Latin American Journal of Aquatic Mammals

ISSN: 2236-1057 | Vol. 20 No. 1, April 2025

Helminth parasites and epizoites in common dolphins (genus *Delphinus*) from coastal Peru and Ecuador

Joanna Alfaro-Shigueto[1, 2, *], Koen Van Waerebeek[1, 3], Julio C. Reyes[4], Marie-Françoise Van Bressem[1, 3], Jorge Samaniego[5], Fernando Félix[6, 7], and Natalia Fraija-Fernández[8]

[1]ProDelphinus, Lima, Peru
[2]Carrera de Biología Marina, Universidad Científica del Sur, Lima, Peru
[3]Cetacean Conservation Medicine Group (CMED), Peruvian Centre for Cetacean Research/ Centro Peruano de Estudios Cetológicos (CEPEC), Museo de Delfines, Lima, Peru
[4]Áreas Costeras y Recursos Marinos (ACOREMA), Pisco, Peru
[5]Guayaquil, Ecuador. Deceased (July 2023)
[6]Pontificia Universidad Católica del Ecuador (PUCE), Quito, Ecuador
[7]Museo de Ballenas, Salinas, Ecuador
[8]Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Paterna, Spain

*Corresponding author: jalfaros@cientifica.edu.pe

Abstract

A twenty-five year old dataset of parasites in long-beaked and short-beaked common dolphins (*Delphinus* spp.), using fisheries as an opportunistic platform of access, registered seven species of helminths and one epizoite, being a unique dataset for the Southeast Pacific. Sampling was conducted in 1985-2000 at six fishing ports in Peru and Ecuador where cetaceans were landed from interactions with small-scale fisheries. From a total of 473 common dolphins examined, we identified helminths including three species of Trematoda: *Nasitrema globicephalae*, *Pholeter gastrophilus,* and *Braunina cordiformis*; three species of Nematoda, including *Anisakis* spp., *Crassicauda* spp., and *Halocercus* sp.; and two cestodes, *Tetrabothrius forsteri* and *Clistobothrium delphini*. No acanthocephalans were observed. No statistically significant sexual and ontogenetic variation in helminth prevalence was detected, after which samples were pooled. The highest prevalences in the long-beaked common dolphin (n = 440) were observed for *N. globicephalae* (87.9%, 29 infested/33 sampled) in cranial sinuses, *Crassicauda* sp1. (80%, 4/5) in mammary glands, followed by *Cl. delphini* (28.6%, 2/7) in the blubber, and *P. gastrophilus* (23%, 26/113) in the pyloric stomach. Although comparative testing was unfeasible due to minimal samples of short-beaked common dolphin (n = 33), several of the same helminth species were found; but not *N. globicephalae* nor *B. cordiformis.* No cyamids were encountered while pseudo-stalked barnacles *Xenobalanus globicipitis* were common. Although no new (global) helminth host records were revealed for common dolphins, this study presents a first checklist of parasites separately for the Southeast Pacific long-beaked and short-beaked common dolphins. Future work should include exhaustive laboratory-based necropsies, enhanced sampling of the short-beaked form, review data from recent parasite collections, focus on intermediate hosts and parasitic pathology, including potential human health impact from consumption of small cetaceans.

Keywords:
bycatch, cetaceans, checklist, long-beaked common dolphin, parasitology, short-beaked common dolphin, Southeast Pacific Ocean

ARTICLE INFO

Manuscript type: Article

Article History
Received: 21 February 2024
Received in revised form: 02 June 2024
Accepted: 02 June 2024
Available online: 23 March 2025
Responsible Editor: Carlos Sacristán

Citation:
Alfaro-Shigueto, J., Van Waerebeek, K., Reyes, J. C., Van Bressem, M-F., Samaniego, J., Félix, F., & Fraija-Fernández, N. (2025). Helminth parasites and epizoites in common dolphins (genus *Delphinus*) from coastal Peru and Ecuador. *Latin American Journal of Aquatic Mammals, 20*(1), 23-35. https://doi.org/10.5597/lajam00344

Introduction

Many studies on the metazoan parasite fauna of marine mammals have focused on their impact on population dynamics through morbidity and mortality (Ridgway & Dailey, 1972; Perrin

& Powers, 1980; Lambertsen, 1986; Morimitsu et al., 1992; Raga et al., 1997) or have studied their use as biological tags (Dailey & Otto, 1982; Van Waerebeek et al., 1990; Dailey & Vogelbein, 1991). Other parasitological research examined marine mammal helminths as potential causes of zoonotic disease in humans and explored their paths of transmission (Miyazaki, 1991; Tantaleán, 1994; McCarthy & Moore, 2000). However, all such studies imply a fair knowledge of the baseline level of parasite burden (prevalence and intensity) on the marine mammal host before they can be successfully interpreted. Unfortunately, such information is often not available.

In the Southeast Pacific (SEP) region, the parasite fauna of three small odontocetes was studied in some detail, *i.e.,* coastal and offshore ecotypes of the common bottlenose dolphin *Tursiops truncatus* (Reyes, 1989; Van Waerebeek et al., 1990), the dusky dolphin *Lagenorhynchus obscurus* (Van Waerebeek, 1992; Van Waerebeek et al., 1993), and the Burmeister's porpoise *Phocoena spinipinnis* (Reyes & Van Waerebeek, 1995). Except for a few records and case studies on helminths from common dolphins *Delphinus* (sub)spp. in Peru (Tantaleán & Escalante, 1987; Alfaro-Shigueto, 1994; Van Waerebeek et al., 1997; Van Bressem et al., 2006), the parasitology of common dolphins of the SEP has not been thoroughly documented. One significant finding was an osteopathological study of skull damage, so-called 'basket-like' osteolytic lesions, diagnostic for some *Crassicauda* species infestation (Raga et al., 1982). Such lesions were encountered in 26.5% of Peruvian common dolphins (n = 98) and did not differ among sex and age classes (Van Bressem et al., 2006). *Crassicauda* sp. was responsible for 78.8% of all osteolytic cranial lesions (Van Bressem et al., 2006).

Landings of small cetaceans in Peruvian fishing ports, both through bycatch and direct takes for consumption and bait, were monitored periodically from 1984 until 2000 before the dolphin capture and landing ban (Read et al., 1988; García-Godos, 1992; Van Waerebeek & Reyes, 1994a, b; Van Waerebeek et al., 1994a, 1997, 1999), which allowed the study of multiple biological and health parameters (*e.g.*, Van Waerebeek, 1992; Van Bressem et al., 2006, 2007; García-Godos et al., 2007). In Ecuador, a dolphin bycatch monitoring programme with limited biological sampling was conducted between 1992 and 1993 (Félix & Samaniego, 1994). The programme in Peru provided a unique opportunity to study the parasitic fauna in samples of bycatches of several small cetacean species. In Ecuador, the sample of short-beaked common dolphins was skewed towards juveniles due to the lack of commercial value of banned species and limited space in the fishing boats, thus the largest animals were discarded offshore and mostly the small individuals were landed.

Although the scope of this study is not the (complex) taxonomy and nomenclature of *Delphinus* spp. in the Eastern Pacific Ocean, which are under debate, it is important to highlight that it documents the parasitology of two distinct hosts, a short-beaked and a long-beaked morphotype. The cosmopolitan short-beaked common dolphin *Delphinus delphis* L. occurs also in, mostly offshore, tropical and temperate areas of the Eastern Pacific. The long-beaked common dolphin in the Northeast Pacific has been referred to as *Delphinus capensis* (after Heyning & Perrin,1994) however it has recently been suggested to represent a subspecies *D. delphis bairdii* Tomilin, 1957 (Perrin, 2022). Recognising the morphological similarity of the neritic long-beaked common dolphin off Peru and north-central Chile with the coastal common dolphins off California and Baja California, this SEP form was also considered as *D. capensis* (Van Waerebeek & Reyes, 1994b; Van Waerebeek et al., 1994a, b). Much further work is needed to evaluate the (sub)specific status of the different morphotypes or ecotypes; however, clearly the long-beaked and short-beaked common dolphins in the SEP present substantial morphological and ecological differences (Van Waerebeek & Reyes, 1994b; Van Waerebeek et al., 1994a, b), much of which remain to be published. They are widely distributed, parapatrically in Peruvian waters and off the north and central coasts of Chile (Van Waerebeek & Reyes, 1994b; Van Waerebeek et al., 1994a, b; Sanino et al., 2003; Reyes, 2009). The large majority (more than 99%) of common dolphins taken in coastal fisheries and landed at Peruvian ports in the 1980s and 1990s were the long-beaked form was assessed (Van Waerebeek et al., 1994a). Whilst in Ecuador only the short-beaked form has been reported (Félix & Samaniego, 1994; Castro & Van Waerebeek, 2019), until recently when a small group of long-beaked specimens was sighted off Santa Clara Island, Ecuador (Félix et al., 2025). From 1985 to 2000 we had access to hundreds of bycaught common dolphins of the SEP Ocean, which allowed for a first checklist and basic epidemiological information of helminths and epizoites. We also compared parasite prevalence from other small cetacean populations in the study region and concisely reviewed published helminth parasite records for common dolphins from other regions.

Material and Methods

We examined 473 common dolphins (genus *Delphinus*) from Peru and Ecuador for the presence of helminth parasites and epizoites. The freshly dead dolphins (code 2, *sensu* Geraci & Lounsbury, 2005) were landed for human consumption and for bait in ports in the period 1985-2000. Most dolphins were captured in neritic waters in multifilament gillnets either as bycatch or as a directed take (harpooned). A smaller number were netted by pelagic purse-seiners (Read et al., 1988; García-Godos, 1992; Félix & Samaniego, 1994; Van Waerebeek & Reyes, 1994a, b; Van Waerebeek et al., 1997). We examined 440 long-beaked common dolphins from Peru and 33 short-beaked common dolphins, 30 from Ecuador and three from Peru. Several juvenile dolphins but no neonates or calves were included in the Peruvian study sample, while in Ecuador 78% of specimens were calves or juveniles of 80-130 cm length.

The principal ports where biological sampling was implemented included (Fig. 1) Cerro Azul (13°03' S, 76°30' W), Pucusana (12°29' S, 76°49' W), Ancón (11°50' S, 77°10' W), and Chimbote (09°04' S, 78°35' W) (Van Waerebeek & Reyes, 1994a) in Peru; and Santa Rosa (02°12' S, 80°57' W), and Puerto López (01°34' S, 80°49' W) (Félix & Samaniego, 1994) in Ecuador.

Sexual maturity status of the sample of long-beaked common dolphin was based on macroscopic inspection of gonads, *i.e.*, presence of semen in epididymides or presence of at least one *corpus albicans* or *corpus luteum* in at least one ovary. For males and females whose gonads could not be examined, maturity was inferred from standard body length (SL), *i.e.*, males and females

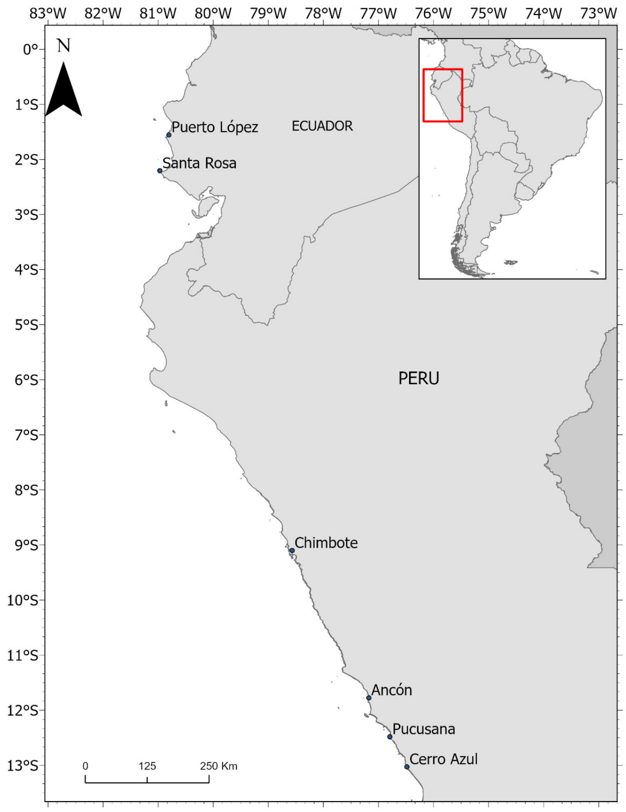

Figure 1. Main ports in Peru and Ecuador where bycaught common dolphins *Delphinus* sp. were examined and sampled for helminth parasites and epizoites in the period 1985-2000.

smaller than, respectively, 215 cm and 200 cm, were considered immature, while males and females larger than, respectively, 220 cm and 210 cm were considered mature (Centro Peruano de Estudios Cetológicos CEPEC data archives, Lima, Peru). Animals of intermediate lengths (males between 215 and 220 cm and females between 200 and 210 cm) were classified 'of unknown maturity' (Van Bressem et al., 2006), and removed from the sample when comparing sexually immature and mature long-beaked common dolphins.

Sampling in Ecuador was performed opportunistically during a fisheries interaction study (Samaniego, 1994). Moreover, the bringing to port of bycaught dolphins depended entirely on the fishermen's goodwill; hence only a small number of mostly juvenile specimens and limited information on parasite prevalence and intensity is available. In Peru, due to high commercial value of dolphin carcasses, access to internal organs in fish markets was limited and depended on the cooperation of fishmongers who sometimes allowed us to collect several organs from the thoracic and abdominal cavities. Sampling methodology followed Van Waerebeek et al. (1993); briefly, the integument and body orifices including blowhole, anus, and urogenital slit, as well as flukes, flippers, and dorsal fins, were macroscopically examined *in situ* for the presence of cutaneous conditions (see Samaniego, 1994; Van Bressem et al., 2006) and epizoites, *i.e.*, barnacles and cyamids. The abdominal and thoracic cavities were accessed through a cut of 80-100 cm length midventral and most of the gastrointestinal tract (*i.e.*, fore-, main, and pyloric stomachs, duodenum including ampulla duodenalis and intestines), gonads and occasionally the lungs, mammary glands, and kidneys were analysed. Heads, after removal of mandibles, were sectioned ventro-laterally as to expose the cranial sinuses, in particular the pterygoid sinus, and the periotic fossa (following terminology in Mead & Fordyce, 2009), which were then thoroughly flushed with seawater over sieves, following Van Waerebeek et al. (1993). The rinsed heads were again inspected macroscopically for any helminths imbedded in the mucosae.

Cetacean sectioning and parasite sampling were normally completed within two to 10 hours after landing. Although evisceration often occurred at night under artificial lighting, the macroscopic examination of organs and parasite quantification was performed during daylight. In Peru, parasites were handled following a standard protocol and were stored in 70% ethanol. Selected trematode specimens were coloured with haematoxylin and mounted in Canada balsam. Nematodes were cleared with lactophenol in permanent slides. Species identification was aided by Dr. R. Verano of the Departamento de Parasitología, Facultad de Ciencias, Universidad Ricardo Palma, Lima. Internal structures were studied and measured with a stereoscope and a binocular compound microscope. Specific voucher specimens and the original dataset (field notes) are archived at the Museo de Delfines, CEPEC, Pucusana, Peru. In Ecuador, dolphins were also examined externally and internally at the landing port. Parasites were stored in an aqueous solution of ethanol (40%), formalin (5%), and glycerin in a proportion 2:2:1. Reference specimens were deposited at the Pontificia Universidad Católica del Ecuador (PUCE) in Quito, Ecuador.

For each host examined (complete specimens or a given organ) the prevalence of infestation was estimated for each parasite species, and the smallest infested and smallest examined host were specified. Intensity of infestation was only occasionally noted. Associated pathology as detected through macroscopic examination is briefly discussed. Eight long-beaked common dolphin specimens of unknown sex were discarded to estimate the prevalence by host sex. In the long-beaked common dolphin we compared the relationship of host sex and the maturity state with the parasite prevalence through a logistic regression analysis. Parasite prevalence (frequency of hosts infected with a specific parasite species) was calculated as the number of infested hosts divided by the total number of hosts examined x100. Confidence intervals (95% CI) for prevalence were computed by the modified Wald method (Agresti & Coull, 1998), which is considered more accurate than the classic so-called 'exact' methods. For comparisons between parasite prevalence, chi-square tests and two-sided Fisher's exact tests were applied. Statistical significance evaluation was set at $\alpha = 0.05$. Cloud-based algorithms were used at https://www.graphpad.com/quickcalcs. To facilitate the comparison with other geographical regions, a chart of metazoan parasites reported for common dolphins *Delphinus* spp. worldwide was produced (Supplementary Material 1).

Results

1. Host: Long-beaked common dolphin *Delphinus delphis* (unnamed subspecies) - formerly *D. capensis* (Peru, n = 440)

Maturity and sexual variation

Numerical data on the prevalence and sample sizes for

Table 1. Prevalence of helminth parasites and epizoites in long-beaked common dolphins *Delphinus* from Peru. Abbreviations: N(ex) = number examined; N(inf) = number infested; Prev = % prevalence; c = complete gastrointestinal tract examined; CI = 95% confidence intervals (modified Wald method)

		MALES			FEMALES			INDET. SEX		POOLED SAMPLE			
	Organ	N (ex)	N (inf)	Prev	N (ex)	N (inf)	Prev	N(ex)	N(inf)	N (ex)	N (inf)	Prev	95% CI
TREMATODA													
Nasitrema globicephalae	cranial sinuses	15	15	100	12	11	91.7	6	3	33	29	87.9	72.1 – 95.8
	main stomach	70	6	8.6	42	1	2.4	1	0	113	7	6.19	2.82 – 12.5
	pyloric stomach	70	11	15.7	42	15	35.7	1	0	113	26	23.0	16.2 – 31.6
	duodenum	39	1	2.6	22	1	4.5	0	0	61	2	3.28	0.25 – 11.8
	c. gastrointestinal tract	34	5	14.7	20	6	30.0	0	0	54	11	20.4	11.6 – 33.1
Braunina cordiformis	main stomach	70	0	0	42	1	2.4	1	0	113	1	0.88	< 0.0001 – 5.33
	pyloric stomach	70	11	15.7	42	8	19	1	0	113	19	16.8	10.9 – 24.9
	duodenum	39	4	10.3	22	1	4.5	0	0	61	5	8.20	3.16 – 18.2
	c. gastrointestinal tract	34	6	17.6	20	5	25	0	0	54	11	20.4	11.6 – 33.1
NEMATODA													
Anisakis sp.	forestomach	70	8	11.4	42	2	4.8	1	0	113	10	8.85	4.71 – 15.7
	duodenum	39	0	0	22	1	4.5	0	0	61	1	1.64	< 0.0001 – 9.55
	c. gastrointestinal tract	34	1	2.9	20	2	10	0	0	54	3	5.56	1.32 – 15.7
Crassicauda sp2.	cranial sinuses	15	1	6.67	12	0	0	6	1	33	2	6.06	0.76 – 21.7
Crassicauda sp1.	mammary glands	0	0	0	5	4	80	0	0	5	4	80.0	36.0 – 97.9
Halocercus sp.	lungs	18	2	11.1	8	0	0	1	0	27	2	7.41	0.96 – 24.5
CESTODA													
Tetrabothrius forsteri	pyloric stomach	70	2	2.9	42	0	0	0	0	112	2	1.79	0.09 – 6.68
	duodenum	39	2	5.1	22	3	13.6	0	0	61	5	8.20	3.16 – 18.2
	intestines	35	1	2.9	21	5	23.8	0	0	56	6	10.7	4.65 – 21.8
	c. gastrointestinal tract	34	5	14.7	20	3	15.0	0	0	54	8	14.8	7.44 – 26.9
Clistobothrium delphini	blubber, anogenital area	5	1	20	2	1	50	0	0	7	2	28.6	7.56 – 64.8
EPIZOITE													
Xenobalanus globicipitis	fluke and flippers	243	13	5.3	124	15	12.1	0	0	365	28	7.67	5.33 – 10.9

parasites of long-beaked common dolphin sampled in Peru are given in Table 1. A series of two-tailed Fisher's tests did not reject the H_0 hypothesis (all $p > 0.074$) of zero difference in prevalence between male and female dolphins for any of the helminth parasites studied. A logistic regression analysis showed that neither significant sexual variation (Logistic: Wald-chi-square = 2.95, $p = 0.085$) nor maturity state (Logistic: Wald-chi-square = 2.70, $p = 0.10$) differences existed in the presence of parasites. Due to a larger sample size for pseudo-stalked barnacles, we ran a logistic regression analysis that showed that females and males are equally likely to be carriers of barnacles (Logistic: Wald-chi-square = 0.57, $p = 0.44$). For every 1 cm increase in body length there was in average 1.025 time as likely (95% Wald's confidence limits = 1.011 - 1.039) that a dolphin be parasitized (Logistic: Wald-chi-square = 12.68, $p = 0.0004$). It was concluded that no significant sexual variation in parasitism existed and therefore the discussion does not further discriminate between the sexes and maturity status of hosts.

1.1. Cranial sinuses (n = 33)

Trematoda: Nasitrematidae

Nasitrema globicephalae (Neiland et al., 1970)

All flukes encountered in the ventral cranial sinuses of the infested long-beaked common dolphins belonged to a single *Nasitrema* morphotype identified as *N. globicephalae* based on the lanceolate and rounded body shape, length range (9.5 - 22 mm) and internal morphology, as described by Neiland et al. (1970) and observed in other small cetacean species from the same study area (Alfaro-Shigueto, 1994). The cranial sinuses of 87.9% of long-beaked common dolphins (n = 33) were parasitized (Table 1), mostly in the pterygoid sinuses but also in the periotic fossa around the earbones. No brain tissue was examined.

The mean intensity was 15.3 flukes per host (SD ± 13.6, range 2 - 57, n = 22). The mucosae of the cranial sinuses showed no macroscopically visible lesions. The smallest infested dolphin (AGG-112, female) measured 170.0 cm. A 136-cm juvenile female (JCR-1108) was negative for this trematode.

Crassicauda sp2. (Leiper and Atkinson, 1914)
Nematoda: Tetrameridae

Adult crassicaudid roundworms of several cm-length were found in the ventral side, in the pterygoid sinuses of two dolphins of the n = 33 examined (prevalence 6.06%; Table 1). Sexual variation in prevalence could not be tested because there was but a single positive dolphin of known sex. That male dolphin had one nematode; intensity for the other was not noted. *Crassicauda* nematodes were partly buried in the air sinus wall of surrounding bone tissue. Their fragile bodies did not permit the collection of complete nematodes under field conditions. Some necrotized, crater-shaped mucosal tissue was evident at the attachment site. The smallest dolphin examined was a 136-cm female. Interestingly, the two dolphins that were infested (KVW-2362, -2366) were landed on consecutive days (10 and 11 January 1993) at Chimbote port and both were immature-sized. Specific identification was not possible as no complete individuals were obtained, and fragments of worms were partially decomposed. Thus, specific diagnostic characters were not observed and DNA extraction and barcoding sequencing were not possible.

1.2. Gastrointestinal tract

Trematoda: Heterophyidae
Pholeter gastrophilus (Kossack, 1910) Odhner, 1914

Pholeter gastrophilus were found as cysts embedded in the mucosae of the gastrointestinal tract (20.4%, n = 54) (Table 1). This fluke was present in the pyloric stomach (23%, n = 113), and less frequently in the main stomach (6.2%, n = 113) and duodenum (3.3%, n = 61), and was entirely absent from the forestomach (n = 113) and post-duodenal intestines (Table 1). *Pholeter gastrophilus* intensity was low, usually one or two flukes per host sampled. The smallest parasitized dolphin was a female of 184.5 cm (KVW-522), although the smallest dolphin examined was a 136-cm female.

Trematoda: Brauninidae
Braunina cordiformis (Wolf, 1903)

Of 54 gastrointestinal tracts studied (forestomach to duodenum), 11 were infested with *B. cordiformis* (prevalence 20.4%, n = 54). The trematode was most commonly found in the pyloric stomach (16.8%, n = 113) and duodenum (8.2%, n = 61), rarely in the main stomach (0.9%, n = 113) and never in the forestomach or the intestines (Table 1). *Braunina cordiformis* occurred mostly as a singleton (median = 1, n = 8) but was also found in clusters of 2-10 individuals, strongly attached to the mucosae although without indications of macroscopic mucosal lesions. This trematode was found in association with *P. gastrophilus* in 5.36% of pyloric stomachs. The smallest host individual examined and infested (in pyloric stomach) was a 136-cm juvenile female.

Nematoda: Anisakidae
Anisakis sp. (Dujardin, 1845)

This nematode was confidently identified only to the genus level. Of 54 complete gastrointestinal tracts examined, three were infested (prevalence 5.6%, n = 54, Table 1). However, anisakid roundworms infested 8.9% of a larger sample of forestomachs examined (n = 113). It was not encountered in the main and pyloric stomachs, but in one 216.5-cm dolphin it was found in the duodenum (1.6%, n = 61). In other parts of the intestine *Anisakis* sp. was not encountered (Table 1). Median intensity of infestation was 1.5 anisakid roundworm (range 1-5, n = 8) and no macroscopic lesions were observed. The smallest parasitized dolphin was a 189.5-cm female (JCR-1851), while the smallest individual examined was a 136-cm female. *Anisakis* spp. nematodes have been registered in the gastrointestinal system of common dolphins worldwide (Supplementary Material 1).

Cestoda: Tetrabothriidae
Tetrabothrius forsteri (Krefft, 1871)

Adult tetrabothrid tapeworms were found in 14.8% of dolphins (n = 54) for which the entire digestive tract was examined (Table 1). *Tetrabothrius forsteri* occurred most often in the duodenum (n = 61) and intestines (n = 56), and rarely in the pyloric stomach (n = 112) (Table 1). The median intensity was two tapeworms per host (range 1-6, n = 9). No cestodes were observed in the forestomachs (n = 112) or main stomachs (n = 61) (Table 1). The smallest dolphin parasitized with *T. forsteri* was a 180-cm male (AGG-023), while the smallest dolphin examined measured 136 cm. This cestode was previously reported worldwide (Supplementary Material 1).

1.3. Lungs (n = 27)

Nematoda: Pseudaliidae
Halocercus sp. (Baylis and Daubney, 1925)

Three *Halocercus* lungworms were extracted from the lung alveoli of a 180-cm, sexually immature male and from another male of 210.5 cm from a total of 27 dolphins examined (prevalence = 7.41%) (Table 1). Taxon could be determined only to genus level due to poor fixation of the specimens. As described in Dailey (1985), the anterior ending was typically embedded in a capsule, probably to protect the parasite from becoming dislodged during forceful expiration by the host. The smallest dolphin examined was a 153-cm juvenile male which was negative for *Halocercus*.

In addition, small cysts, mostly less than 5 mm in diameter and partly consisting of necrotized tissue, were found in the lung tissue in low to high densities in 23.1% of examined dolphins (n = 27). However, these cysts were not found to correspond to any metazoan parasite.

1.4. Pancreatic duct, spleen, kidneys, and liver (n = 17)

The pancreatic ducts of 17 long-beaked common dolphins (eight females and nine males) were dissected, but none presented helminth parasites. The smallest dolphin examined was a juvenile male of 189.5 cm (JCR-1851). No parasites were found macroscopically in eight (paired) kidneys (five females, three males) and three livers.

1.5. Blubber, mesenteries, and mammary glands (n = 7)

Cestoda: Phyllobothriidae

Clistobothrium delphini (Bosc, 1802) Caira, Jensen, Pickering, Ruhnke, & Gallagher, 2020 (previously known as *Phyllobothrium delphini*)

Two of seven dolphins studied (28.6%), a mature female and a 197-cm male, showed small white cysts of merocercoids of *C. delphini* in the blubber, primarily concentrated in the anogenital area (Table 1). However, given the often-large number of cysts and because we had no permission to make multiple sections in the blubber, the total number of merocercoids per dolphin could not be counted. The smallest infested and examined hosts consisted, respectively, of a 197-cm male (MFB-264) and a 161-cm male (AGG-371).

Cestoda: Phyllobothriidae

Clistobothrium grimaldii (Moniez, 1899) Caira, Jensen, Pickering, Ruhnke & Gallagher, 2020 (previously known as *Monorygma grimaldii*)

The lack of complete dissections of dolphin carcasses precluded a thorough examination and prevalence estimation for this parasite. However, only one 214.5-cm female long-beaked common dolphin (JCR-1069) was found to be parasitized by merocercoids of *C. grimaldii* cysts in the mesenteries, showing the occurrence of this species in Peruvian waters.

Crassicauda sp1. The mammary glands of four of five (80%) females examined (all of which were immature animals) were infested with *Crassicauda* sp1. (Table 1). As was the case for the cranial sinuses, no complete nematode specimens could be extracted from the mammary glands in the field and thus species identification was not possible morphologically. Attempts to extract DNA failed, presumably due to degraded samples. Median intensity per positive host was two nematodes (range 1-7, n = 5). The smallest infested dolphin, also the smallest one examined, a 173-cm female (AGG-488), presented *Crassicauda* worms firmly anchored in both the mammary glands and in the surrounding hypodermis and subcutaneous tissue.

1.6. Integument, orifices, and appendages (n = 365)

Thoracica: Balanidae

Xenobalanus globicipitis (Steenstrup, 1851)

Pseudo-stalked barnacles were attached primarily to the trailing edge of the flukes, but also to the dorsal fin and flippers in 7.67% of 365 long-beaked common dolphins examined (Table 1). A slightly higher prevalence of females was infested (p = 0.0346) compared to males. Although the barnacle's calcareous base is incrusted into the skin, *X. globicipitis* did not cause inflammation or any other macroscopically detectable cutaneous pathology, as was also observed in other Peruvian odontocetes (Van Waerebeek et al., 1993; Reyes & Van Waerebeek, 1995). The smallest infested and examined specimens were respectively a 149-cm male (KVW-1334) and a 136-cm female (JCR-1108).

Amphipoda: Cyamidae

No cyamids (whale-lice) were found on any of the 178 long-beaked common dolphins for which the integument, appendages, and orifices were carefully examined. These included dolphins of both sexes and a full range of body lengths, proxy for age classes.

2. Host: Short-beaked common dolphin *Delphinus delphis* (n = 33)

Peru

Only limited data could be collected from three short-beaked common dolphins (KVW-568, KVW-569, and JSM-10). No helminths were found in the cranial sinuses of a 216-cm male (JSM-10). Stomachs (fore-, main, and pyloric) and livers of the three dolphins were found to be negative for helminths, with the exception of one main stomach (KVW-568, mature male) that contained the trematode *P. gastrophilus*. No barnacles, nor cyamids were detected.

Ecuador

2.1. Gastrointestinal tract

Nematoda: Anisakidae

Anisakis sp. (Dujardin, 1845)

Anisakid roundworms were collected from seven short-beaked common dolphins (n = 30; prevalence = 23.3%). Nematodes were predominantly encountered in the forestomach.

Cestoda: Tetrabothriidae

Tetrabothrium sp.

A single tetrabothrid tapeworm was collected at an unspecified location of the gastrointestinal tract, although most likely from the intestine, of a 186-cm male short-beaked common dolphin (Z2SR170). The poor state of preservation of the tapeworm precluded identification beyond genus level.

Cestoda: unidentified tetraphyllidean larvae

Some 20 procercoid stage tetraphyllidean larvae, probably ingested and released from infested fish or squid, were found free in the digestive tract of a juvenile (144 cm) male dolphin (Z2SR080).

2.2. Lungs

Nematoda: Pseudaliidae

Halocercus sp.

The lungs of one short-beaked common dolphin (n = 30), a 108-cm male calf (Z2SR002), contained the lungworm *Halocercus* sp.

2.3. Kidneys

Kidneys of 30 dolphins were sectioned and examined macroscopically, but no parasites were found.

2.4. Mesenteries and blubber

Cestoda: Phyllobothriidae

Clistobothrium delphini and *Clistobothrium grimaldii*

Merocercoids of *C. delphini*, which we called "cysts" in field notes, were collected from the blubber around the anogenital area in two specimens (n = 30), a 170-cm male (Z2SR186) and a 178-cm female (Z2SR171). A single *Cl. grimaldii* larva was recovered opportunistically from near the intercostal muscle of a male short-beaked common dolphin (Z2SR084).

2.5. Integument, orifices, and appendages

Thoracica: Balanidae

Xenobalanus globicipitis

A 91-cm male calf, the only animal amongst 30 *D. delphis* examined (3.3%), presented *X. globicipitis.* Remarkably, the pseudo-stalked barnacles were present with high intensity, with *ca.* 50 specimens attached to flippers and flukes (Samaniego, 1994).

Discussion

All species of helminth parasites documented in this study in long-beaked and short-beaked common dolphins from coastal waters of Peru and Ecuador were previously reported elsewhere for other *Delphinus* spp. populations, however typically without distinction between common dolphin (sub)species or ecotypes. Due to very small or indeterminate sample sizes for the short-beaked common dolphin, it was unfeasible to statistically compare parasite loads between the two morphs of the SEP. Also, most helminths and epizoites reported here for *Delphinus* spp. have also been encountered in other small odontocete species from the Southeast Pacific region.

Trematoda

The cranial sinus fluke *N. globicephalae* showed high prevalence in both inshore (80%) and offshore (94.1%) ecotypes of the common bottlenose dolphin (Reyes, 1989; Van Waerebeek et al., 1990) and in the Peruvian dusky dolphin (78.3%; Van Waerebeek et al., 1990, 1993), but only occasionally parasitized the Burmeister's porpoise (9.3%) (Reyes & Van Waerebeek, 1995). The higher prevalence compared to the porpoises may be explained by differences in the prey composition, related to the porpoises' more neritic distribution or to a dissimilar susceptibility to *Nasitrema* infection.

Nasitrema globicephalae was previously documented in common dolphins in the Northern Pacific (Supplementary Material 1). In Peru, *N. globicephalae* is known to infest also the southern right whale dolphin *Lissodelphis peronii*, short-finned pilot whale *Globicephala macrorhynchus,* and false killer whale *Pseudorca crassidens* (Van Waerebeek & Oporto, 1990; Alfaro-Shigueto, 1994). Another host record in Pacific South America includes the Chilean dolphin *Cephalorhynchus eutropia* (Brieva & Oporto, 1991). This trematode has been encountered also in the long-finned pilot whale *Globicephala melas* from Argentina's Tierra del Fuego (Raga et al., 1994). Trematodes of the genus *Nasitrema* and nematodes of the genus *Crassicauda* have been suggested as a cause of stranding and morbidity in small cetaceans (Dailey & Stroud, 1978; Dailey & Walker, 1978; Dailey, 1985; Morimitsu et al., 1992). Comparable to what was found in Peruvian dusky dolphins (Van Waerebeek et al., 1993), we did not detect any macroscopic lesions of mucosae in the cranial sinuses related to the presence of *Nasitrema*. Also, we identified no strandings of common dolphin other than fisheries-related or of unknown causes, and the question of serious parasitic morbidity remains unanswered. Other studies reported this trematode in free-ranging cetaceans obtained from fisheries and from strandings (Supplementary Material 1).

Pholeter gastrophilus is distributed in the North and South Atlantic oceans, as well as in the Mediterranean, Black, and North seas. For the Pacific Ocean just a few records exist for the Peruvian coast (Supplementary Material 1) and South Australia and, for the Indian Ocean, *P. gastrophilus* samples are restricted to the Red Sea (Fraija-Fernández et al., 2017). The trematode species *P. gastrophilus* and *B. cordiformis* were previously mentioned for the common dolphin in the western South Atlantic and the Adriatic Sea (Supplementary Material 1). They were also documented in Peru in both *T. truncatus* ecotypes (*Pholeter* only in the offshore form) (Reyes, 1989; Van Waerebeek et al., 1990), in dusky dolphin (Van Waerebeek et al., 1993), and in the Burmeister's porpoise (Reyes & Van Waerebeek, 1995).

Necropsies of *D. delphis* in the Patagonian coast of Argentina showed the presence of *B. cordiformis* in the forestomach (Berón-Vera et al., 2007), which expresses a different pathobiology than in the long-beaked common dolphin here sampled in Peru where none were registered in the 70 forestomachs examined but were present in 16.8% of pyloric stomachs (Table 1). Previous records of *P. gastrophilus* in *D. delphis* exist also for the Atlantic, west Pacific, and Black Sea (see Supplementary Material 1 for references).

Nematoda

The low prevalence (3.7%) of cranial crassicaudiasis, as estimated by infestation with *Crassicauda* sp2. nematodes in the ventral cranial sinuses of long-beaked common dolphin in Peru mirrors their absence in the Peruvian dusky dolphin (n = 97) (Van Waerebeek et al., 1993), a sympatric species with a highly similar diet (García-Godos et al., 2007) that often forms mixed schools (Van Waerebeek, 1994). Cranial osteolysis, diagnostic for *Crassicauda* spp. infestation, was however encountered in museum specimens at a significantly higher prevalence (26.5%, n = 98) in Peru (Van Bressem et al., 2006) suggesting that common dolphins that recovered from active infestation, however, did not resolve osteopathy. In Peru *Crassicauda* spp. was also commonly found in offshore *T. truncatus* (Van Waerebeek et al., 1990) but was absent in the inshore ecotype and in *P. spinipinnis*, both of which feed in neritic habitat (Van Waerebeek et al., 1990; Reyes & Van Waerebeek, 1995; Alfaro-Shigueto et al., 2008; Reyes, 2009). Other cases include those for *D. delphis* from the Eastern Tropical Pacific (Walker & Cowan, 1981) and from England and Wales (Gibson et al., 1998).

Anisakis spp. are nematodes commonly present in hosts inhabiting temperate waters (Davey, 1971). They affect a large number of cetacean species (Baylis, 1932; Delyamure, 1955; Dailey & Brownell, 1972), including also short-beaked common dolphins from the Northeast Atlantic, the Northeast Pacific and long-beaked common dolphin from South Africa, California, and Venezuela's Caribbean coast (Mignucci-Giannoni et al., 1998; Colom-Llavina, 2005). Murga et al. (1986) briefly commented on *Anisakis* sp. in '*D. delphis*' from Chimbote, Peru. However, the majority of common dolphins landed at Peruvian ports, including Chimbote, have been the long-beaked form (Van Waerebeek et al., 1994a). In Peru, *Anisakis typica* was documented in both offshore (61.9%) and inshore (37.5%) ecotypes of the common bottlenose dolphin (Reyes, 1989; Van Waerebeek et al., 1990) and in 28.1% of Burmeister's porpoises (Reyes & Van Waerebeek, 1995). Interestingly *Anisakis* sp. was encountered in 40% (n = 218) of Peruvian dusky dolphins (Van Waerebeek et al., 1993), a significantly higher prevalence (two-tailed Fisher's, $p < 0.0001$) than the 8.8% of common dolphins. Despite extensive group mixing, this suggests that important differences exist in ecological niches, or in susceptibility to infestation.

Anisakis sp. is reported here for *D. delphis* from Ecuador and was found in a larval form, with a higher prevalence, in Atlantic *D. delphis* (Berón-Vera et al., 2007) (Supplementary Material 1). This nematode affects also some other small odontocete hosts of the study region including the Chilean dolphin and Burmeister's porpoise in Chilean waters (Torres et al., 1992).

Halocercus sp. has previously been reported to infest lungs of common dolphins *D. delphis* s.l. in the Atlantic and Pacific oceans, and the Mediterranean and Black seas (Supplementary Material 1). In the present study only two long-beaked (prevalence = 7.4%) and one short-beaked common dolphin had a low-intensity *Halocercus* sp. lungworm infestation. For the SEP only one other case was mentioned for dusky dolphin (Van Waerebeek et al., 1993) and three cases in Burmeister's porpoise (Reyes & Van Waerebeek, 1995). *Halocercus* lungworms may cause verminous pneumonia and possibly death (Dailey, 1985). Dailey et al. (1991) found evidence of prenatal infection of *Halocercus lagenorhynchi* in *T. truncatus*, which begs the question whether transplacental transmission occurs exceptionally or frequently. Though *H. delphini* and *H. kleinenbergi* were reported in common dolphins from various oceanic regions (Supplementary Material 1), they were absent in *D. delphis* from the Patagonian coast of Argentina (Berón-Vera et al., 2007).

Cestoda

Tetrabothrium forsteri was present in both forms of common dolphin (Table 1). Three other final hosts for this cestode have been documented for the SEP, *i.e.,* southern right whale dolphin in central Chile (Fernández, 1987) and inshore (prevalence = 16.7%) and offshore (70.6%) forms of *T. truncatus* in Peru (Van Waerebeek et al., 1990). In both short-beaked common dolphins from Ecuador and long-beaked common dolphins from Peru we found the merocercoids *C. grimaldii* and *C. delphinii*. In the field the small phyllobothrid tapeworm larvae found in the blubber of delphinids (see Van Waerebeek et al., 1990, 1993) were classified as *Phyllobothrium delphini* (Bosc, 1802) and the significantly larger larvae encountered in multiple organs and tissues including serous membrane as *Monorygma grimaldii* (Moniez, 1899), according to earlier understandings (Testa & Dailey, 1977; Geraci et al., 1978). However, recent taxonomic studies, based on both molecular genetics and morphology, have renamed these, respectively, *Clistobothrium delphini* and *C. grimaldii* (Caira et al., 2020; Agustí et al., 2005a, b), nomenclature used in this paper. The taxonomic identity of these species has been in dispute for years (Agustí et al., 2005a, b; Aznar et al., 2007). Recently, Caira et al. (2020), using broad phylogenetic data, have shed light on their nomenclature. These larval cestodes showed molecular affinities with *Clistobothrium* species, whose adults commonly occur in sharks (Caira et al., 2005). The cestodes *C. delphini* and *C. monorygma* from either stranded or captured cetaceans have been reported mostly in the Atlantic and North Pacific oceans. Both species may serve as bio-indicators in *T. truncatus*, as they are present only in the offshore population (Reyes, 1989; Van Waerebeek et al., 1990), presumably because the latter often feeds on squid (García-Godos et al., 2007), a likely intermediate host (Walker & Cowan, 1981). *Clistobothrium delphini* parasitized also 70.0% of Peruvian dusky dolphins (Van Waerebeek et al., 1993).

Acanthocephala

No acanthocephalans were found in SEP *Delphinus*, analogous to checklists of helminth faunas in Peruvian dusky dolphin, Burmeister's porpoise, and common bottlenose dolphin (Reyes, 1989; Van Waerebeek, 1990, 1993; Reyes & Van Waerebeek, 1995). This suggests acanthocephalans are rare in small cetaceans of this region. Recent reviews of the diversity of marine acanthocephalans in Peru identified the South American sea lion (*Otaria byronia*) as the only known marine mammal host, namely for *Corynosoma obtuscens* (Morales et al., 2005; Tantaleán et al., 2005). However, studies in the Atlantic, Mediterranean, and Australia revealed acanthocephalans such as *Bolbosoma vasculosum*, *C. cetaceum,* and *Corynosoma* sp. in common dolphins (Delyamure, 1955; Abollo et al., 1998; Costa et al., 2005; Berrón-Vera et al., 2007), most of which are thought to be short-beaked common dolphin.

In several organs subjected to macroscopic examination, no metazoan parasites were encountered, including the spleen (n = 3), kidneys (n = 8 paired), and liver (n = 3). This finding is consistent with the study by Ross (1984), which neither found helminths in the kidneys (n = 10), liver (n = 6), lungs (n = 8), and hearts (n = 4) of long-beaked common dolphin from the southeast coast of South Africa (see Samaai et al., 2005). A 185-cm female was the smallest dolphin for which spleen, kidneys, and liver were examined in Peru.

Crustacea

This study documented the epizoite *X. globicipitis* on both SEP common dolphin forms. Previous records of *Xenobalanus* in *D. delphis* exist from the North Atlantic, western Mediterranean (4%), and North Pacific (Dollfus, 1968; Pilleri, 1970; Dailey & Walker, 1978). This pseudo-stalked barnacle is very common in Peruvian waters and has been found in the dusky dolphin with high prevalence, namely 38.9%, CI 35.4-42.5 (Van Waerebeek et al., 1993; Van Bressem et al., 2006), in Burmeister's porpoise with prevalence = 23.8%, CI 13.3-38.7 (Huamán & Reyes, 1986; Reyes & Van Waerebeek, 1995), and in common bottlenose dolphins with prevalence = 6.8% (Van Waerebeek et al., 1990). However, in Ecuador, 42.3% of offshore bottlenose dolphins were infested with this epizoite (Félix & Castro, 2023). From photographs of free-ranging animals, the prevalence of *X. globicipitis* in the short-beaked and long-beaked common dolphin in the Eastern Tropical Pacific Ocean was estimated as 2.9% and 1%, respectively (Kane et al., 2008). These are considerably lower values compared to the samples from coastal Peru. The high productivity linked to year-round upwelling in the Humboldt Current Large Marine Ecosystem (Gutiérrez et al,. 2016), we suggest, creates a particularly favourable environment for a sessile filter-feeder like *Xenobalanus*, alongside providing a high abundance of phoretic hosts. Prevalence estimates derived from at-surface photographs of free-ranging dolphins (Kane et al., 2008) will inevitably underestimate true values considering that a number of barnacles will not be detected on largely submerged caudal and pectoral fins.

As was the case in Peruvian dusky dolphins (Van Waerebeek et al., 1993), this study found no associated cyamids despite the close inspection of hundreds of carcasses of long-beaked common dolphin. This shared absence is consistent with these dolphin species frequently forming mixed schools in coastal Peru (Van Waerebeek, 1994) which hypothetically would facilitate cyamid transmission. In contrast, *Isocyamus* sp. was occasionally encountered on Burmeister's porpoises landed in Peru (Reyes & Van Waerebeek, 1995) and also on a few common bottlenose dolphins (CEPEC, unpublished data). In the Atlantic, *Isocyamus delphini* has been documented for *D. delphis* (Leung, 1967), while cyamids for South African long-beaked common dolphin had also been reported (Ross, 1984) (Supplementary Material 1).

The presence of most gastrointestinal helminth parasites in marine mammals is directly related to their diet habits, as both fish and squid act as intermediate hosts (Dans et al., 1999; Berón-Vera et al., 2007). While there is a paucity of information on helminth fauna in prey species, we know more on the feeding ecology of the principal odontocetes of the study region. By far the main prey item of long-beaked common dolphin is the Peruvian anchovy *Engraulis ringens*. Other species include silverside *Odontesthes regia*, Peruvian pilchard *Sardinops sagax*, mackerel *Trachurus picturatus*, hake *Merluccius gayi*, and various squids (García-Godos et al., 2007). A study of the metazoan parasites of *E. ringens* in Chilean waters revealed the occurrence of *Anisakis* sp. (Valdivia et al., 2007) which may plausibly explain why common dolphins are infested. Also, the complete lack of parasites observed in the pancreatic duct of 17 long-beaked common dolphins in Peru contrasts with the high prevalence rate (76.7%) of *Oschmarinella rochebruni* found in the ducts of long-beaked specimens from California (Cowan et al., 1986). This finding suggests a significantly different feeding ecology and/or parasitic susceptibility which may have a genetical base and may reflect a phylogenetic distance between these two long-beaked common dolphin populations.

In order to improve sample sizes, establish time series, and help reveal helminth life cycles and hosting, we recommend systematic, standardized parasite sampling from dolphin bycatch in the study region, and most especially from short-beaked common dolphins to allow a comparative analysis between both common dolphin forms. Surveys of marine mammal helminth fauna in the SEP region linked to detailed, laboratory-based necropsies, unfeasible under the field conditions of the present study (*i.e,* time constraints due to simultaneous sampling of specimens, impacting the number of all organs analysed) should yield better information on pathological processes including clinical signs, and contribute to the understanding of verminous morbidity and mortality, and ultimately the impact on the general health status of cetacean populations. Conceivably, cetacean helminths may have some relevance also for human health, considering that dolphins and porpoises are still occasionally consumed in Peru (Alfaro-Shigueto et al., 2008; Mangel et al., 2010; Tzika et al., 2010). Other studies with a zoonotic focus (Miyazaki, 1991; Tantaleán, 1994; McCarthy & Moore, 2000; Goldsmid, 2005) have discussed precautions to prevent the accidental transmission of helminth parasites to humans through the handling and consumption of insufficiently cooked cetacean products, so-called aquatic bushmeat or 'wild meat' prevalent in many regions of the world (*e.g.*, Ofori-Danson et al., 2003; Clapham & Van Waerebeek, 2007).

Acknowledgments

We greatly acknowledge support with field work by biologists Laura Chávez-Lisambarth, Ignacio García-Godos, David Montes, Karina Ontón, Andrew Read, Anne-Catherine Lescrauwaet, and Jeffrey McKinnon. We are grateful to Dr. Raúl Verano, emeritus head of the Department of Parasitology, Universidad Ricardo Palma, Lima, for the identification or confirmation of some helminths and to Dr. Juan Antonio Raga, Cavanilles Institute of Biodiversity and Evolutionary Biology, Universitat de València, for key comments that greatly improved previous drafts. Field collecting in Peru (1985-2000) was financed by various research grants: Leopold-III Fonds voor Natuuronderzoek en Natuurbehoud, IUCN Cetacean Specialist Group, UNEP, Cetacean Society International, Whale and Dolphin Conservation Society, and the Consejo Nacional de Ciencia y Tecnología (CONCYTEC, Peru). Data analysis and initial reporting was supported by grants from the International Whaling Commission (Research Proposal SC/52/SM34) and the International Fund for Animal Welfare. The field study in Ecuador was financed by UNEP and the Research Fellowship Program for Conservation Ecociencia (Wildlife Conservation Society). KVW was supported by ProDelphinus, and (in 2021) by the Center for Chinese White Dolphin Research and Conservation, Beijing Institute of Technology at Zhuhai, Guangdong, China.

Conflict of interest

The authors declare that no conflict of interest related to the implementation of this research exists.

References

Abollo, E., López, A., Gestal, C., Benavente, P., & Pascual, S. (1998). Macroparasites in cetaceans stranded on the northwest Spanish Atlantic coast. *Diseases of Aquatic Organisms, 32*(3), 227-231. https://doi.org/10.3354/dao032227

Agresti, A., & Coull, B. A. (1998). Approximate is better than "exact" for interval estimation of binomial proportions. *American Statistician, 52*(2), 119-126. https://doi.org/10.1080/00031305.1998.10480550

Agustí, C., Aznar, F. J., Olson, P. D., Littlewood, D. T. J., Kostadinova, A., & Raga, J. A. (2005a). Morphological and molecular characterization of tetraphyllidean merocercoids (Platyhelminthes: Cestoda) of striped dolphins (*Stenella coeruleoalba*) from the western Mediterranean. *Parasitology, 130*(4), 461-474. https://doi.org/10.1017/S0031182004006754

Agustí, C., Aznar, F. J., & Raga, J. A. (2005b). Tetraphyllidean plerocercoids from western Mediterranean cetaceans and other marine mammals around the world: a comprehensive morphological analysis. *Journal of Parasitology, 91*(1), 83-92. https://doi.org/10.1645/GE-372R

Alfaro-Shigueto, J. (1994). *Estudio del género* Nasitrema *en algunos cetáceos de la Costa Peruana* [BSc thesis, Universidad Ricardo Palma, Lima].

Alfaro-Shigueto, J., Mangel, J. C., & Van Waerebeek, K. (2008). *Small cetacean captures and CPUE estimates in artisanal fisheries operating from a port in northern Peru, 2005-2007* (Publication No. SC/60/SM19). International Whaling Commission Scientific Committee.

Aznar, F. J., Agustí, C., Littlewood, D. T. J., Raga, J. A., & Olson, P.D. (2007). Insight into the role of cetaceans in the life cycle of the tetraphyllideans (Platyhelminthes: Cestoda). *International Journal for Parasitology, 37*(2), 243-255. https://doi.org/10.1016/j.ijpara.2006.10.010

Baylis, H. A. (1932). A list of worms parasitic in Cetacea. *Discovery Reports, 6*, 393-418.

Berón-Vera, B., Crespo, E. A., Raga, J. A., & Fernández, M. (2007). Parasite communities of common dolphins (*Delphinus delphis*) from Patagonia: the relation with host distribution and diet and comparison with sympatric hosts. *Journal of Parasitology, 93*(5), 1056-1060. https://doi.org/10.1645/GE-1070R.1

Brieva, L. M., & Oporto, J. A. (1991). Prevalencia e intensidad de la infección por tremátodos del género *Nasitrema* en el delfín chileno *Cephalorhynchus eutropia* (Cetacea: Delphinidae). *Archivos de Medicina Veterinaria, 23*(1), 97-100.

Caira, J. N., Jensen, K., Pickering, M., Ruhnke, T. R., & Gallagher, K. A. (2020). Intrigue surrounding the life-cycles of species of *Clistobothrium* (Cestoda: Phyllobothriidea) parasitising large pelagic sharks. *International Journal for Parasitology, 50*(13), 1043-1055. https://doi.org/10.1016/j.ijpara.2020.08.002

Caira, J. N., Richmond, C., & Swanson, J. (2005). A revision of *Phoreiobothrium* (Tetraphyllidea: Onchobothridae) with descriptions of five new species. *Journal of Parasitology, 91*(5), 1153-1174. https://doi.org/10.1645/GE-3459.1

Castro, C., & Van Waerebeek, K. (2019). *Strandings and mortality of cetaceans due to interactions with fishing nets in Ecuador, 2001-2017* (Publication No. SC/68A/HIM/17). International Whaling Commission Scientific Committee.

Clapham, P., & Van Waerebeek, K. (2007). Bushmeat, the sum of the parts. *Molecular Ecology, 16*(13), 2607-2609. https://doi.org/10.1111/j.1365-294X.2007.03378.x

Colom-Llavina, M. M. (2005). *Metazoan parasites of marine mammals from the Caribbean and western coast of North America* [MSc thesis, University of Puerto Rico].

Costa, G., Chubb, J. C., & Veltkamp, C. J. (2005). Cystacanths of *Bolbosoma vasculosum* in the black-scabbard fish, *Aphanopus carbo*, oceanic horse mackerel *Trachurus picturatus* and common dolphin *Delphinus delphis* from Madeira, Portugal. *Journal of Helminthology, 74*(2), 113-120. https://doi.org/10.1017/S0022149X00700770

Cowan, D. F., Walker, W. A., & Brownell Jr, R. L. (1986). Pathology of small cetaceans stranded along southern California beaches. In M. M. Bryden, & R. Harrison (Eds.), *Research on Dolphins* (pp. 323-367). Oxford University Press.

Dailey, M. D., & Brownell Jr, R. L. (1972). A checklist of marine mammal parasites. In S. H. Ridgway (Ed.), *Mammals of the Sea, Biology and Medicine* (pp. 528-589). C. C. Thomas.

Dailey, M. D. (1985). Diseases of Mammalia: Cetacea. In O. Kinne (Ed.), *Diseases of Marine Animals* (pp. 805-844). Biologische Anstalt Helgoland.

Dailey, M. D., & Stroud, R. K. (1978). Parasites and associated pathology observed in cetaceans stranded along the Oregon Coast. *Journal of Wildlife Diseases, 14*(4), 503-511. https://doi.org/10.7589/0090-3558-14.4.503

Dailey, M. D., & Walker, W. A. (1978). Parasitism as a factor (?) in single strandings of southern California cetaceans. *Journal of Parasitology, 64*(4), 593-596. https://doi.org/10.2307/3279939

Dailey, M. D., & Otto, K. A. (1982). *Parasites as biological indicators of the distributions and diets of marine mammals common to the eastern tropical Pacific* (Publication No. LJ-82-13C). NMFS, SWFSC.

Dailey, M. D., Walsh, M., Odell, D., & Campbell, T. (1991). Evidence of prenatal infection in the bottlenose dolphin, with the lungworm *Halocercus lagenorhynchi* (Nematoda: Pseudaliidae). *Journal of Wildlife Diseases, 27*(1), 164-165. https://doi.org/10.7589/0090-3558-27.1.164

Dailey, M. D., & Vogelbein, W. K. (1991). Parasite fauna of 3 species of Antarctic whales with reference to their use as potential stock indicators. *Fishery Bulletin, 89*(3), 355-365. https://scholarworks.wm.edu/vimsarticles/607

Dans, S. L., Reyes, L. M., Pedraza, S. N., Raga, R. A., & Crespo, E. A. (1999). Gastrointestinal helminths of the dusky dolphin, *Lagenorhynchus obscurus*, off Patagonian coasts, in the Southwestern Atlantic Ocean. *Marine Mammal Science, 15*(3), 649-660. https://doi.org/10.1111/j.1748-7692.1999.tb00834.x

Davey, J. T. (1971). A revision of genus *Anisakis* Dujardin 1845 (Nematoda, Ascaridata). *Journal of Helminthology, 45*(1), 51-72. https://doi.org/10.1017/S0022149X00006921

Delyamure, S. L. (1955). Helminthofauna of Marine Mammals (Ecology Phylogeny). Academy of Sciences USSR (Translated by the Israel Program for Scientific Translations for 1968 for the US Department of Interior and National Science Foundation). National Technical Information Service.

Dollfus, R. (1968). *Xenobalanus globicipitis* Steenstrup (Cirripedia, Thoracica) recolté sur *Tursiops truncatus* (Montagu) à proximité de la Côte Nord du Maroc. *Bulletin Institut des Pêches Maritimes du Maroc, 16*, 55-60.

Félix, F., & Samaniego, J. (1994). Incidental catches of small cetaceans in the artisanal fisheries of Ecuador. *Report of the International Whaling Commission* (*Special Issue 15*), 475-483.

Félix, F., & Castro, C. (2023). Occurrence, abundance and some ecological aspects of the offshore bottlenose dolphin off Ecuador's central coast. *Latin American Journal of Aquatic Mammals, 18*(2), 175-185. https://doi.org/10.5597/lajam00310

Félix, F., Van Waerebeek, K., Macías, R., Platt, M., & Castro, C. (2025). First record of the long-beaked common dolphin in Ecuador. *Latin American Journal of Aquatic Mammals, 20(1), 60-65.* https://doi.org/10.5597/ lajam00343

Fernández, J. C. (1987). Nuevos registros de parásitos en mamíferos marinos chilenos. *Parasitología al Día, 11*, 120-25.

Fraija-Fernández, N., Fernández, M., Lehnert, K., Raga, J. A., Siebert, U., & Aznar, F.J. (2017). Long-distance travellers: phylogeography of a generalist parasite, *Pholeter gastrophilus,* from Cetaceans. *PLoS ONE, 12*(1), e0170184. https://doi.org/10.1371/journal.pone.0170184

García-Godos, I. (1992, August 2-7). *Captura estacional de cetáceos menores en la caleta de Ancón* [Paper presentation]. X Congreso Nacional de Biología, Lima, Peru.

García-Godos, I., Van Waerebeek, K., Reyes, J. C., Alfaro-Shigueto, J., & Arias-Schreiber, M. (2007). Prey occurrence in the stomach contents of four small cetacean species in Peru. *Latin American Journal of Aquatic Mammals, 6*(2), 171-183. https://doi.org/0.5597/lajam00122

Geraci, J. R., & Lounsbury, V. J. (2005). *Marine Mammals Ashore, A field guide for strandings.* Texas A&M University Sea Grant College Program.

Geraci, J. R., Dailey, M. D., & St Aubin, D. J. (1978). Parasitic mastitis in the Atlantic white-sided dolphin, *Lagenorhynchus acutus*, as a probable factor in herd productivity. *Journal of the Fisheries Research Board of Canada, 35*(10), 1350-1355. https://doi.org/10.1139/f78-210

Gibson, D. I., Harris, E. A., Bray, R. A., Jepson, P. D., Kuiken, T., Baker, J. R., & Simpson, V. R. (1998). A survey of the helminth parasites of cetaceans stranded on the coast of England and Wales during the period 1990-1994. *Journal of Zoology London, 244*(4), 563-574. https://doi.org/10.1111/j.1469-7998.1998.tb00061.x

Goldsmid, J. M. (2005). Zoonotic infections – An overview. In J. M. Goldsmid & P. A. Leggat (Eds.), *Primer of Tropical Medicine* (pp 14.1-14.14). Australasian College of Tropical Medicine Publications.

Gutiérrez, D., Akester, M., & Naranjo, L. (2016). Productivity and sustainable management of the Humboldt Current Large Ecosystem under climate change. *Environmental Development, 17*(1), 126-144. https://doi.org/10.1016/j.envdev.2015.11.004

Heyning, J. E., & Perrin, W. F. (1994). Two forms of common dolphins (genus *Delphinus*) from the eastern North Pacific; evidence for two species. *Contribution in Science (Los Angeles), 442*, 1-35.

Huamán, P., & Reyes, J. C. (1986, May 25-31). Xenobalanus globicipitis *Steenstrup, 1851 (Thoracica, Coronulidae), cirrípedo epizoo de la 'marsopa espinosa'* Phocoena spinipinnis *Burmeister, 1865 (Cetacea, Phocoenidae)* [Paper presentation]. VIII Congreso Nacional de Biología y VIII Simposio de Educación en Ciencias Biológicas, Arequipa. Peru.

Kane, E. A., Olson, P. A., Gerrodette, T., & Fiedler, P. C. (2008). Prevalence of the commensal barnacle *Xenobalanus globicipitis* on cetacean species in the eastern tropical Pacific Ocean, and a review of global occurrence. *Fishery Bulletin, 106*(4), 395-404.

Lambertsen, R. H. (1986). Disease of the common fin whale (*Balaenoptera physalus*): Crassicaudosis of the urinary system. *Journal of Mammalogy, 67*(2), 353-366. https://doi.org/10.2307/1380889

Leung, Y-M. (1967). An illustrated key to the species of whale-lice (*Amphipoda, Cyamidae*), ectoparasites of Cetacea, with a guide to the literature. *Crustaceana, 12*(3), 279-291. https://www.jstor.org/stable/20102847

Mangel J. C., Alfaro-Shigueto, J., Van Waerebeek, K., Caceres, C., Bearhop, S., Witt, M. J., & Godley, B. (2010). Small cetacean captures in Peruvian artisanal fisheries: High despite protective legislation. *Biological Conservation, 143*(1), 136-143. https://doi.org/10.1016/j.biocon.2009.09.017

McCarthy, J., & Moore, T. A. (2000). Emerging helminth zoonosis. *International Journal of Parasitology, 30*(12-13), 1351-1360. https://doi.org/10.1016/s0020-7519(00)00122-3

Mead, J. G., & Fordyce, R. E. (2009). The Therian skull: A lexicon with emphasis on the odontocetes. *Smithsonian Contributions to Zoology, 627*, 1-248. https://doi.org/10.5479/si.00810282.627

Mignucci-Giannoni, A., Hoberg, E. P., Siegel-Causey, D., & Williams Jr, E. H. (1998). Metazoan parasites and other symbionts of cetaceans in the Caribbean. *Journal of Parasitology, 84*(5), 939-946. https://doi.org/10.2307/3284625

Miyazaki, I. (1991). *An illustrated book of helminthic zoonoses.* International Medical Foundation of Japan.

Morales, E., Sarmiento, L., Sánchez, L., Floríndez, D., & Lamas, G. (2005). Material tipo de helmintos en el Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, (MUSM), Lima, Perú. *Revista Peruana de Biología, 12*(3), 463-472. https://doi.org/10.15381/rpb.v12i3.2423

Morimitsu, T., Kawano, H., Torihara, K., Kato, E., & Koono, M. (1992). Histopathology of eighth cranial nerve of mass stranded dolphins at Goto Islands, Japan. *Journal of Wildlife Diseases, 28*(4): 656-58. https://doi.org/10.7589/0090-3558-28.4.656

Murga, G., Moreno, R., & Escalante, A. H. (1986, May 25-31). *Helmintos parásitos de* Delphinus delphis *procedentes de la zona norte del Mar Peruano* [Paper presentation]. VIII Congreso Nacional de Biología y III Simposio de Educación en Ciencias Biológicas, Arequipa, Peru.

Neiland, K. A., Rice, D. W., & Holden, B. L. (1970). Helminths of marine mammals, I. The genus *Nasitrema*, air sinus flukes of delphinid Cetacea. *Journal of Parasitology, 56*(2), 305-316. https://doi.org/10.2307/3277662

Ofori-Danson, P. K., Van Waerebeek, K., & Debrah, S. (2003). A survey for the conservation of dolphins in Ghanaian coastal waters. *Journal of the Ghana Science Association, 5*(2), 45-54.

Perrin, W. F., & Powers, J. E. (1980). Role of a nematode in natural mortality of spotted dolphins. *Journal of Wildlife Management, 41*(4), 960-963. https://doi.org/10.2307/3808335

Perrin, W. F. (2022) *World Cetacea Database.* Delphinus delphis bairdii *Tomilin, 1957*. https://www.marinespecies.org/aphia.php?p=taxdetails&id=384522

Pilleri, G. (1970). *Xenobalanus globicipitis* Steenstrup on *Delphinus delphis*, *Stenella styx* and *Tursiops truncatus* of the western Mediterranean. *Investigations on Cetacea, 2*, 248-249.

Raga, J. A., Casinos, A., Filella, S., & Raduan, A. (1982). Notes on cetaceans of the Iberian coasts. V. *Crassicauda grampicola* Johnston & Mawson, 1941 (Nematoda), cause of injuries in the pterygoids of some specimens of *Grampus griseus. Saugetierkündliche Mitteilungen, 30*(4), 315-318.

Raga, J. A., Abril, E., Goodall, R. N. P., & Balbuena, J. A. (1994). *Nasitrema* sp. (Digenea; Nasitrematidae) from the long-finned pilot whale (*Globicephala melas*), off Tierra del Fuego; a new host record. *Report of the International Whaling Commission, 44*, 371-374.

Raga, J. A., Balbuena, J. A., Aznar, J., & Fernández, M. (1997). The impact of parasites on marine mammals: a review. *Parassitologia, 39*, 293-296.

Read, A., Van Waerebeek, K., Reyes, J. C., McKinnon, J. S., & Lehman, L. C. (1988) The exploitation of small cetaceans in coastal Peru. *Biological Conservation, 46*(1), 53-70. https://doi.org/10.1016/0006-3207(88)90108-5

Reyes, J. C. (1989). *Helmintos parásitos de* Tursiops truncatus *(Cetacea: Delphinidae) en aguas de la costa peruana* [BSc Thesis, Universidad Ricardo Palma, Lima].

Reyes Robles, J. C. (2009). *Ballenas, delfines y otros cetáceos del Perú. Una fuente de información*. Squema Ediciones.

Reyes, J. C., & Van Waerebeek, K. (1995). Aspects of the biology of Burmeister's porpoise from Peru. *Report of the International Whaling Commission (Special Issue 16)*, 349-364.

Ridgway, S. H., & Dailey, M. D. (1972). Cerebral and cerebellar involvement of trematode parasites in dolphins and their possible role in stranding. *Journal of Wildlife Diseases, 8,* 33-43. https://doi.org/10.7589/0090-3558-8.1.33

Ross, G. J. B. (1984). The smaller cetaceans of the southeast coast of southern Africa. *Annals of the Cape Provincial Museums (Natural History), 15*(2), 173-410.

Samaai, T., Best, P. B., & Gibbons, M. J. (2005). The taxonomic status of common dolphins *Delphinus* spp. in South African waters. *African Journal of Marine Science, 27*(2), 449-458. https://doi.org/10.2989/18142320509504103

Samaniego, J. (1994). *Aspectos biológicos de 4 especies de delfines capturados casualmente, y estudio del impacto de las pesquerías artesanales en las poblaciones de cetáceos menores en Ecuador* [BSc Thesis, Pontificia Universidad Católica del Ecuador].

Sanino, G. P., Van Waerebeek, K., & Yañez, J. (2003). Revisión de la distribución del género *Delphinus* y registros documentados de *D. capensis* en Chile. *Boletín del Museo Nacional de Historia Natural de Chile, 52*, 97-102.

Tantaleán, M. (1994). Nuevos helmintos de importancia médica en el Perú. *Revista Peruana de Medicina Tropical de la Universidad Nacional Mayor de San Marcos, 8*(1-2), 87-91.

Tantaleán, M., & Escalante, H. (1987). Nota sobre la presencia de *Synthesium tursionis* (Marchi, 1873) Price, 1932 (Trematoda: Campulidae) en *Delphinus delphis* L. (Cetacea: Odontoceti) de la Costa Peruana. *Parasitologia al Día, 11*, 39-40.

Tantaleán, M., Sánchez, L., Gómez, L., & Huiza, A. (2005). Acanthocephalan from Peru. *Revista Peruana de Biología, 12*(1), 83-92. https://doi.org/10.15381/rpb.v12i1.2361

Testa, J., & Dailey, M. D. (1977). Five new morphotypes of *Phyllobothrium delphini* (Cestoda: Tetraphyllidea), the relationship to existing morphotypes, and their zoogeography. *Bulletin of the Southern California Academy of Sciences, 76*(2), 99-110. https://doi.org/10.3160/0038-3872-76.2.99

Torres, P., Oporto, J. A., Brieva, L. M., & Escare, L. (1992). Gastrointestinal helminths of the cetaceans *Phocoena spinipinnis* (Burmeister, 1865) and *Cephalorhynchus eutropia* (Gray, 1846) from the southern coast of Chile. *Journal of Wildlife Diseases, 28*(2), 313-315. https://doi.org/10.7589/0090-3558-28.2.313

Tzika, A. C., D'Amico, E., Alfaro-Shigueto, J., Mangel, J. C., Van Waerebeek, K., & Milinkovitch, M. C. (2010). Molecular identification of small cetacean samples from Peruvian fish markets. *Conservation Genetics, 11*, 2207-2218. https://doi.org/10.1007/s10592-010-0106-8

Valdivia, I. M., Chávez, R. A., & Oliva, M. E. (2007). Metazoan parasites of *Engraulis ringens* as tools for stock discrimination along the Chilean coast. *Journal of Fish Biology, 70*, 1504-1511. https://doi.org/10.1111/J.1095-8649.2007.01429.X

Van Bressem, M-F., Van Waerebeek, K., Montes, D., Kennedy, S., Reyes, J. C., García-Godos, I. A., Ontón-Silva, K., & Alfaro-Shigueto, J. (2006). Diseases, lesions and malformations in the long-beaked common dolphin *Delphinus capensis* from the Southeast Pacific. *Diseases of Aquatic Organisms, 68*, 149-165.

Van Bressem, M-F., Van Waerebeek, K., Reyes, J. C., Félix, F., Echegaray, M., Siciliano, S., di Beneditto, A. P., Flach, L., Viddi, F., Avila, I. C., Herrera, J. C., Tobón, I. C., Bolaños-Jiménez, J., Moreno, I. B., Ott, P. H., Sanino, G. P., Castineira, E., Montes, D., Crespo, E., Flores, P. A. C., Haase, B., Medonça de Souza, S. M. F., Laeta, M., & Fragoso, A. B. (2007). A preliminary overview of skin and skeletal diseases and traumata in small cetaceans from South American waters. *Latin American Journal of Aquatic Mammals, 6*(1), 7-42. https://doi.org/10.5597/lajam00108

Van Waerebeek, K. (1992). *Population identity and general biology of the dusky dolphin* Lagenorhynchus obscurus *(Gray, 1828) in the Southeast Pacific* [Doctoral dissertation, University of Amsterdam].

Van Waerebeek, K. (1994). A note on the status of the dusky dolphins *Lagenorhynchus obscurus* off Peru. *Report of the International Whaling Commission (Special Issue 15)*, 525-528.

Van Waerebeek, K., & Oporto, J. A. (1990, November 12-15). *Observaciones preliminares sobre la biología de* Lissodelphis peronii *(Delphinidae) en el Pacífico sureste* [Paper presentation]. IV Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Valdivia, Chile.

Van Waerebeek, K., & Reyes, J. C. (1994a). Interactions between small cetaceans and Peruvian fisheries in 1988/1989 and analysis of trends. *Report of the International Whaling Commission (Special Issue 15)*, 495-502.

Van Waerebeek, K., & Reyes, J. C. (1994b). Post-ban small cetacean takes off Peru: a review. *Report of the International Whaling Commission (Special Issue 15)*, 503-520.

Van Waerebeek, K., Reyes, J. C., Read, A. J., & McKinnon, J. S. (1990). Preliminary observations of bottlenose dolphins from the Pacific coast of South America. In S. Leatherwood, & R. R. Reeves (Eds.), *The Bottlenose Dolphin* (pp.143-154). Academic Press. https://doi.org/10.1016/B978-0-12-440280-5.50011-1

Van Waerebeek, K., Reyes, J. C., & Alfaro, J. (1993). Helminth parasites and phoronts of dusky dolphins *Lagenorhynchus obscurus* (Gray, 1828) from Peru. *Aquatic Mammals, 19*(3), 159-169.

Van Waerebeek, K., Van Bressem, M-F., Reyes, J. C., Alfaro, J. A., Bello, R., Echegaray, M., García-Godos, A., & Ontón, K. (1994a). *Illegal exploitation of small cetaceans in Peru.* Final report to United Nations Environment Programme, and WDCS.

Van Waerebeek, K., Reyes, J. C., & Van Bressem, M-F. (1994b). *Presencia de dos especies de* Delphinus *en el Pacífico sureste* [Paper presentation]. 6a RT Especialistas em Mamíferos Aquáticos da América do Sul, Florianópolis, Brazil.

Van Waerebeek, K., Van Bressem, M-F., Félix, F., Alfaro-Shigueto, J., García-Godos, A., Chávez-Lisambart, L., Ontón, K., Montes, D., & Bello, R. (1997). Mortality of dolphins and porpoises in coastal fisheries off Peru and southern Ecuador in 1994. *Biological Conservation, 81*(1-2), 43-49. https://doi.org/10.1016/S0006-3207(96)00152-8

Van Waerebeek, K., Van Bressem, M-F., Alfaro-Shigueto, J., Sanino, G. P., Montes, D., & Ontón, K. (1999). *A preliminary analysis of recent captures of small cetaceans in Peru and Chile* (Publication No. SC/51/SM17). International Whaling Commission Scientific Committee.

Walker, W. A., & Cowan, D.F. (1981). *Air sinus parasitism and pathobiology in free-ranging common dolphins* (Delphinus delphis) *in the Eastern Tropical Pacific* (Publication No. LJ-81-23C). National Oceanic and Atmospheric Administration.

Supplementary material

Supplementary Material 1 - Overview of known metazoan parasites and epizoites in common dolphins *Delphinus* spp.