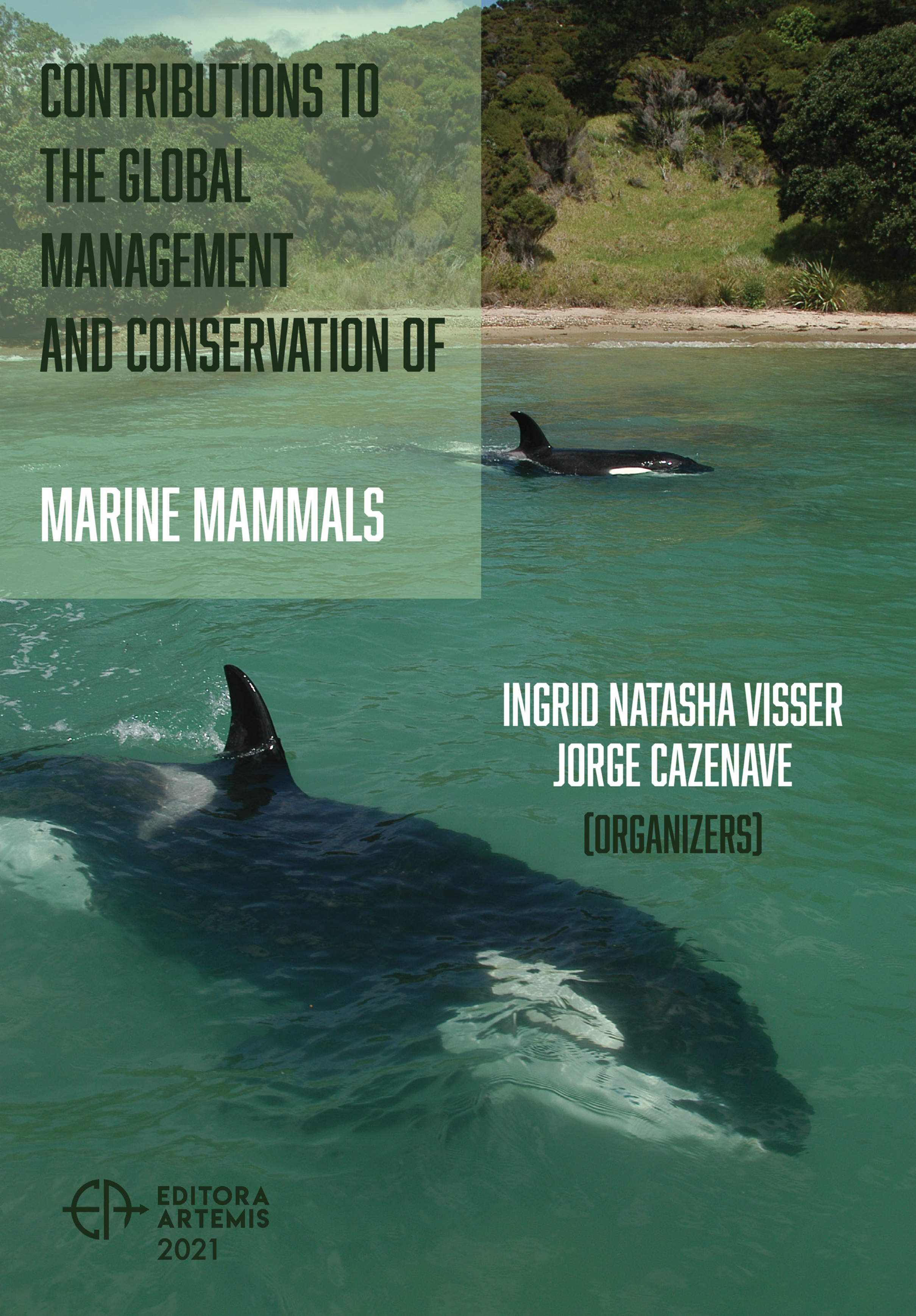

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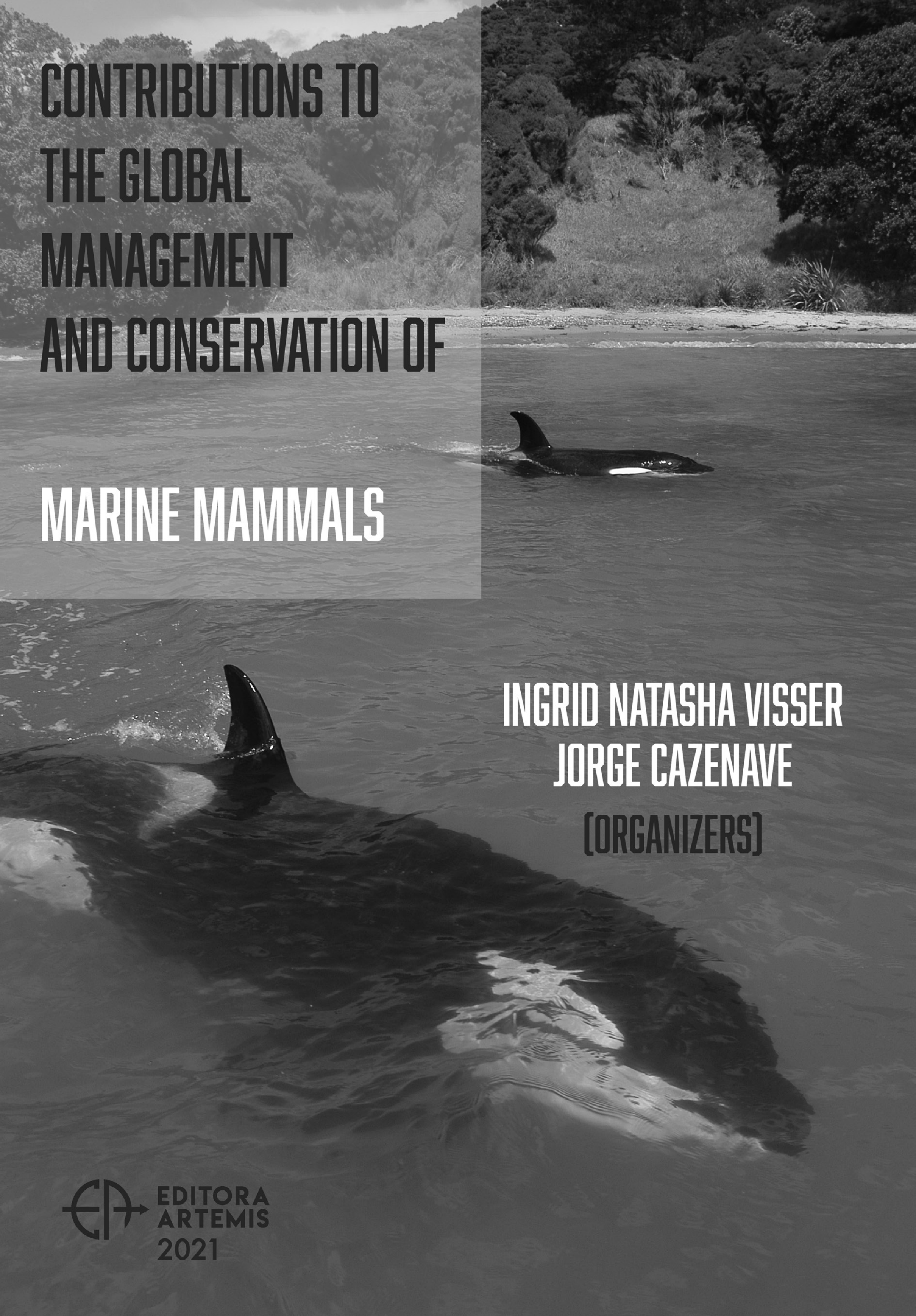

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PREFACE

Contributions to the Global to Management and Conservation of Marine Mammals.

I write the introduction to this book after just having returned from a day out researching wild orca along the New Zealand coastline. During that encounter I had the opportunity to not only see the orca hunting for rays in the shallow waters, but an adult male orca, known to me since he was born, became stranded as he followed his family over a sand bank. His calm demeanour was indicative to me that he had experienced such an event before. Whilst stranded, he patiently tested the water depth, and his ability to get off the sand bank, by gently rolling from side to side every 10 mins or so. During the time that he was stranded our team poured water over him in order to prevent his skin drying out. Eventually the tide had returned enough for him to focus all his energy into getting off and into deeper water. Within minutes of freeing himself he was back with his family and within an hour he was catching rays again. It struck me as I was watching him, that he was around 30 years old, older than I was when I started studying his family. The changes he had seen in his lifetime are changes that I've documented too. Encroachment into his habitat with new marinas, wharfs, reclamation and dredging. Exclusion from prime hunting area from all of these man-made features as well as aquaculture farms expanding so fast it is hard to document them all. He has seen the numbers of vessels increase exponentially and the volume of noise pollution expand with it. He has experienced raw sewage flowing around him when he has entered into harbours and he has swum past floating garbage and viewed sunken junk discarded in his home. He has seen members of his social network drown when entangled, die when stuck on a beach and suffer from severe wounds when hit by boats. It is a wonder he has survived as long as he has with all this and more that he must contend with. But, despite all these negative aspects, there is some hope; New Zealand now has more than 30 marine reserves (protected areas to prevent fishing and habitat destruction). Although they are comprised of only a tiny part of the entire coastline, they are a start. I also see a growing number of scientists, lawyers, researchers and field biologists interested in contributing towards conservation and management issues. My hope is that this volume will provide a platform for some of those studies to reach a wide audience and to make a difference for individual cetaceans, their populations and the habitats that they not only live in but require to survive. The book is arranged by author, rather than, species, region or topic as the first two categories ranged across multiple species and around the globe and yet at times also overlapped, whilst the topics were just as diverse.

Ingrid N. Visser (PhD), New Zealand

In December 2019, the Society for Marine Mammalogy (SMM) and the European Cetacean Society (ECS) jointly hosted the World Marine Mammal Conference in Barcelona, Catalonia, Spain. That conference, the starting point for gathering the authors of this book, was the largest gathering of marine mammologists that had ever occurred, with over 2,700 registered attendees, from more than 90 countries. It was only the second World Marine Mammal Conference, with the first being in 1998 in Monte Carlo, Monaco (and where approximately 1,200 people from 50 countries attended). With the Covid-19 pandemic now rampant across the globe it may be many years before such a similar gather occurs again. Regardless, the work of all those conference attendees will continue and this volume is just one of the many published works that are resulting from ongoing research.

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CHAPTER 3

PARASITES AS INTEGRAL ELEMENTS OF CETACEAN BIOLOGY: THE DIGENEAN *PHOLETER GASTROPHILUS* AS A CASE STUDY

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ABSTRACT: Cetaceans harbor a rich and high-specific parasite fauna that can influence hosts' population dynamics and be used to unveil aspects on their biology. Furthermore, these biotic associations are interesting models to investigate coevolutionary processes in the marine environment. In this chapter, we select a digenean exclusive to cetaceans, *Pholeter gastrophilus*, as a case study to illustrate the potential of parasitological studies to understand historical and present-day host-parasite interactions in this group of marine mammals. First, we present a brief account of the helminth diversity in cetaceans, as well as the systematics and host records for *P. gastrophilus*. Second, we discuss evidence on the origin of the association and phylogeography of this species with cetaceans, emphasizing the gaps in basic aspects such as the life cycle and the population structure, especially of Pacific and Black Sea populations. Third, we sum up information on microhabitat selection and life-history strategy, also identifying the relevant spatial scales and host sampling scheme necessaries for future research. Finally, we examine the pathogenic effects of *P. gastrophilus* and its potential impact at individual and population level. Our bottom-line message is that a comprehensive analysis of parasites of marine mammals also sheds light on host and ecosystem features.

KEYWORDS: *Pholeter gastrophilus*, phylogeography, life history, microhabitat selection, pathogenic potential.

PARASITAS COMO ELEMENTOS INTEGRAIS DA BIOLOGIA DOS CETÁCEOS: O DIGÊNEO PHOLETER GASTROPHILUS COMO ESTUDO DE CASO

RESUMO: Os cetáceos abrigam uma fauna parasitária rica e altamente específica que pode influenciar a dinâmica populacional dos hospedeiros e ser usada para revelar aspectos de sua biologia. Além disso, essas associações bióticas são modelos interessantes para investigar processos coevolucionários no ambiente marinho. Neste capítulo, selecionamos um digeneano exclusivo para cetáceos, *Pholeter gastrophilus*, como um estudo de caso para ilustrar o potencial dos estudos parasitológicos para compreender as interações parasita-hospedeiro históricas e atuais neste grupo de mamíferos marinhos. Primeiramente, apresentamos um breve relato da diversidade de helmintos em cetáceos, bem como a sistemática e registros de hospedeiros de *P. gastrophilus*. Em segundo lugar, discutimos evidências sobre a origem da associação e filogeografia desta espécie com cetáceos, enfatizando as lacunas em aspectos básicos como o ciclo de vida e a estrutura populacional, especialmente das populações do Pacífico e do Mar Negro. Terceiro, resumimos as informações sobre a seleção de microhabitats e estratégia de história de vida, também identificando as escalas espaciais relevantes e os esquemas de amostragem de hospedeiros necessários para pesquisas futuras. Finalmente, examinamos os efeitos patogênicos de *P. gastrophilus* e seu impacto potencial a nível individual e populacional. Nossa mensagem final é que uma análise abrangente de parasitas de mamíferos marinhos também esclarece as características do hospedeiro e do ecossistema.

PALAVRAS CHAVE: *Pholeter gastrophilus*, filogeografia, história de vida, seleção de microhabitat, potencial patogênico.

1. THE IMPORTANCE OF PARASITISM IN CETACEANS

Parasites are an inextricable element of the biology of their hosts since they stablish relationships of close dependency with them. Precisely because of the nature of these associations, parasites are suitable entities to reveal a broad range of aspects on their host's biology. For instance, many parasites of cetaceans have been used as biomarkers in studies concerning, *inter alia*, the behavior, health status or population structure of their hosts (AZNAR et al. 2002; FRAIJA-FERNÁNDEZ et al. 2016b and references therein). Furthermore, by definition, parasites exert a negative effect, sometimes generating a considerable population impact on their hosts (AZNAR et al. 2002). Among microparasites, for instance, cetacean morbilliviruses are of particular concern because they can cause mass mortality events in wild host populations (WEISS et al. 2020 and references therein). Likewise, parasites of genus *Crassicauda*, which occur in the urogenital system, mammary glands, abdominal muscle and cranial sinuses of cetaceans, may provoke serious pathologies including bone lesions (GERACI and AUBIN, 1987; VAN BRESSEM et al. 2020) or congestive renal failure (LAMBERTSEN, 1986). These pathogenic effects have been proposed as a major cause of natural mortality of hosts (LAMBERTSEN, 1986; GERACI and AUBIN 1987; AZNAR et al. 2002). In short, there is evidence that parasites can significantly impact cetacean populations and, since several cetacean species are seriously endangered, conservation programs should include parasites as a relevant component of assessment.

Although cetaceans harbor a rich and highly specific parasite fauna (see below), a great deal of viruses, bacteria, as well as parasitic protozoans and metazoans, are yet to be described (AZNAR et al. 2002; RAGA et al. 2009; FRAIJA-FERNÁNDEZ et al. 2016b). Moreover, our knowledge about the biology of these parasites, as well as about the relationships they stablish with their hosts, is still very scarce in most cases. It is particularly challenging to obtain information about life cycles due to the cryptic nature of these animals, the difficulties of field sampling and the virtual impossibility of experimental approaches (e.g. HERMOSILLA et al. 2015; LEMPEREUR et al. 2017). However, it is worth making an effort to undertake a biological and ecological study of these parasites, not only for the reasons stated above, but also because parasites of cetaceans are models of great interest to investigate coevolutionary phenomena in the marine environment, especially oceanic.

In this chapter, we select a species of digenean exclusive to cetaceans, i.e. *Pholeter gastrophilus*, as a case study. This species infects a large number of odontocetes (FRAIJA-FERNÁNDEZ et al. 2016b; 2017) and represents a suitable model to illustrate the type of research that can be carried out regarding host-parasite associations in this group of marine mammals. First, we will place this species in the context of helminth diversity in cetaceans. Second, we will trace the taxonomic history of the species and its relationship with allied taxa. Third, we will discuss the origin of the association of *P. gastrophilus* with cetaceans and their phylogeographic patterns. Fourth, we will point out what is known about its ecology, including its life cycle and life history strategies, as well as their microhabitat selection in cetaceans. Finally, we will comment on the pathogenic impact of this species. We will conclude with a brief reflection on the implications of these findings and the areas for future research.

2. HELMINTH DIVERSITY IN CETACEANS

To date, 175 species of helminths have been reported in cetaceans (FRAIJA-FERNÁNDEZ et al. 2016b; EBERT et al. 2017) belonging to Acanthocephala (20 spp); Cestoda (38 spp.); Nematoda (62 spp.) and Digenea (54 spp.).

Acanthocephalans of cetaceans belong to genera *Bolbosoma* and *Corynosoma* (family Polymorphidae) and, similarly as other acanthocephalans infecting endotherms, they occur in the intestine of mysticetes and odontocetes (FRAIJA-FERNÁNDEZ et al. 2016b); a striking exception is *Corynosoma cetaceum*, which mainly favours the stomach of dolphins (AZNAR et al. 2001). Life cycles of these parasites have not been fully elucidated but, presumably, pelagic euphausiids and copepods act as intermediate hosts, fishes as paratenic (i.e. transport) hosts and marine mammals as final hosts (RAGA et al. 2009). Marine mammals, including cetaceans, are thought to have ancestrally acquired polymorphids due to a host switching event involving aquatic birds (GARCÍA-VARELA et al. 2013).

Among cestodes, the families Diphyllobothriidae, Tetrabothriidae and Phyllobothriidae contain species infecting cetaceans (FRAIJA-FERNÁNDEZ et al. 2016b). Species of the first two families inhabit the intestines of mysticetes and odontocetes, which are known to be final hosts (RAGA et al. 2009); data about the rest of the life cycle is limited, although zooplanktonic crustaceans are known to serve as first intermediate hosts for other cestodes in the oceanic realm (RAGA et al. 2009). Available evidence suggests that marine mammals acquired tetrabothriids from marine birds in the Tertiary (HOBERG et al. 1999). On the other hand, larvae of phyllobothriids are found in the subcutaneous blubber, the mesenteries of the abdominal cavity and the digestive tract of many odontocetes; apparently, large sharks are final hosts and get infected when feeding on cetaceans (AZNAR et al. 2007; RANDHAWA 2011). Historically, cetaceans were likely incorporated as intermediate hosts in a pre-existing life cycle that involved crustaceans and teleosts as intermediate hosts, and sharks as definitive hosts (AZNAR et al. 2007; RAGA et al. 2009).

Nematodes reported in cetaceans are grouped into the families Anisakidae, Pseudaliidae and Tetrameridae (FRAIJA-FERNÁNDEZ et al. 2016b). Species of the Anisakidae use invertebrates as first intermediate hosts, fishes and cephalopods as paratenic hosts, and marine mammals as final hosts, where worms typically inhabit the stomach (MATTIUCCI and NASCETTI, 2008). Some anisakids (i.e. *Anisakis* spp.) occur worldwide in mysticetes and odontocetes, whereas others (i.e. some species of *Pseudoterranova* and *Contracaecum*) are restricted to a few odontocete species (FRAIJA-

FERNÁNDEZ et al. 2016b). The anisakids infecting marine mammals appear to have a marine origin, with a secondary colonization of *Anisakis* spp. in some freshwater dolphins (HOBERG and KLASSEN, 2002; RAGA et al. 2009). Pseudaliids, on other hand, exploit a wide range of microhabitats of mysticetes and odontocetes, including the respiratory system, the middle ear, the eustachian tube and the cranial sinuses (MEASURES 2001; LEMPEREUR et al. 2017). Information concerning their life cycle is rather scarce, although there is convincing evidence for vertical transmission in some species (MEASURES 2001; POOL et al. 2020), and data on putative paratenic fish hosts in others (LEHNERT et al. 2010). It is thought that pseudaliids have a terrestrial origin and made it to the sea with ancestors of marine mammals (LEHNERT et al. 2010 and references therein). Finally, the family Tetrameridae is represented by *Placentonema gigantisima*, which is restricted to the placenta of sperm whales (*Physeter macrocephalus*), (DHERMAIN, SOULIER and BOMPAR, 2002) and species of *Crassicauda*, which are typically found in the circulatory and urogenital system of both mysticetes and odontocetes, and in the cranial pterygoid sinuses of odontocetes (KEEMAN-BATEMAN et al. 2018; MARCER et al. 2019; VAN BRESSEM et al. 2020). The life cycles of tetramerids are also poorly known, but some species of *Crassicauda* are thought to reach cetaceans by trophic transmission (LEMPEREUR et al. 2017).

Digeneans are the most specific taxa at species level among cetacean helminths, and are distributed into four families, i.e. Brachycladiidae, Brauninidae, Notocotylidae and Heterophyidae (FRAIJA-FERNÁNDEZ et al. 2015a, 2016b; EBERT et al. 2017). The family Brachycladiidae is the only one whose members exclusively infect marine mammals as final hosts (FRAIJA-FERNÁNDEZ et al. 2016a; KREMNEV et al. 2020). Seven of its genera are restricted to mysticetes and odontocetes, occurring in bile ducts, intestine, lungs and air sinuses (DAILEY et al. 2007; FRAIJA-FERNÁNDEZ et al. 2016a). The life cycle of some brachycladiid species infecting pinnipeds has been elucidated recently; it appears to comprise gastropods as first intermediate hosts and bivalves as second intermediate hosts (KREMNEV et al. 2020). However, transmission pathways for species dwelling in oceanic cetaceans are still an enigma (FRAIJA-FERNÁNDEZ et al. 2016a). The association of brachycladiids with marine mammals likely resulted from a host-switching event from fishes to the ancestors of odontocetes that preyed on them; subsequent colonization of mysticetes followed (RAGA et al. 2009; FRAIJA-FERNÁNDEZ et al. 2016a). The family Brauninidae contains a single species i.e. *Braunina cordiformis*, which attach to the stomach wall and in the duodenal ampulla of several odontocetes (FRAIJA-FERNÁNDEZ et al. 2015a; 2016a); its life cycle is not known (TORRES et al. 1992). With regard to family

Notocotylidae, species of the genus *Ogmogaster* infect the intestines of mysticetes (FRAIJA-FERNÁNDEZ et al. 2015a, 2016a); whales are thought to acquire these parasites when feed on crustaceans. Both the associations of *B. cordiformis* and *Ogmogaster* spp. with cetaceans appear to have resulted also from host-switching events (FRAIJA-FERNÁNDEZ et al. 2015a). Finally, *Pholeter gastrophilus* (Fig.1) is the only species of family Heterophyidae that exhibits an exclusive association with cetaceans; this species selects the wall of the stomach (rarely the duodenum) of odontocetes (FRAIJA-FERNÁNDEZ et al. 2015a, 2016b). The life cycle of this species, as well as other aspects of its biology, are addressed in what follows.

3. THE BIOLOGY OF *PHOLETER GASTROPHILUS*

3.1 Specificity and geographical distribution

The genus *Pholeter* Odhner, 1914 (Digenea: Heterophyidae) currently comprises two species: *Pholeter gastrophilus* (Kossack, 1910) Odhner, 1914 and *Pholeter anterouterus* Fischthal and Nasir, 1974.

The taxonomic affiliation of species of *Pholeter* has been controversial. *Pholeter gastrophilus* (Fig. 1) was firstly described as *Distomum gastrophilum* Kossack, 1910, from an intestinal cyst of a harbor porpoise (*Phocoena phocoena*) in the Baltic Sea. Later, Odhner (1914) provided a more detailed description and included this species within the family Troglotrematidae Odhner, 1914 (PRICE, 1932) as *Pholeter gastrophilus*. Troglotrematids comprised a miscellaneous group of parasites that where not phylogenetically related but that all shared the trait of living within nodules of host tissue (BLAIR, TKACH and BARTON, 2008). Given the artificial nature of troglotrematids as a taxon, Dollfus (1939) included the genus *Pholeter* in a specific family, Pholeteridae, which was in turn included into superfamily Heterophyoidea Odhner, 1914 (currently known as Opisthorchioidea Looss, 1899) (PEARSON and COURTNEY, 1977). Later, Yamaguti (1958) reduced the family Pholeteridae to subfamily status (i.e. Pholeterinae) and it was included within the family Opisthorchiidae Looss, 1899 (PEARSON and COURTNEY, 1977; RAGA, RADUAN and BLANCO, 1985).

Courtney and Forrester (1974) reported a probable new species of *Pholeter* in the small intestine of two pelican species from Florida, but no morphological description was provided. Almost simultaneously, Fischthal and Nasir (1974) described *P. anterouterus* from the intestine of a neotropical cormorant (*Phalacrocorax olivaceus*) and suggested that Courtney and Forrester's finding was very likely *P. anterouterus*. The new species was included together with *P. gastrophilus* within the family Opisthorchiidae, with an emended diagnosis of the genus (PEARSON and COURTNEY, 1977). Few decades later, and due to morphological similarities with other heterophyids, members of the genus *Pholeter* were finally assigned to the family Heterophyidae Leiper 1909 (PEARSON and COURTNEY, 1977; BLAIR, TKACH and BARTON, 2008).

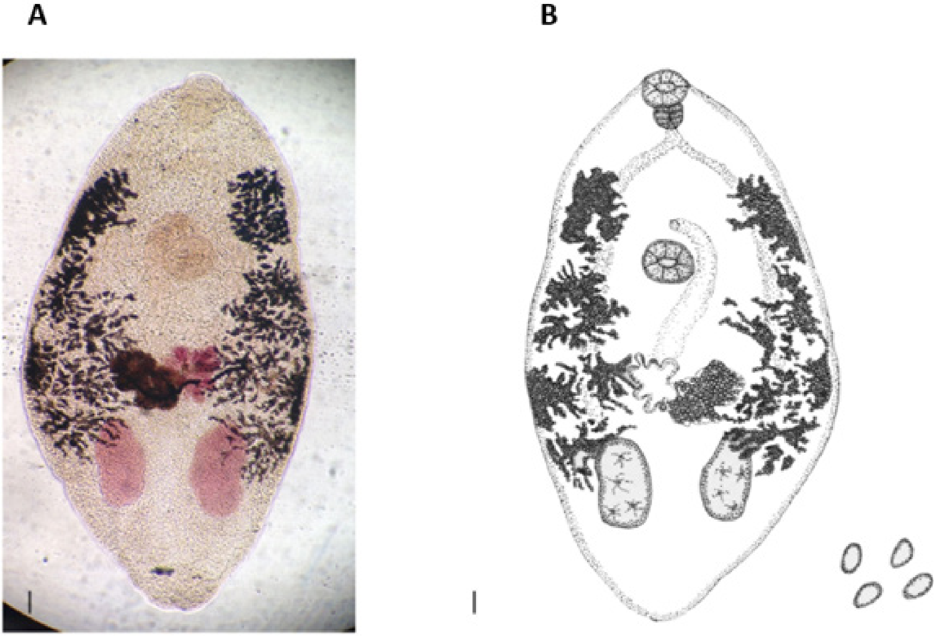

Figure 1. Adult of *Pholeter gastrophilus*. A) microscopic view. B) Schematic drawing, including eggs (on the right). Scale-bars: 0.1mm.

Currently, records of *P. gastrophilus* are well documented (Table 1). Fraija-Fernández et al. (2017) reported the last update in terms of distribution and host-parasite associations, which included 21 odontocetes worldwide belonging to 6 families, mostly delphinids. Only one host species was missed in this review, namely, the pygmy killer whale (*Feresa attenuata*) (CONTI and FROHLICH, 1984) as well as a few host records in the North Sea (Table 1). Recently, Groch et al. (2018) found numerous trematode eggs compatible with those from *P. gastrophilus* in the pyloric stomach of Guiana dolphin (*Sotalia guianensis*). Accordingly, the list of definitive hosts for *P. gastrophilus* currently includes 23 spp. (Table 1).

Table 1. Updated list of definitive host species and geographical areas where the digenean *Pholeter gastrophilus* (Trematoda: Heterophyidae) has been recorded. Abbreviations: AR, Amazon River; AO, Atlantic Ocean; BaS, Baltic Sea; BlS, Black Sea; MS, Mediterranean Sea; NS, North Sea; PO, Pacific Ocean; RS, Red Sea; SA, South Australia.

Host species	Locality	References
Family Delphinidae		
Cephalorhynchus commersonii. Commerson's dolphin	AO	[1] [2]
Delphinus delphis. Short-beaked common dolphin	AO, BlS, SA	[1] [11]
Feresa attenuata. Pygmy killer whale	AO	[3]
Globicephala macrorhynchus. Short-finned pilot whale	AO	[2]
Globicephala melas. Long-finned pilot whale	AO, NS, MS	[4] [5] [1] [2] [6]
Grampus griseus. Risso's dolphin	AO, MS	[1] [2]
Lagenodelphis hosei. Fraser's dolphin	AO	[2]
Lagenorhynchus acutus. Atlantic white-sided dolphin	AO, NS	[1] [2] [7]
Lagenorhynchus albirostris. White-beaked dolphin	AO, NS	[1] [2] [7]
Lagenorhynchus obscurus. White-sided dolphin	AO, PO	[1] [2]
Sotalia guianensis. Guiana dolphin (*)	AO	[7]
Stenella frontalis. Atlantic spotted dolphin	AO	[1] [2]
Stenella coeruleoalba. Striped dolphin	AO, MS	[1] [2]
Steno bredanensis. Rough-toothed dolphin	AO	[1] [2]
Tursiops aduncus. Indo-pacific bottlenose dolphin	RS	[1] [2]
Tursiops truncatus. Common bottlenose dolphin	AO, BlS, MS, PO	[1] [2]
Family Iniidae		
Inia geoffrensis. Amazon river dolphin (¹)	AR	[1] [2]
Family Kogiidae		
Kogia breviceps. Pygmy sperm whale	AO	[2]
Kogia sima. Dwarf sperm whale	AO	[2]
Family Phocoenidae		
Phocoena phocoena. Harbor porpoise	AO, Bas, BlS, NS	[9] [10] [1] [2] [11]
Phocoena spinipinnis. Burmeister's porpoise	AO, PO	[1] [2]
Family Physeteridae		
Physter macrocephalus. Sperm whale	AO	[2]
Family Pontoporiidae		
Pontoporia blanvillei. Franciscana	AO	[1] [2]

References: [1] FRAIJA-FERNÁNDEZ et al. 2016b and references therein; [2] FRAIJA-FERNÁNDEZ et al. 2017 and references therein; [3] CONTI and FROHLICH, 1984; [4] JAUNIAUX et al. 2002; [5] IJSSELDIJK et al. 2015; [6] IJSSELDIJK and GRÖNE, 2019; [7] SCHICK et al. 2020; [8] GROCH et al. 2018; [9] HERRERAS et al. 1997; [10] SIEBERT et al. 2006; [11] VAN ELK et al. 2019. (*) Eggs compatible with *P. gastrophilus*, but no morphological description was given; (¹): this record requires further confirmation.

3.2 Origin and phylogeographic patterns

How the exuberant diversity of digeneans became associated with the ancestors of cetaceans been extensively debated during the recent decades; a major issue was the extent to which such associations are of terrestrial or marine origin. We can assume that the terrestrial ancestors of cetaceans harbored their own parasite fauna, but life-cycles were likely compromised when these definitive hosts began to colonize the marine environment (HOBERG and KLASSEN, 2002; RAGA et al. 2009). Even though some parasites could have exceptionally cope with the new marine conditions, there is consensus that mass extinctions of parasites must have happened (HOBERG and KLASSEN, 2002; RAGA et al. 2009). Thus, most of the current helminth fauna of cetaceans was probably acquired via host switching events in the ocean. Since marine mammals radiated after seabirds and teleost fishes in the marine realm (PYENSON, KELLEY and PARHAM, 2014), cetaceans could most likely acquire marine parasites from the later taxa, an scenario that is supported by phylogenetic evidence (FERNÁNDEZ et al. 1998; FRAIJA-FERNÁNDEZ et al. 2015a).

Pholeter gastrophilus is included in the family Heterophyidae, whose members use fish as intermediate hosts and fish-eating birds and mammals as final hosts. Specifically, adults of the putative sister taxon of *P. gastrophilus* (i.e. *P. anterouterus*) are found in fibrotic nodules of the intestinal wall of at least 3 families of fish-eating birds (Table 2). Thus, it seems plausible that the presence of *Pholeter* spp. in non-related hosts, i.e., odontocetes and seabirds, was driven by the similarity of hosts' trophic guild that historically favored contacts with infective stages, and potential exchange of parasites. In fact, ancient odontocetes were presumably piscivorous (THEWISSEN et al. 2009 and references therein). Although the available evidence does not allow to clarify whether cetaceans acquired *Pholeter* spp. from aquatic birds or vice versa, the affinities of allied heterophyid taxa with birds point to the possibility that the association of *P. gastrophilus* with cetaceans occurred at sea. Once this association got established, *P. gastrophilus* could have expanded its host range into other piscivorous cetaceans; this is a phenomenon that has been reported in other digeneans from cetaceans, i.e. the family Brachycladiidae (FERNÁNDEZ et al. 1998; FRAIJA-FERNÁNDEZ et al.2016a).

Table 2. Records of the digenean Pholeter anterouterus (Trematoda: Heterophyidae). Abbreviations: FL, Florida; Ven: Venezuela.

Host species	Locality	References
Family Ardeidae		
Ardea alba. Great egret	FL	[1]
Egretta caerulea. Blue heron	FL	[2]
Family Phalacrocoracidae		
Phalacrocorax olivaceus. Neotropic cormorant	Ven	[3] [4]
Family Pelicanidae		
Pelecanus erythrorhynchos. American white pelican	FL	[5] [6]
Pelecanus occidentalis. Brown pelican	FL	[7(*)] [5]

References: [1] SEPÚLVEDA et al. 1999; [2] SEPÚLVEDA et al. 1996; [3] FISCHTHAL and NASIR, 1974; [4] NÚÑEZ, 1999; [5] PEARSON and COURTNEY, 1977; [6] KINSELLA, SPALDING and FORRESTER, 2004; [7] COURTNEY and FORRESTER, 1974. (*): Probably *P. anterouterus*: no morphological description was given.

As noted above, *P. gastrophilus* is the most generalist and geographically widespread digenean species that infects cetaceans (FRAIJA-FERNÁNDEZ et al. 2017). This raises the question of whether or not *P. gastrophilus* may actually comprise a complex of sibling species, a phenomenon that has been documented in other generalist helminths of cetaceans (e.g. MATTIUCCI and NASCETTI, 2008). However, FRAIJA-FERNÁNDEZ et al. (2015b; 2017) did not detect significant genetic divergence between specimens from different cetacean species, or between populations geographically apart (south western vs. north eastern Atlantic). This apparently suggests that there is ample genetic flow between populations and *P. gastrophilus* represent a single species. However, this should be confirmed by including molecular data from individuals from Pacific and Black Sea populations (Table 1), which presumably are the most ecologically and geographically isolated.

In fact, among the surveyed populations, FRAIJA-FERNÁNDEZ et al. (2017) found a certain degree of genetic structure at a regional scale. In particular, worms sampled in hosts from the North Sea showed significant divergence with respect to those from other Atlantic and Mediterranean populations. This was related to at least two ecological factors that limit gene flow (FRAIJA-FERNÁNDEZ et al. 2017 and references therein). First, gene flow in digeneans is crucially related with the dispersion potential of its most mobile hosts (typically the definitive hosts), and the species of cetaceans that were sampled in North Sea are sedentary and strongly linked to coastal areas. Second, the southern Bay of Biscay represent a transition zone between boreal and subtropical regions, acting as an oceanographic barrier to marine organisms, including some cetaceans. Further studies are required to investigate gene flow in other presumably isolated areas, e.g., the Black Sea.

3.3 Life cycle and life history strategies

Among parasitic taxa, digeneans exhibit particularly complex life cycles (CRIBB et al. 2003; FRAIJA-FERNÁNDEZ et al. 2017) that involve at least three distinct generations of both parasitic and free-living forms (CRIBB, BRAY and LITTLEWOOD, 2001). As a general scheme, ciliated miracidia emerge from the eggs released to the aquatic environment; miracidia swim and look for the first intermediate host (typically a mollusc) and penetrate in them. After a series of metamorphoses inside the mollusc, miracidia turn into cercariae, which leave the mollusc and actively look for the second intermediate host, which can be an invertebrate (typically an arthropod), or a vertebrate (typically a fish). Within the second intermediate host, cercariae lose their capacity to swim and transform into encysted metacercariae. Finally, when the second intermediate host is ingested by the final host, metacercariae are released from prey and migrate into the characteristic microhabitat within the host body where they reach sexual maturity and reproduce. These adult worms release eggs to the aquatic environment through the host feces (CRIBB, BRAY and LITTLEWOOD, 2001).

In the case of *P. gastrophilus*, currently there is only evidence about the identity of the final hosts (Table 1). Speculation on the specific identity of intermediate hosts has been made using the information available from allied digenean species, given the similarity among the stages in their life cycles. Digeneans show a high level of phylogenetic conservatism regarding their first intermediate host (CRIBB, BRAY and LITTLEWOOD, 2001). Since the first intermediate hosts known for heterophyids include 3 superfamilies of bottom-dwelling snails, namely Cerithioidea, Littorinoidea and Rissoidea, it is plausible that the first intermediate host (s) for *P. gastrophilus* is (are) species from any of these superfamilies, although the specific identity may vary depending on the geographical area (FRAIJA-FERNÁNDEZ et al. 2017 and references therein). This hypothesis would be supported by the fact that *P. gastrophilus* infects both neritic and oceanic cetaceans and, therefore, its first intermediate host(s) is (are) expected to tolerate a wide bathymetric range, as most cerithoids and rissoids do (WELCH, 2010).

The second intermediate hosts in other heterophyids are typically fish (CRIBB, BRAY and LITTLEWOOD, 2001). Interestingly, most cetaceans in which *P. gastrophilus* has been reported are mainly piscivorous (PAULY et al. 1998). However, this parasite has been extensively detected in cetaceans that consume a great variety of fish prey (neritic, oceanic, pelagic and demersal), as well as in cetaceans that feed almost exclusively on cephalopods (AZNAR et al. 2006). These observations strongly suggest that *P. gastrophilus* must use many prey species of both fish and cephalopod to infect its final hosts. In this context, it is rather striking that metacercariae of *P. gastrophilus* have never been detected after many decades of parasitological surveys on both fish and cephalopods that serve as prey for cetaceans (MATEU et al. 2015).

In any event, the completion of the life cycle of *P. gastrophilus* in the oceanic environment is particularly challenging. Oceanic ecosystems are characterized by low productivity, meaning less density of organisms, and therefore less probabilities for infective stages to contact hosts compared with neritic habitats, which are by far more productive (FRAIJA-FERNÁNDEZ et al. 2015b and references therein). In particular, the tiny miracidia of *P. gastrophilus* should be able to contact the putative mollusk first intermediate host in both the vast and “empty” oceanic space, and the more “friendly” coastal area. How could this be accomplished? Available evidence preliminarily suggests that individuals of coastal and oceanic populations of *P. gastrophilus* make different investments in offspring. Although the number of eggs *in utero* does not seem to differ between worms infecting an oceanic cetacean, the striped dolphin (*Stenella coeruleoalba*), and a coastal cetacean, the common bottlenose dolphin (*Tursiops truncatus*), eggs are significantly larger in the former. Apparently, worms infecting the oceanic cetacean would make a greater provision of resources per capita for their offspring to withstand their lower probability of contacting the first intermediate host (FRAIJA-FERNÁNDEZ et al. 2015b). Conversely, in a costal habitat with more intermediate hosts available it would be wiser to divide the investment into more offspring. This hypothesis assumes that a larger egg translates in both longer times for hatching and larger hatched miracidia, and these two factors would increase the chances of initial survival in a harsh environment. However, the study by FRAIJA-FERNÁNDEZ et al. (2015b) was based on just two host species, and replication using other coastal and oceanic cetaceans is peremptory to confirm this pattern.

3.4 Microhabitat selection in cetaceans

The study of habitat selection by parasites can be approached at different hierarchical scales, from the most general (the choice of host) to the most specific environment (i.e. the microhabitat) and, at each scale, the processes driving habitat occupation may be shaped by different selective pressures and phylogenetic restrictions (AZNAR et al. 2006 and references therein). The case of *Pholeter gastrophilus*, is particularly complex (Fig. 2).

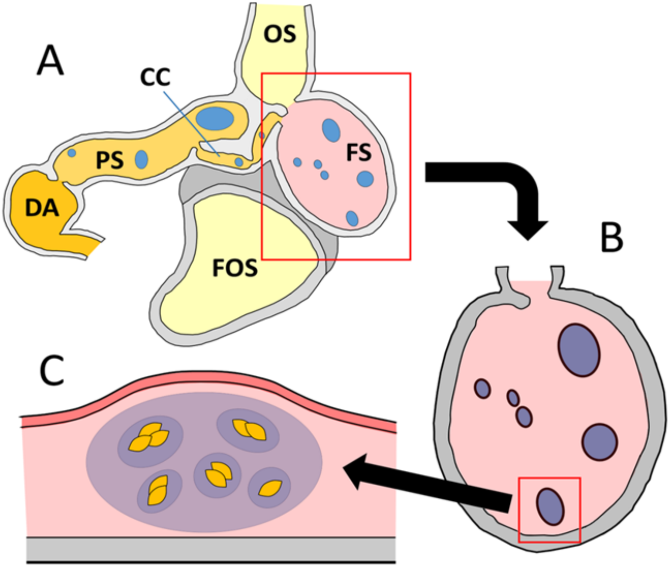

Figure 2. Spatial scales at which the microhabitat selection by the digenean *Pholeter gastrophilus* can be investigated in cetaceans. A) Among stomach chambers. The oesophagus (OS) expands to form a so-called forestomach (FOS), which, in turn, connects to the fundic stomach (FS). A narrow connecting channel (CC) regulates the pass of chyme into the pyloric stomach (PS). The pyloric sphincter separates the stomach from the intestine which, in most cetaceans, begins with a funnel-shaped expansion of the duodenum, the duodenal ampulla (DA). *Pholeter gastrophilus* favours the stomach proper, where it form nodules (in blue). However, the distribution among chambers can differ between cetacean species. B) Within chambers. Worms form aggregations (nodules) of variable size and distribution in each chamber. C) Within nodules. Nodules are composed of a number of cavities containing a variable number of worms (typically 2-3). (See the text for details).

At the broadest scale, the habitat selected by *P. gastrophilus* is the stomach of odontocete cetaceans. This organ is composed of 3 chambers (i.e. forestomach, fundic and pyloric stomachs) that differ in both morphology and physiology (Fig. 2A). There is also a narrow connecting channel between the last two chambers. The forestomach (actually an oesophageal pouch) stores prey and starts the mechanical and chemical digestion thanks to digestive enzymes coming from the fundic stomach. The main chemical digestion takes place in the latter. The connecting channel regulates the passage of food (at this point, in state of chyme) to the pyloric stomach, where its pH is regulated before it passes into the duodenum (HARRISON, JOHNSON and YOUNG,1970).

AZNAR et al. (2006) found that, at this (organ) scale, *P. gastrophilus* is restricted to the glandular part of the stomach, namely, the fundic and pyloric chambers, as well as the connecting channel. However, the distribution among chambers were found to differ between cetacean species. In both common bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*), which are mainly piscivorous, *P. gastrophilus* tended to occupy the fundic stomach; in long-finned pilot whales (*Globicephala melas*), which mostly feed on cephalopods, it was more commonly found in the pyloric stomach; in striped dolphins, which have a mixed diet of both fish and squid, the distribution of *P. gastrophilus* was more even among chambers. Accordingly, the location of *P. gastrophilus* along the 3 compartments would be driven, at least in part, by the digestive physiology of cetaceans and the energetic content of prey. In particular, it would take longer to digest fishes than cephalopods due to their higher caloric content and elevated lipid concentration, as well as their higher resistance of their tissues to enzymatic action. Thus, fish prey would stay in the fundic stomach for longer, which would give more time to the infective stages of *P. gastrophilus* to excyst and attach to the wall of this chamber. On the contrary, in a diet dominated by cephalopods digestion is presumably faster, thus excystation would tend to occur in the pyloric stomach. This hypothesis is based on two reasonable assumptions that are yet to be confirmed, i.e. that (1) *P. gastrophilus* uses both fish and cephalopods as intermediate hosts and (2) chambers do not differ in quality as microhabitats.

At a lower spatial scale, i.e. within chambers, the distribution of *P. gastrophilus* is clearly not random (Fig. 2B). After excystation, infective stages are thought to penetrate the stomach wall down into the submucosa where they become adult, reproduce, and eventually die. Eggs are void to the stomach lumen through narrow conducts (Fig. 3A, black arrows). Obviously, the host's immunity system reacts to the presence of worms by forming fibrotic nodules to isolate them (JABER et al. 2006; HRABAR et al. 2017, and references therein). Interestingly, nodules of different sizes are clearly recognizable on the stomach wall (Fig. 3A), and this begs one obvious question, i.e., what are the factors that drive the aggregation of worms and the distribution of such aggregations in the stomach? It is striking that, in a microhabitat with high physical disturbance (the stomach lumen), the worms released from prey may end up aggregating in groups of variable size. In fact, nodules can encompass from just 1 to 300 worms (unpub. data). An additional question here is whether worms from the same nodule belong to one or several recruits. The occurrence in the same nodules of worms from several infection events would suggest that the first colonizers may attract other worms. These interesting questions should be addressed in the future.

At an even lower spatial scale, individuals of *P. gastrophilus* are neither randomly distributed within nodules (Fig. 2C). Worms are found isolated in cavities containing a variable number of individuals, but most commonly two or three (Fig. 3B). Apparently, cavities are the basic "units" that are connected with the lumen of the stomach through ducts (unpub. data). Although there are obvious functional reasons for worms to congregate in pairs (i.e., exogamy), it is very intriguing how they adaptively interact with the host's immune response to generate the complex architecture found in the nodules, and how they manage to keep multiple (an perhaps interconnected?) ducts open during the reproductive period. These questions definitively deserve a closer look.

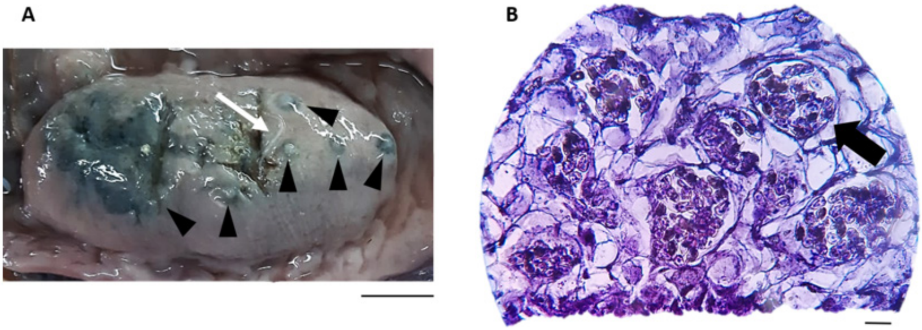

Figure 3. Microhabitat of *Pholeter gastrophilus* (Trematoda: Heterophyidae) within the glandular stomach of odontocetes. A) Oval nodule in the pyloric stomach of a common bottlenose dolphin (*Tursiops truncatus*) stranded in the Galician coast (Spain) in 2019. Black arrows: holes of the ducts connecting cavities containing worms to the stomach lumen. White arrow: larva of *Anisakis* sp. emerging from an ulcer presumably caused by the nematode after the nodule was formed. Scale-bar: 1cm. B) Histological cross section of a nodule found in the fundic stomach of a common bottlenose dolphin (*Tursiops truncatus*) stranded in the Mediterranean coasts of Valencia (Spain) in 2018. Black arrow: Cavity full of eggs. Scale-bar: 1mm.

3.5 Pathogenic potential

Infections by *Pholeter gastrophilus* cause an intense inflammatory response in cetaceans, characterized by the formation of fibrotic cysts that severely affect the stomach submucosa (WOODARD et al. 1969; GERACI and AUBIN, 1987; see above). This gastro-intestinal pathology (pholeterosis), properly described as an infiltrated fibrogranulomatous gastritis (BIRKUN et al. 2002; LEHNERT, RAGA and SIEBERT, 2005) also implies an acute accumulation of cytotoxic T-cells, proinflammatory cytokines and the execution phase of cell apoptosis in the altered area (JABER et al. 2006; HRABAR et al. 2017).

In mild infections, pholeterosis leads to limited pathological consequences (WOODARD et al. 1969; JAUNIAUX et al. 2002; HRABAR et al. 2017) thus being rarely associated with severe disease in cetaceans. However, heavy infections of *P. gastrophilus* can seriously comprise host health. Firstly, they can cause pyloric stenosis, which has been reported as the direct cause of death of common bottlenose dolphins (*Tursiops truncatus*) (KIRKWOOD et al. 1997; JAUNIAUX et al. 2002). Secondly, profuse alteration of the stomach wall due to nodule formation can produce hemorrhages and the perforation of the gastric cavity (BIRKUN et al. 2002), eventually leading to peritonitis (JABER et al. 2006). Thirdly, the damage caused in the gastric walls may facilitate the entry of other pathogens, especially in the area where the opening of the cyst connects the inner tissues of the host with the lumen (Fig. 3A, black arrows). Accordingly, not only bacterial infections can occur, but also other gastric parasites can benefit from the previous damage, particularly those that attach to the walls such as Anisakis spp. (Fig. 2A, big arrow) (C. Pons-Bordas personal observations). Finally, massive infections dispersed throughout the entire stomach cavity can lead to the fibrotic connection of nodules, hardening most of the wall of the gastric chamber (C. Pons-Bordas personal observations) or tearing the muscular fibers (Woodard et al. 1969).

The pathological effects associated to *P. gastrophilus* has hitherto been analyzed from the point of view of individual hosts. It would also be interesting to investigate what the role is (if any) of this parasite at a population level.

4. CONCLUSIONS

Based on the previous discussion we hope that the reader is now convinced that the digenean *Pholeter gastrophilus* represents an excellent example of how parasites can reveal important facets of coevolutionary processes between host-parasite associations in the marine realm. However, there are many gaps in our knowledge of this host-parasite system. In what follows, we summarize key areas of further research that should be addressed in the near future:

1. A complete phylogeographic analysis is peremptory to establish whether *P. gastrophilus* is a single species regardless of geographic area and species of cetacean host. To this end, molecular data are required from the Pacific and Black Sea populations. Furthermore, to shed light on the origin of the association between *Pholeter* spp. and marine vertebrates, it would be necessary to carry out a co-phylogenetic study of the family Heterophyidae, including both *P. gastrophilus* and *P. anterouterus*.

2. The identity of the intermediate hosts should urgently be ascertained. At a minimum, this would require, in suitable localities, (i) a thorough visual examination of large samples of common prey of the most infected cetacean hosts, as well as benthic and pelagic gastropods and bivalves; (ii) the use of new sampling techniques, such as environmental DNA (TABERLET et al. 2018). In addition, the putative differences of life history traits between coastal and oceanic populations of *P. gastrophilus* should be confirmed using other cetaceans, and further aspects (e.g. local adaptation vs. phenotypic plasticity) should be explored with molecular methods.

3. Patterns of habitat selection should be investigated at a more inclusive (host specificity) and more detailed (within chamber, within nodule) scales. I would be important to explore how, and why, individuals become aggregated in different points on the surface of the stomach, and how individuals of *P. gastrophilus* adaptively interact with the host's immune response to generate nodules that seems to be clearly dynamic in both architecture and size.

4. As it is the case for other helminths from cetaceans (AZNAR et al. 2002), the virulence of *P. gastrophilus* should be put into a host population context. Beyond the harm produced in individual hosts, it would be worth to investigate whether *P. gastrophilus* may play a significant (additive) role in shaping host population dynamics.

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ABOUT THE ORGANIZERS

Ingrid N. Visser

Ingrid has had a passion for cetaceans since she was a child. She gained her first University degree, in Zoology, after having spent her teenage years sailing around the world. This was soon followed by a Masters degree also in Zoology. When she started her PhD in Environmental and Marine Science, with the topic of the New Zealand coastal orca, she founded the Orca Research Trust. That non-profit continues to this day and is the foundation for the data collected in Chapter 6. Her research has featured in a number of documentaries, for companies such as BBC, National Geographic, Discovery Channel. Ingrid has observed more than half of the worlds marine mammals and visited all seven continents in her quest to learn more about these fascinating animals. She has published more than 30 scientific articles, along with numerous popular-style articles for wildlife magazines and children's books and an autobiography. Since 2010 she has divided her time between working with wild cetaceans and advocating for those in captivity (see Chapter 5). As part of that work, Ingrid has observed 15 different species of cetaceans (plus other marine mammals; i.e., pinnipeds, sirenians, marine otters and polar bears), in 50 facilities around the world. She has appeared as an expert witness in Environmental and High Courts, as well as before Governments who are investigating the issues of keeping marine mammals in captivity. As part of her conservation work, she has founded (or co-founded) seven non-profit organisations, all with a focus on marine mammals, such as Punta Norte Orca Research (Chapter 1) and Whale Rescue (Chapter 6).

Jorge Cazenave

Jorge started his professional career as a lawyer in Argentina, however after 10 years in this field he switched to tourism. He co-founded (and was President of) Agricultural Tour Operators International and was on the board of the National Tour Association, both whilst photographing wildlife. As an experienced naturalist, he currently guides guests to view and photograph wildlife around the world, specialising in apex predators such as puma, jaguar and orca. His expertise is sought after by documentary making companies such as the BBC, ZED and National Geographic. Since 2001, Jorge has been photographing the unique orca of Punta Norte on the remote Península Valdés, Argentina (see Chapter 1), who exhibit a range of unique behaviours including intentionally stranding to capture sea lion pups. His work with conservation extends to include collaboration with several projects in different regions of Argentina, including Punta Norte Orca Research, of which he is a board member.

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