalence. This 'quantitative gap' problem is worsened by the selective 'picking' of positive records, i.e., there is a tendency to report on the occurrence, but not on the absence, of epibionts in descriptive surveys on cetaceans. Consequently, it can be difficult to draw accurate pictures of the degree of specificity and, especially, geographic distribution of epizoic taxa. Another source of bias concerns epibiont size. Studies on large, visible barnacles such as *Xenobalanus globicipitis* are far more numerous than those focusing on minute creatures such as *Balaenophilus unisetus* (Badillo et al., 2007) or species of Cyamidae infecting dolphins (Fraija-Fernández et al., 2017). The genetic information available also varies among epibiotic taxa: 28 out of 54 species lack sequenced genetic material. Among these, some are poorly known species, but others have a long study history and numerous records (e.g., *Odontobius ceti vs. Coronula reginae*).

There is also an uneven coverage and research effort on cetaceans as basibionts, which can result in somewhat biased impressions on epibiont diversity among cetaceans. For instance, baleen whales as a group exhibit the greatest epibiont diversity most likely because they are large, slow-swimming hosts with a number of skin folds and callosities that provide suitable microhabitats for epibiont settlement (Berzin and Vlasova, 1982; see Fraija-Fernández et al., 2017). Moreover, the occurrence of certain epibionts on whales (e.g., coronulids) promotes the settlement and/or population growth of others (e.g., lepadids, cyamids), acting as pioneers (e.g., Matthews, 1937; Rice, 1963). However, mysticetes also are a well-studied cetacean group and, not surprinsingly, only the pygmy right whale, *Caperea marginata* (Gray, 1846), and Omura's whale, *Balaenoptera omurai* Wada et al., 2003, described in 2003 (Wada et al., 2003), still lack records of epibiotic fauna. Conversely, odontocetes may exhibit relatively poor epizoic fauna because many of them (e.g., delphinids) are fast-swimming hosts with small, smooth surfaces. Moreover, there are riverine dolphins, i.e. species of *Inia*, *Neophocaena*, *Orcaella*, *Platanista*, and *Sotalia* that can seldom, if at all, be exposed to epibiotic taxa of marine origin. Research effort is also low for many odontocetes, and no studies are indeed available from species of *Orcaella* Gray, 1866, *Platanista* Wagler, 1830, and *Tasmacetus* Oliver, 1937. The overall point is, therefore, that epibiotic richness in the less studied cetaceans likely has an unassessed degree of underestimation.

The spatial distribution of data is also heterogeneous. First, records from oceanic waters are far less common than those from coastal areas. Second, most geographic records concentrate in the Southern Ocean, Mediterranean Sea, off South Africa, and California, followed by other Northern Pacific regions (Eastern waters and Japan) and the North Sea. However, other vast areas have few surveys, or even none, including the Arctic, Black Sea, Red Sea, Indian Ocean (except South African waters), and the Southwestern Pacific and adjacent seas (e.g., Sulu-Celebes Sea). In this context, it is worth noting that the higher number of records in particular regions does not necessarily result from higher epizoite diversity or abundance, but rather from higher sampling effort. Whaling was a fundamental source of data but focused mainly on areas and seasons where the target species occurred at higher densities, e.g., Antarctic whaling during the austral summer or Saldanha and Durban whaling stations in South Africa (see Findlay and Best, 2016; IWC, 2021). Also, the Mediterranean and U.S. stranding networks have been working for several decades (Becker et al., 1994), while other areas have recently started to gather data on cetaceans (e.g., the Western Indian Ocean region; Plön et al., 2020) or lack active stranding or research programs (i.e., eastern Russian Arctic).

Finally, we still know very little about biology of the epibiotic fauna of cetaceans; a problem which results, at least in part, from the difficulties of dealing with organisms that depend on marine hosts whose accessibility is often limited due to economical, logistic, and legal constraints for sampling. We call this the 'association gap'; we often do not know basic aspects of many epibiont taxa, such as the complete life cycle or the actual nature of the interactions (commensal, parasitic or mutualistic).

The Nature of Epibiotic Associations and Their Indicator Potential

The origin of epibiotic associations of some animal groups with cetaceans is an exciting evolutionary issue since this epibiont fauna was acquired after the ancestors of these mammals colonized the sea (Aznar et al., 2001). Thus, there are instances of a simple use of cetaceans as additional substrata for facultative epibionts such as the Lepadidae (Newman and Abbott, 1980); host-switching events from prior obligate associations with other marine vertebrates, resulting in co-speciation, e.g., the Coronulidae (Frick et al., 2011; Hayashi et al., 2013; Buckeridge et al., 2019) and, perhaps, *B. unisetus* (Badillo et al., 2007); or putative colonization without speciation, e.g., in the case of *Pennella balaenoptera* (Fraija-Fernández et al., 2018). As far as we are aware, the Cyamidae could represent the only case of a potential primary adaptation to parasitism on cetaceans from a putative marine free-living ancestor (see Lowry and Myers, 2013). The nature of each type association brought about a variable degree of modifications in morphology, dependency of host/basibiont, and life history traits yet to be investigated in detail (see, e.g., Pugliese et al., 2012; Dreyer et al., 2020, for the case of *X. globicipitis*). These features define the potential of each epibiont as a tool to uncover aspects of cetaceans' biology. In what follows, we condense the key biological data shown above for the main epibiotic groups, i.e., amphipods, cirripeds, and copepods; we also summarize their use as indicators. Other members of the epibiotic fauna of cetaceans are certainly interesting from ecological and evolutionary points of view, e.g., the roundworm *Odontobius ceti* or the whalesucker *Remora australis*. However, their usefulness as indicators are, in principle, more limited, and will not be further discussed here.

The level of host specificity varies greatly among whale lice species; some species have been reported only, or preferentially, on single cetacean species (e.g., *Cyamus boopis*, *C. catodontis*, *C. ceti*, *C. eschrichtii*, *Neocyamus physeteris*) or clades (e.g., *Balaenocyamus balaenopterae*, *C. erraticus*, *C. gracilis*), whereas others appear to be more generalist (e.g., *Syncyamus aequus*).

The combination of bodily transmission and high specificity makes cyamids especially useful to shed light on phylogeography and social interactions of cetaceans (see references above). Moreover, cyamids can outlive their host for several days, thus providing a rough proxy of the time of death of cetaceans (Leung, 1976; Lehnert et al., 2007). However, when dealing with stranded cetaceans (a common scenario nowadays), these parasites can readily dislodge from hosts, which represents a potential drawback if quantitative infection data are to be used (Fraija-Fernández et al., 2017).

All epibiotic barnacles of cetaceans are filter-feeders whose life cycle includes a series of planktotrophic naupliar stages followed by a non-feeding cyprid, which permanently attaches to the basibiont (Darwin, 1851; Anderson, 1994; Høeg et al., 2003). Coronulids typical from whales tend to be selective and preferentially settle on single host species. For instance, *Coronula diadema* is associated to humpback whales (*ca.* 70% of records of *C. diadema*) and occurs on nearly all whales examined in surveys (Nishiwaki, 1959; Rice, 1963). In contrast, the basal representative of coronulids colonizing cetaceans, namely, *Xenobalanus globicipitis*, has been found on a total of 41 odontocete and mysticete species worldwide. The actual and potential indicator value of coronulids are thus defined by the commensal mode of feeding, the strict dependence on cetacean epidermis for attachment, and the variable degree of basibiont specificity. Species of this family have been used to unveil hydrodynamic features of cetaceans (Kasuya and Rice, 1970; Fish and Battle, 1995; Carrillo et al., 2015; Moreno-Colom et al., 2020) or systemic disease (Aznar et al., 1994; Aznar et al., 2005; Flach et al., 2021). However, their utility to inform on other aspects of cetacean biology, particularly movements and stock identification, are still far from full exploitation. For instance, Bushuev (1990) found significant differences of prevalence of *X. globicipitis* on Antartic minke whales from different Antarctic sectors, and interpreted them as evidence that whales used different wintering areas and did not mix in the Southern Ocean. However, this interpretation relies on the untested assumption that barnacle recruitment can only occur at low latitudes.

The second group of barnacles occurring on cetaceans, i.e., members of the Lepadidae, includes generalist dwellers on any type of hard substrata available in oceanic waters (e.g., Farrapeira et al., 2007; Wegner and Cartamil, 2012). Perhaps the most interesting species in this respect is *Conchoderma auritum* because, as noted above, it tends to be associated to cetaceans, either directly (on teeth) or indirectly (via the shell of coronulids, or the body of the mesoparasite *P. balaenoptera*). This raises the interesting question over the extent to which individuals of *C. auritum* recognize cetaceans as preferential substrata, and whether their populations depend on these basibionts for long-term stability. In any event, lepadids are fast-growing organisms that can be amenable for observational and experimental studies to determine their growth rate at different temperatures (Evans, 1958; Rasmussen, 1980; Dalley and Crisp, 1981; Eckert and Eckert, 1987; Inatsuchi et al., 2010). This makes them suitable as indicators of drifting time of their 'living platforms' (Fraser et al., 2011; Magni et al., 2015; López et al., 2017; Ten et al., 2019), and other aspects yet to be explored in cetaceans.

Two copepods have also developed intimate associations with cetaceans. *Balaenophilus unisetus* occurs on the baleen plates of four *Balaenoptera* spp. and is believed to feed on baleen's keratin (or the associated microfilm) as an obligate commensal (Vervoort and Tranter, 1961; Ogawa et al., 1997; Fernandez-Leborans, 2001; Badillo et al., 2007). Interestingly, available evidence for the congeneric species *B. manatorum* suggests that direct contact is necessary for transmission of *Balaenophilus* spp. (Domènech et al., 2017). This feature has allowed to draw striking inferences on unexpected contacts between otherwise solitary juveniles of marine turtles (Domènech et al., 2017). However, the indicator value of *B. unisetus* seems much more limited because accessibility to whale samples is very restricted.

Females of the world-largest known copepod, *Pennella balaenoptera*, act as mesoparasite of at least 24 cetacean species, penetrating the blubber and musculature to feed on blood (Schmidt and Roberts, 2009; Hogans, 2017). Recent evidence has shown that there are not clear diagnostic morphological traits to differentiate this species from its congener *P. filosa* except for the use of different hosts (Abaunza et al., 2001; Hogans, 2017). Moreover, molecular data do not support segregation between specimens collected from cetaceans and the swordfish in the western Mediterranean (Fraija-Fernández et al., 2018). *Pennella filosa* parasitizes a broad spectrum of large marine fishes in the oceanic realm (Román-Reyes et al., 2019 and references herein). Apparently, then, the occurrence of *P. balaenoptera* (= *filosa*) in oceanic cetaceans could have resulted from and co-accommodation of the parasite on further hosts sharing the same habitat. However, this conclusion should be confirmed by analyzing more specimens of *P. balaenoptera* collected from other fish and cetaceans in other geographical regions. This is paramount because both *P. balaenoptera* and *P. filosa* exhibit low host specificity, contrary to other members of the family Pennellidae, which infect one or two hosts (Hogans, 2017). Thus, the possibility that cryptic speciation have occurred in *P. balaenoptera* (= *filosa*) cannot be ruled out. This taxonomic issue is also relevant to assess the usefulness of *P. balaenoptera* as an indicator species. So far, the species has been used as an indicator of host's health status, i.e., heavy loads of this parasite could reflect poor health of the affected cetacean (Vecchione and Aznar, 2014). However, population inferences are more dependent on whether or not fishes should be included as part of the actual host community supporting the local population of *P. balaenoptera* (= *filosa*).

CONCLUDING REMARKS

Every epibiotic organism must first contact a potential basibiont, attach, and then successfully thrive on it (Crisp and Barnes, 1954; Crisp, 1955; Mullineaux and Butman, 1991). Accordingly, its presence on a vagile animal implies prior coincidence in time and space between both organisms and the suitability of the basibiont/host as a habitat. In addition, since epibionts essentially live in the ecotone between the basibiont/host surface and the marine environment, abiotic conditions (e.g., temperature, salinity) must also fit the auto-ecological requirements of the epibionts during all their life-span, regardless of the migratory activity of the basibiont/host (see Moreno-Colom et al., 2020, and references therein). All these features are the ones that potentially allow to draw inferences on hosts' biology and ecology at individual, population, or community levels. However, the absence of epibionts is also informative, particularly at population level. For instance, investigating marine-mammal breeding and feeding grounds, and migratory routes, is especially important for conservation (Pompa et al., 2011), and can be elucidated, not only by the presence of selected epibionts, but also by their absence. We therefore encourage cetologists to report on both the presence or absence of epibionts whenever possible. Also, quantitative data (e.g., prevalence, mean number of individuals per host) would be most welcome.

Lastly, it is not an overstatement to claim that cetacean epibionts bear intrinsic value, thus should benefit from explicit consideration in conservation policies (see Whiteman and Parker, 2005; Aznar et al., 2011; Kwak et al., 2020). This becomes highly relevant for specific taxa associated to threatened cetaceans (e.g., whale lice), which are also on the verge of unnoticed extinction (see Buckeridge, 2012).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**. Further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

ST carried out literature search, wrote the initial version of the manuscript, and prepared the figures. FJA participated in developing the ideas and organizing and writing the manuscript, and JAR revised the text. All authors read manuscript drafts and contributed content to the developing paper. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.846558/full#supplementary-material

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