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Helminth Load in Feces of Free-Ranging Blue and Fin Whales from the Gulf of California

Lavinia Flores-Cascante[1,3] · Jaime Gómez-Gutiérrez[1] · María del Carmen Gómez del Prado-Rosas[2] · Diane Gendron[1]

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Abstract

Introduction This is the first worldwide systematic and quantitative study to count and identify helminth parasites from 100 blue and 44 fin whale fecal samples collected in the Gulf of California during winter (1993–2014).

Results Blue and fin whale feces had similar prevalence of adult acanthocephalans (*Bolbosoma* sp.) in feces (18.2% and 14.6%, respectively), but blue whales had significantly higher helminth egg prevalence in feces (100%) and mean intensity (443 ± 318 eggs/g) compared to fin whales (61%, 252 ± 327 eggs/g). *Diphyllobothrium* sp. eggs were identified in blue whale feces and Diphyllobothridae, *Ogmogaster* sp. and *Crassicauda* sp. eggs were identified in fin whale feces. We tested the hypothesis that egg intensity in blue whale's feces varies as a function of age class, reproductive status, sex, preservation and sampling years using a Generalized Linear Model. This model explained 61% of the variance in the helminth egg intensity, but it was not significant. Eighteen blue whale individuals were resampled over time without significant difference between consecutive samples.

Conclusions Thus, all individual blue whales that migrate to the Gulf of California during winter are permanently parasitized with helminths, while the resident fin whales showed lower prevalence and intensity. This helminth load difference is likely due to their different diets duringsummer–fall, when blue whales feed on other krill species in the California Current System and fin whales shift to school fish prey types in the Gulf of California.

Keywords *Balaenoptera musculus* · *Balaenoptera physalus* · McMaster's technique · Parasitism · Eggs · Prevalence intensity · Mexico

Introduction

In wild marine mammal populations, the interactions that occur among individuals, the environment and disease agents are complex and difficult to assess [24]. Thus, the monitoring of parameters and ecological factors are necessary to investigate population health. Long-term studies on stranded cetaceans have been useful to explore parasite diversity, intensity and prevalence [83]. Historically, odontocetes have been more intensively studied than mysticetes due to their smaller body size and the relatively higher stranding frequency associated with their greater population sizes compared to mysticetes [24, 71, 75]. High helminth intensities and prevalence have been cited among the causes linked to stranding of common odontocetes along the North Atlantic coast of England [31]. However, whether information concerning parasite infections based on stranded animals is representative of a wild population is still under debate [74].

Monitoring health in live cetacean populations that are distributed over an extensive geographical range, exhibit periodic migrations and that are protected by distinct country laws is logistically complex. Thus, parasite communities have rarely been evaluated in free-ranging cetacean populations and could provide valuable information about feeding

✉ Diane Gendron
dianegendroncicimar@gmail.com

[1] Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, Av. Instituto Politécnico Nacional s/n, Col. Playa Palo de Santa Rita, 23096 La Paz, Baja California Sur, Mexico

[2] Departamento Académico de Biología Marina, Universidad Autónoma de Baja California Sur, Carretera al Sur Km 5.5, 23080 La Paz, Baja California Sur, Mexico

[3] Present Address: Ingeniería en Biotecnología, Universidad Abierta y a Distancia de México, Av. Insurgentes No. 423, Col. Unidad Nonoalco Tlatelolco, 06900 Mexico City, Distrito Federal, Mexico

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habits and health conditions of individuals and populations [83]. Parasites also potentially serve as biological tags [7, 24, 75]. Information about intestinal parasites from live cetaceans has been obtained from feces and analyzed qualitatively using molecular methods identifying the parasites from genus-to-phylum levels [20, 38, 46]. Because these studies lack a quantitative estimation of prevalence, intensity and population structure in feces as a function of whale hosts (sex, size or reproductive phase), few inferences can be achieved about the parasite–host populations. Monitoring studies, involving long-term biological sampling, preferably associated with a natural history database of photo-identified individuals, would be required to investigate parasite intensity and prevalence in wild populations of free-ranging cetaceans.

The present study is part of 22 years (1993–2014) of cetacean research carried out in the southwestern region of the Gulf of California and takes advantage of the collected individual photo-identification data and biological sampling (skin, feces and subcutaneous fat) from individual blue whales *Balaenoptera musculus* [29] and fin whales *Balaenoptera physalus*. Blue whale is a seasonal migrant [8, 27] while fin whale is resident of the Gulf of California and highly isolated from the North Pacific population [9]. Both baleen whale species co-occur during winter and spring, when the marine productivity is enhanced by wind-driven upwelling and tidal mixing [4]. During this period they feed on dense swarms of the numerically dominant krill *Nyctiphanes simplex* [11, 26]. Morphological analysis of prey remnants contained in their feces collected in the Gulf of California revealed they feed mostly on *N. simplex* and scarcely on *Nematoscelis difficilis* [19, 26, 41, 82]. Molecular scatology conducted on the same set of fecal samples of the present study showed evidence that both baleen whale species also prey on lantern fish: Family Myctophidae [41]. The significances of baleen whale spatio-temporal shifts in diet on trophic-transmitted parasites are unknown.

We present the first systematic quantification of helminth parasites (egg intensity and adult prevalence contained in feces) of individual blue and fin whales based on the quantitative McMaster technique applied to cetaceans [23] and compare the prevalence and intensity of helminths that interact with blue and fin whale species sampled in the Gulf of California. We propose the hypothesis that although blue and fin whales presumably feed on the same prey types (krill and lantern fish) during the winter–spring period in the Gulf of California [41], differences in their diet when they distribute in distinct regions during summer–fall [67] cause differences in parasite prevalence and species composition. Because the large sample size of blue whale feces were linked with photo-identification information of the individuals, we also tested the hypothesis that the parasite intensity (number of helminth eggs per gram of feces) in individual would vary according to sex, female reproductive status and age class, presumably due to inherent hormonal and physiological variations in individuals of such population categories. Our ultimate goals were to define a quantitative baseline useful for monitoring these populations and to identify potential health changes that may occur in the future.

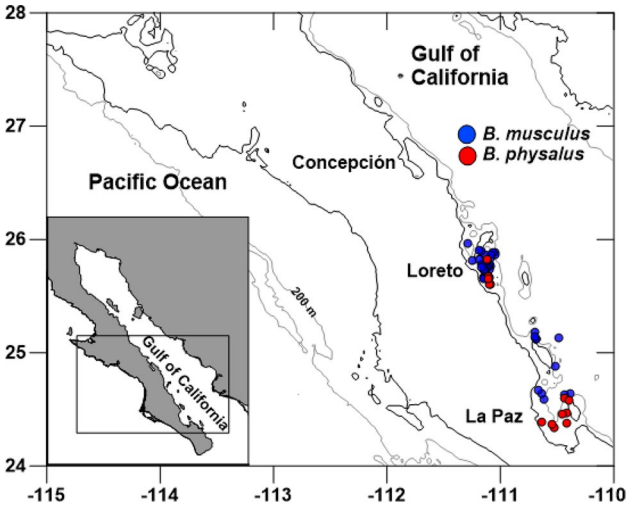

Fig. 1 Area of study located along the southwestern coast of the Gulf of California where blue whale feces (blue circles) were collected during their annual winter migration (January to May 1996–2014). Fin whale feces (red circles) were collected throughout the year (1993–2009). Black circles are the geographical positions of the fecal samples analyzed in the present study (color figure online)

Materials and Methods

Area and Population of Study

A total of 100 blue whale and 44 fin whale fecal samples were collected at sea surface between January and May from 1993 to 2014 along the southwestern coast of the Gulf of California, Mexico (Bahía de La Paz 24°30′N to Loreto 26°20′N) (Fig. 1). Blue whale individuals of both sexes, different maturity and reproductive states feed in this region during Dec–May. The blue whale, in particular, has been systematically monitored every year beginning in 1993 [29]. Most of the blue whale samples (81%) were linked to photo-identified individuals using the method described Gendron and Ugalde-de la Cruz [29]. Age class (juvenile or adult) of individuals was estimated using the length data obtained with a standard photo-sequence method to estimate the total length of each individual (Ortega Ortiz [69]). Blue whale females and males reach sexual maturity at 22 m total length [25, 54]. Females accompanied by calves were considered to be lactating, females sampled during the following year of lactation were considered post-lactating females and resting

females were those females with no observable evidence of recent lactation.

Fieldwork

Feces of blue and fin whales were opportunistically collected between 1993 and 2008 when observed at sea surface during our annual photo-identification census along the southwestern Gulf of California. However, since 2009 most samples come from the intentional search for feces during focal surveys [3], during which the strategy was to follow anindividual for many hours during each sampling day, typically from sunrise to sunset. This strategy increased the probability of finding feces and provided a relatively large amount per sampling season. This strategy increased the probability of finding their feces and provided a relatively large number of feces per sampling season. A bucket or colander was used for sea surface collection of the compact feces (typically red-colored) floating at surface and usually observed when the baleen whale started a dive [23]. Subsamples of 150–250 ml were stored in 500 ml jars, preserved in formalin at 5% or 10% or in non-denatured ethanol at a range between 50 and 96% concentration. Due to technical issues related to the quality of preservation and the amount of sample available for parasitological analysis, only 82 out of the 100 blue whale fecal samples were analyzed for adult parasite identification and 88 for quantification of helminth eggs. In the case of fin whale, from a total of 44 fecal samples collected, 11 were analyzed for adult parasite identification and prevalence in feces and 31 samples for helminth egg quantification.

Sample Processing

Adult parasites and eggs extracted from blue whale and fin whale feces preserved in formalin or ethanol were found typically in poor morphological condition. The eggs were never completely spherical or ovoid. The fecal samples analyzed for macroscopic adult parasites were previously filtered through a 400-µm mesh sieve. The adult specimens were measured, photographed and observed using an Olympus SZ61 stereomicroscope to detect external morphological structures useful for identification at the most precise taxonomic level. The best-preserved adult helminth specimens were processed for scanning electron microscopy (Hitachi S-3000 N), while other specimens were stained and transparent processed for taxonomic identification [77].

The adult helminth identification was carried out using available taxonomic literature and identification keys [5, 16–18, 52, 86, 92].

Parasite eggs from feces were observed from samples preserved in formalin and ethanol. From blue whale feces, the eggs were isolated with (1) a modification of the Ritchie technique, (2) by flotation using Zinc sulfate solution and (3) by Baermann technique from a saline culture at room temperature using six fresh blue whale fecal samples collected during 2011. For fin whale fecal samples Zinc sulfate flotation solution was exclusively used. Observation of eggs from feces was done using a compound microscope Olympus CX40 (10×, 40×, and 100× magnifications). Independently of the preservation method used, the eggs were stained with iodine or crystal violet to facilitate the detection of morphological structures of diagnostic taxonomic value, based on the helminth parasite identification key for marine mammals [17, 18].

Quantification of parasite eggs was standardized as number of eggs per gram of dry feces (eggs/g, EPG) using the McMaster technique modified for free-ranging cetaceans [23]. Each fecal sample was homogenized just before each parasitological analysis and counts were done in duplicate. The egg counts were calculated from dehydrated fecal samples of 88 blue whales and 31 fin whales. Their dry weight was obtained by air-drying. Due to drying and the characteristics of the McMaster chamber, morphological internal or external structures in eggs could not be clearly observed; therefore, the parasite egg load for the entire time series was estimated by identifying them only as helminth eggs.

Statistical Analysis

We calculated the prevalence and mean intensity of parasite eggs and adults in baleen whale feces according to the formulas described by Bush et al. [12]. Confidence limits were calculated using Bootstrap iteration (Bias corrected and accelerated percentile method, BCa) in Quantitative Parasitology on the Web 1.0 [78]. Mann–Whitney *U* test was used for testing significant differences in the median of helminth egg counts between blue whales and fin whales.

A general linear model (GLM, SPSS 17.0) was used to investigate the effects of the combination of all blue whale variables: age class, reproductive status (females), sex, preservation and sampling years in the parasite egg intensity. This GLM was not carried out with fin whales due to the lack of information about individuals (sex, total length and age composition).

Wilcoxon signed rank test was used to compare whether egg intensities of blue whales in consecutive fecal samples of the same individual with sampling intervals of days, months or years (non-independent samples) were significantly different. We assumed that mean intensity of helminth eggs would not change significantly in whales resampled the same year and among years. Because adult parasites were observed at a relatively low prevalence and intensity in feces of both baleen whale species, no statistic tests were attempted.

Table 1 Measurements of range and mean of length and width (µm) of protists and ten types of helminth eggs found in blue whale (1996–2014) and fin whale (1993–2009) feces collected from the southwest region of the Gulf of California (Loreto to Bahía de La Paz, BCS), Mexico

Type of parasites	Number of specimens *n*	Length range (mean) µm	Width range (mean) µm
Host blue whales			
Protist	5	22–33 (26.3)	13–20 (16.1)
Diphyllobothrium sp.	4	59–76 (68)	40–55 (49.7)
Unidentified egg	1	115.0	75.0
Nematoda egg	1	50.0	48.0
Cestoda coracidium	6	26–36 (30.3)	15–20 (16.3)
Embryonated unidentified eggs	4	35–73 (57.25)	31–71 (49.75)
Host fin whales			
Group of unidentified eggs	6	90–140 (125)	90–140 (118.3)
Diphyllobothriidae	2	40–57 (48.5)	27–48 (37.5)
Ogmogaster sp.	4	120–140 (127.5)	10–11 (10.3)
Unidentified egg	1	140.0	140.0
Crassicauda sp.	2	40–45 (42.5)	30–40 (35)

Results

Overall, adult *Bolbosoma* sp. (Acanthocephala) were observed in feces of both baleen whale species. *Diphyllobothrium* sp. (Cestoda) and Nematoda eggs, Cestoda coracidium and protists were identified in blue whales and Diphyllobothridae (Cestoda), *Ogmogaster* sp. (Trematoda) and *Crassicauda* sp. (Nematoda) eggs were identified in fin whale feces (Table 1).

Helminth Egg Parasites in Whale Feces

In blue whales, the parasites were classified as protists and embryonated, plus four morphotypes of helminth eggs. The small size and external morphology of some parasites suggested that they were protists (Fig. 2a–c). These were not dyed with either iodine or crystal violet. The first morphotype egg (Fig. 2d, e) had a double shell wall, poorly defined operculum and a shell thickness of 3 µm. These were morphologically similar to those described for eggs of Cestoda of the genus *Diplogonoporus* (Diphyllobothriidae). Waeschenbach et al. [90] concluded with molecular evidence that *Diplogonoporus* is the junior synonym of *Diphyllobothrium* (Diphyllobothriidae). However, there is a lack of information concerning the characterization of the eggs of *Diphyllobothrium* at species level [18, 56]. The second egg morphotype was 115 µm long and 75 µm wide (Fig. 2f). The third egg morphotype was 50 µm long and 45 µm wide, possibly belonging to the family Anisakidae (Nematoda) (Fig. 2g). The fourth egg morphotype (Fig. 2h), recovered exclusively from fresh cultures of feces collected in 2011, resembled the first stage of a coracidium (Cestoda). Several embryonated eggs were also found from fresh cultures; lengths and widths varied with the volume of the morula (Fig. 2i, j).

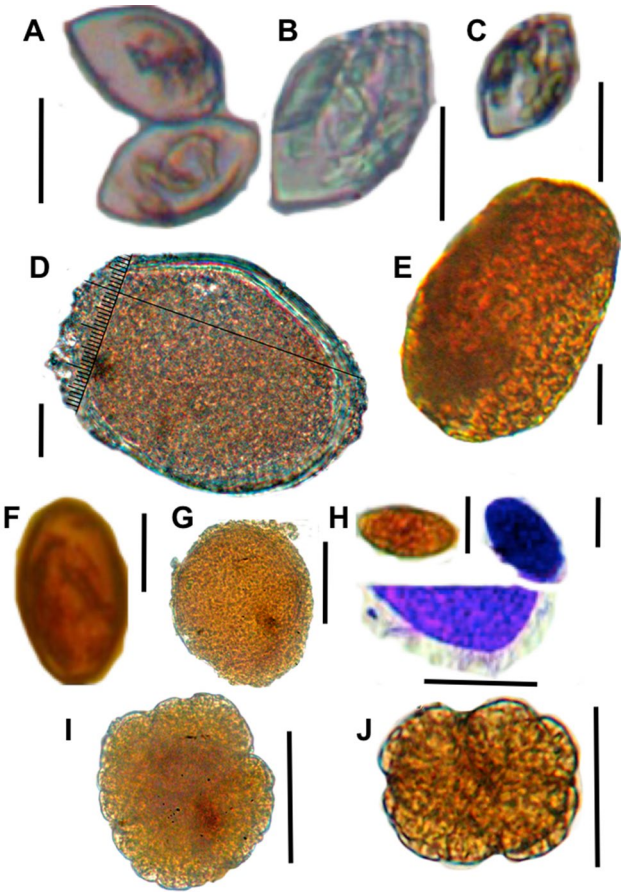

Fig. 2 Parasite types found in blue whale feces. **a–c** possible protists. **d**, **e** eggs identified as *Diphyllobothrium* sp., **f**, **g** eggs unidentified, **h** unidentified Cestoda, **i**, **j** embryonated helminth eggs (scale bar: **a**, **b**, **e** = 15 µm; **c**, **h** = 20 µm; **d** = 10 µm, **g** = 25 µm; **f**, **i**, **j** = 50 µm)

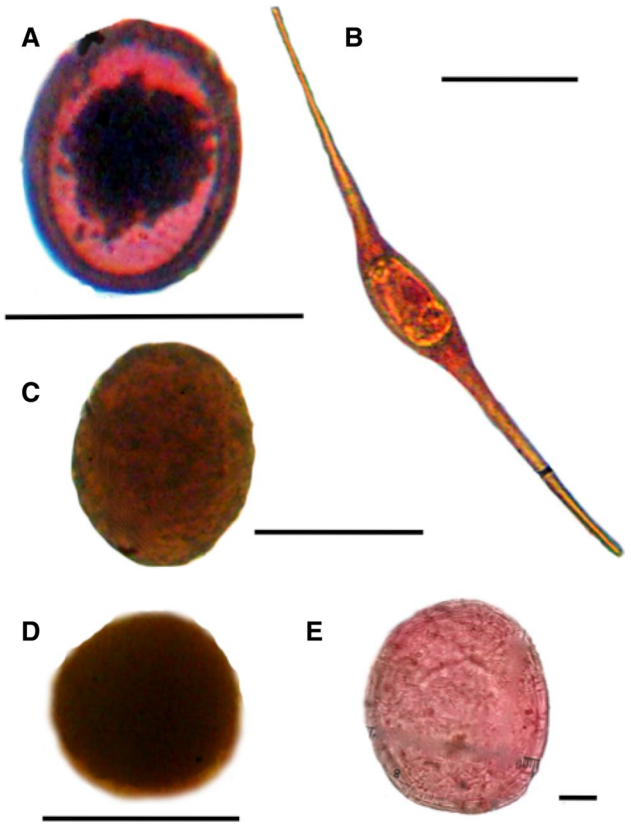

Fig. 3 Egg parasites found in fin whale feces. **a** Nematode eggs of the genus *Crassicauda* unidentified egg, **b** digenea egg of the genus *Ogmogaster*, **c** eggs identified as Diphyllobothriidae, **d**, **e** unidentified eggs. Scale bars **a** = 50 µm; **b** = 25 µm; **c** = 50 µm, **d**, **e** = 100 µm

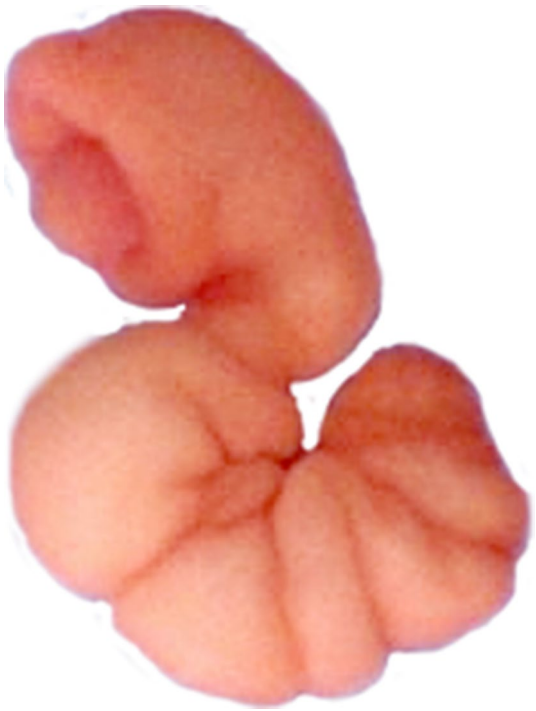

Fig. 4 Adult parasite found in the blue whale feces. (*Bolbosoma* sp.) Scale bar = 2.5 mm

In fin whale samples, an egg morphotype (42.5 ± 3.5 µm long, 35 ± 7 µm wide) was identified as *Crassicauda* (Nematoda), due to its oval shape, thick cuticle and size (36–57 µm long, 25–38 µm wide) [18, 51] (Fig. 3a). *Crassicauda* eggs have been reported with inner morulated material and with a larva inside [51]. *Crassicauda* eggs were found in only two fin whale feces. *Ogmogaster* sp. eggs were identified because they had two long polar filaments, even longer than the egg diameter (Fig. 3b). These eggs measured 19.2 ± 1.1 µm in length and 10.2 ± 0.5 µm in width, but the length including polar filaments reached 127.5 ± 9.5 µm. Eggs of the genus *Ogmogaster* were previously reported for *B. physalus and B. musculus* measuring between 15 and 35 µm in length, 7 and 20 µm in width and the total length of the egg including polar filaments between 100 and 560 µm. Eggs of the Diphyllobothriidae family (Fig. 3c) had barely visible operculum with average dimensions of 48.5 ± 12 µm in length and 37.5 ± 14.8 µm. An unidentified egg morphotype appeared several times in three fin whale feces samples, having an average diameter of 125 ± 19 µm length and 118 ± 18 µm width (Fig. 3d). It had a semi-spherical appearance with irregular borders (Fig. 3d). Finally, a spherical unidentified egg morphotype appeared in a fecal sample (140 µm) and had a thick cuticle of ~ 5 µm thickness (Fig. 3e). The mean and range of protists and ten types of helminth egg length and width found in feces of blue and fin whales are shown in Table 1.

Adult Parasites

A total of 38 complete adult parasites and other parasitic structures in different degrees of fragmentation were found in blue and fin whale samples. Average length of the intact adult specimens from blue whale feces was 8.1 ± 5.1 mm (n = 19) (Fig. 4). Optical microscopic and scanning electron microscopy observations showed the following: (1) anterior part of the trunk was bulbous, (2) lack of genital spines, (3) body free of spines (except for the proboscides and the bulbous) (Fig. 5a, b, d) and (4) proboscides with 25 hook rows (each with 5–7 hooks) (Fig. 5c, d). These morphological characteristics are consistent with acanthocephalans of the genus *Bolbosoma* (12–26 rows of hooks, 5–9 hooks per row) and in particular with *Bolbosoma hamiltoni* that has 24–26 rows with 7–8 hooks each [92]. However, adult size reported for this species is 50 mm long [92]. We did not collect any specimen of such length in the samples analyzed, although we do not rule out the possibility of adults with that size inside the body of the whale (not expelled in the feces).

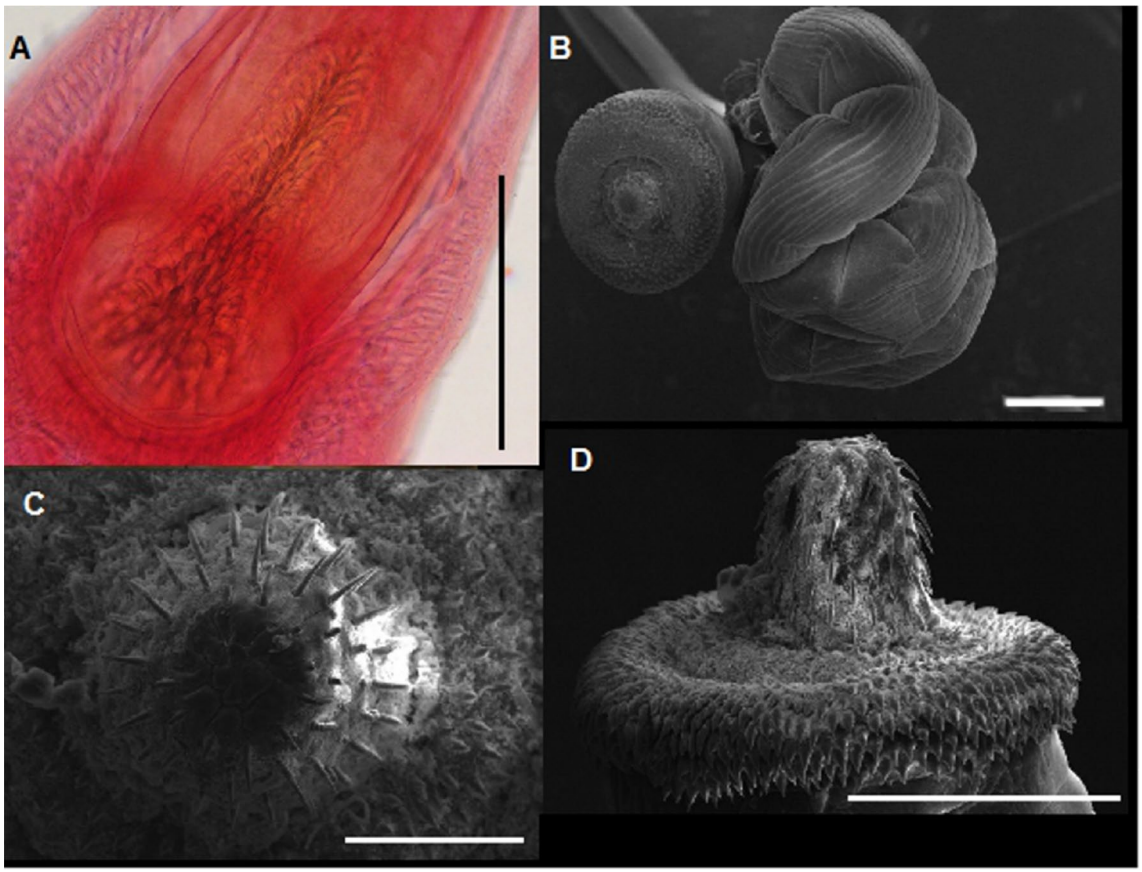

Fig. 5 Adult parasites found in blue whale feces identified as *Bolbosoma* sp. **a** proboscis invaginated in a receptacle with double-walled muscular sac. **b** free body spines. **c**, **d** proboscis with 25 rows of hooks and 5–7 hooks per row. Scale bars **a**, **b**, **d** = 1000 µm; **c** = 200 µm

The 19 adult acanthocephalans from fin whale feces measured on average 6.2 ± 0.7 mm length (Fig. 6). The specimens showed the proboscis receptacle had a double wall (Fig. 6a). The anterior part of the trunk was swollen considerably and was separated by a narrow constriction (Fig. 6b). Specimens had cylindrical proboscis with alternating longitudinal rows of hooks and both sexes lacked genital spines (Fig. 6c, d). All these morphological characteristics indicate that specimens collected from *B. physalus* feces are acanthocephalans of the genus *Bolbosoma*.

Prevalence

The prevalence of adult helminths in blue whales in feces was 35% ($n = 82$ analyzed fecal samples) and specifically the acanthocephalan identified as *Bolbosoma* sp. had a prevalence in feces of 14.6% (Fig. 5a). The prevalence of adult acanthocephalan *Bolbosoma* sp. in fin whales was 18.2% ($n = 11$ analyzed fecal samples) (Fig. 6a). The rest of the helminths found in blue whales' feces were fragmented; therefore, taxonomic identification was not possible. The helminth egg prevalence observed in blue whales with the McMaster chamber was 100% ($n = 88$ feces) compared to 61.2% ($n = 31$ feces) in fin whales. The prevalence per type of eggs varied from 3.2 to 12.9% for fin whales.

Helminth Egg Intensity in Feces

The mean and standard deviation of helminth egg intensity from blue whale was 443 ± 318 eggs/g (range: 100–1400 eggs/g, 95% confidence limits of the mean: 383–514 eggs/g). For fin whales mean and standard deviation of helminth egg intensity was 252 ± 327 eggs/g (range: 100–1300 eggs/g, 95% confidence limits of the mean: 105–400 eggs/g). The helminth egg intensity in blue whale was significantly larger than in fin whale feces (Mann–Whitney test $U = 372$, $p = 0.0001$).

Variation in Helminth Egg Intensity in Individual Blue Whales

From the 88 blue whale samples analyzed, 58 were from females, 14 from males and 16 from individuals of unknown

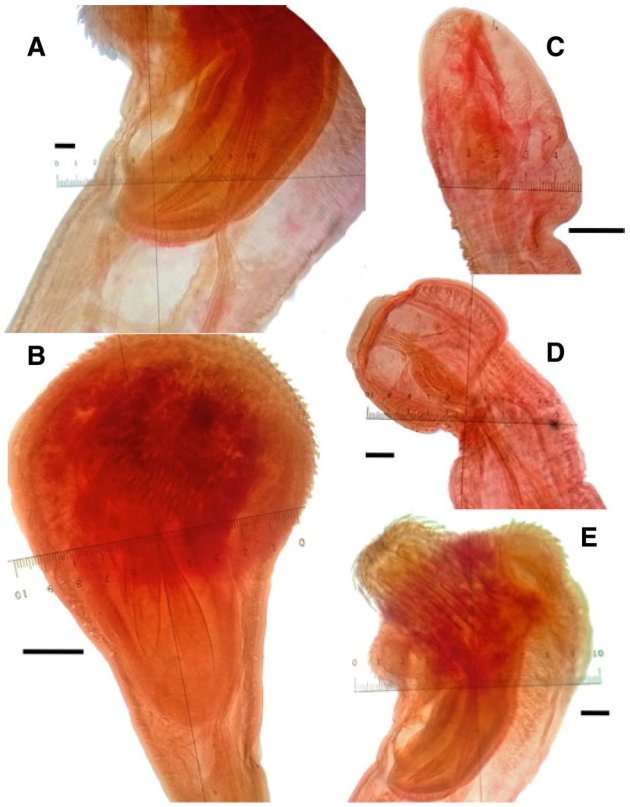

Fig. 6 Adult parasites found in fin whale feces identified as *Bolbosoma* sp. **a** proboscis receptacle with double-walled muscular sac. **b** anterior part of the trunk swollen considerably and separated by a narrow constriction. **c**, **d** both sexes without genital spines, **e** cylindrical proboscis with several hook in rows alternating considerably. Scale bars **a**, **d** = 50 µm**, b**, **c** = 200 µm, **e** = 200 µm

Fifty-one fecal samples were associated with individuals whose sexual maturity was estimated based on their total length. Immature blue whale individuals (15–21 m total length) had a mean intensity of 487 ± 356 eggs/g, ($n = 8$) and adults (22–28 m total length) had a mean intensity of 495 ± 351 eggs/g ($n = 43$).

A general linear model analysis of the variables to predict parasite egg load, using the combined effect of sexual maturity × reproductive status × sex × preservation × sampling years, explained 61% of the variance in the total parasite helminth egg load, but was not significant ($F_{5.28} = 1.280$, $p = 0.566$). This result implies that all the blue whale population sampled had the same probability to be parasitized with similar intensity.

Fourteen fecal samples (15.9%) from 13 blue whale individuals showed EPG counts above the upper limit of the overall standard deviation (761 eggs/g, Fig. 7). These outliers were considered as "wormy animals" indistinctly represented by individuals of both sex, different sexual maturity and female reproductive status (Fig. 7). Two fin whale samples out of 19 analyzed (10.5%) also showed EPG counts above the upper limit of the overall standard deviation (579 eggs/g).

Feces from 18 blue whale individuals were resampled more than once at different time scales. Low and high variability in the EPG counts were found between these replicates (Table 2). No statistical difference was found between the first and the last EPG count of all individuals sampled in different years, ($n = 10$, Wilcoxon test $W = 33.5$, $p = 0.19$); within the same year ($n = 12$, Wilcoxon test $W = 33.5$, $p = 0.96$), or on the same day ($n = 8$, Wilcoxon test $W = 19$, $p = 0.39$). Some of these individuals were "wormy animals"; thus the results here indicate that the "wormy" status is likely not permanent (Table 2).

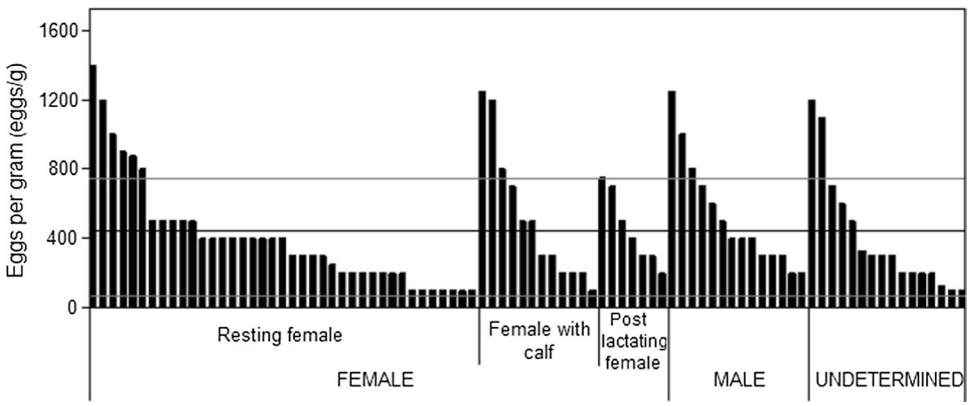

Fig. 7 Eggs per gram counts of individual blue whales. Black line: Mean intensity; Gray line: standard deviation. Wormy animals are specimens with eggs per gram counts higher than the standard deviation (upper gray horizontal line)

sex. Mean intensity was 434 ± 317 eggs/g for females and 525 ± 313 eggs/g for males. Based on the sighting histories, 58 samples were associated with females of known reproductive state. Mean egg intensity was 520 ± 391 eggs/g for lactating females ($n = 12$), 450 ± 210 eggs/g for post-lactating females ($n = 7$) and 405 ± 310 eggs/g for resting females ($n = 39$).

Table 2 Photo-identified blue whales whose feces were resampled in several times between 1996–2014 in the southeast of the Gulf of California

ID	Sex	No. feces	No. years	Sampling years (EPG per year)			EPG
				1st sampling year	2nd sampling year	3rd sampling year	Mean (±STD)
12	M	5	3	2007 (400)	2010 (300)	2014 (300, 400, 400)	360 (±54)
124	F	5	3	2008 (200)	2009 (100, 300, 200)	2010 (500)	260 (±151)
65	F	4	2	2008 (400, **1200**)	2009 (400, 200)	–	550 (±443)
59	F	2	2	1999 (700)	2009 (300)	–	500 (±282)
192	F	2	2	2000 (100)	2002 (500)	–	300 (±282)
249	M	2	2	2001 (200)	2007 (200)	–	200 (±0)
398	F	2	2	2007 (**1400**)	2009 (100)	–	750 (±919)
41	F	2	2	2010 (100)	2011 (200)	–	150 (±70)
75	F	2	2	2011 (**1200**)	2014 (100)	–	650 (±777)
667	F	2	2	2011 (200)	2013 (500)	–	350 (±212)
119	F	2	1	2001 (500, 300)	–	–	400 (±141)
251	F	2	1	2008 (750, 300)	–	–	525 (±318)
253	F	2	1	2009 (250, 200)	–	–	225 (±35)
267	F	2	1	2009 (100, 400)	–	–	250 (±212)
298	F	2	1	2014 (300, 300)	–	–	300 (±0)
334	F	2	1	2009 (200, 400)	–	–	300 (±141)
477	F	2	1	2009 (**1000**, 400)	–	–	700 (±424)
536	F	2	1	2013 (500, **900**)	–	–	700 (±282)

Bold font = individuals with egg intensities larger > one standard deviation (outliers)

EPG Egg per grams of feces are shown between parenthesis

Discussion

Interspecific Comparison of Parasites Between Baleen Whale Species

We systematically compared the prevalence and intensities of helminthes (adults and eggs) from feces of blue whales that annually migrate from California Current System (summer-autumn) to the Gulf of California (winter-spring) [8, 27] and the resident and highly isolated population of fin whale from the Gulf of California [9]. We concluded that there was similar diversity of helminths in fin whales to that in blue whales (considering the current level of precision in the taxonomic identification), but blue whale feces showed higher prevalence and mean intensities of helminth parasites than fin whale feces. This was clearly observed in helminth egg counts with a mean of 444 eggs/g and a prevalence of 100% for blue whale compared with a mean of 252 eggs/g and prevalence of 61% for fin whale feces. Fin whales were parasitized with four different parasite taxa (Nematoda, Cestoda, Trematoda and Acanthocephala) compared with only three taxa (Acanthocephala and Cestoda, and Nematoda) in blue whales. This contrasts with overall helminth diversity known for these two baleen whale species [24]. Such parasitological differences of trophic-transmitted parasites would be expected from whale species with different morphological specializations, hydrodynamic performance, ecological niche and/or feeding strategies [91]. These two large baleen whales also have similar short diving behavior and high energetic cost when foraging by lung feeding [14, 32]. However, those prevalence and egg intensity differences were not expected from two species that cohabit during winter–spring in the Gulf of California, where they feed on dense krill aggregations of *N. simplex* [19, 26, 82] and lantern fish [41]. There is, however, evidence that these species feed on distinct trophic level during summer–fall, which coincide with the stomach analysis of commercial captures from the North Pacific [22, 43, 66]. Fin whales shift their diet to higher trophic prey during summer–autumn [28] when krill abundance considerably decreases [11, 84] whilst blue whales feed on temperate krill species (mostly *Thysanoessa spinifera*) off California [21, 67].

Baleen whales require consumption of abundant prey that form swarms and schools, such as euphausiids and small pelagic fish. Euphausiids interact with 18 types of symbionts, including helminths that can be trophically transmitted to baleen whales [33, 34]. *Nyctiphanes simplex*, the most abundant and common prey of both whale species in the Gulf of California, is infected with seven of helminth species (Cestoda 98.8%, Acanthocephala 0.56%, Trematoda 0.37%, Nematoda 0.18%), while *N. difficilis* is known to be parasitize with one trematode species [33, 63]. In California, the

dominant krill *T. spinifera* and *Euphausia pacifica* are parasitized with the nematode *Anisakis simplex* [81]. Because Myctophidae DNA was found in feces of both baleen whale species in the the Gulf of California [41], several of the Myctophidae parasites could be found in the whales' feces. Myctophids from the California Current System are parasitized with Monogenea [70], *Diphyllobothrium* (Cestoda) [47, 48], Digenea and Nematoda [58]. A dietary DNA metabarcoding of 18 feces from blue whales from the Northern Indian Ocean showed that they fed mostly (87%) on deep-sea pelagic sergestid shrimps; but were only parasitized with Acanthocephala [20].

Body size is one of the most important determinants of metabolic rate, digestive efficiency and total caloric requirements [1, 72, 80]. Blue whale and fin whale are the two largest species of mysticetes and need to consume high biomass of prey [32]. Our blue whale information did not show significant parasitic prevalence or intensity correlation with age class (juveniles vs adults). Infection of krill swarms is a binomial variable (with infected or not infected krill individuals), with the result that any blue whale individual, independently of the sex, age or reproductive status has the same probability to ingest infected or non-infected krill swarms. This probably leads to a permanent infection with helminths that found the conditions appropriate for their reproduction, resulting in a continuous deposit of eggs in baleen whale feces. Here, we argue that differences in diet compositions of the whale species likely explain differences in prevalence and taxonomic composition of helminth eggs and adults in both host species.

From all the parasites observed in blue whale and fin whale feces in the present study (acanthocephalan *Bolbosoma,* nematode *Crassicauda*, cestode *Diphyllobotrium, and trematode Ogmogaster,* Table 1) only *Bolbosoma* has been observed parasitizing krill in the Gulf of California [33, 63] or other krill species around the world [34]. In the North Atlantic, *Nyctiphanes couchii* are intermediate host of *Bolbosoma balanae* [35]. *Bolbosoma* species have been widely reported in baleen whales, including blue whales [24, 60, 61] and fin whales [79]. Particularly, Rice [76] reported *Bolbosoma nipponicum* and *Crassicauda crassicauda* from two individual blue whales caught off California.

The eggs identified at genus or family level in the present study were recovered directly from compact stools (see [23]) that decrease the possible mix of free-swimming parasites contained in surface seawater. As expected, adult parasites were less prevalent than parasite eggs in the baleen whales' feces. This is because the eggs are released in the feces as part of the parasite life cycle, while adult presence in feces implies a mortality event for the parasites inhabiting the gastrointestinal tract. Our observed adult *Bolbosoma* sp. prevalence of 14.6% in feces of blue whale and 18.2% in fin whale in the Gulf of California is similar to 18.8% of Acanthocephala observed from dietary DNA metabarcoding of fecal sample analysis of blue whale from Sri Lanka [20]. This is of general ecological interest since two blue whale populations that predominantly feed on distinct pelagic crustaceans, euphausiids in the Gulf of California and sergestid shrimps in the region off Sri Lanka, have similar Acanthocephala prevalence.

Population Structure and Parasites

The parasitological record of stranded cetaceans has provided valuable but partial information about taxonomy of parasites and types of diseases [7, 18, 31, 39, 59, 60, 73, 83]. However, for monitoring purposes of wild populations, information obtained exclusively from stranded animals cannot be used as baseline because they do not represent a "normal" sample of individuals of the population [74].

There are few studies describing the parasite load from stranded blue and fin whales. The available information for blue whale is poorly updated, mostly qualitative and often was not systematically recorded [40, 55, 60, 61]. The same is true for fin whale parasite species composition and parasitic load [51, 59, 68]. The observation of the Cestoda "*Diplogonoporus"* sp. eggs (currently known as *Diphyllobothrium* [90] in our study) matches three previous reports from stranded blue whales from the Atlantic and Arctic oceans [30, 49, 56]. *Diphyllobothrium* eggs found in feces of baleen whales match in morphology but not in morphometry with eggs obtained from the uterus of *Diphyllobothrium balaneopterae* infecting a human [15].

Our quantitative results were restricted to intensity (egg counts identified only to the helminth level) and prevalence (adults *Bolbosoma* sp., unidentified structures of parasites and per type of eggs in fin whale feces). Taxonomic information for eggs of *Bolbosoma* is limited and adult specimens are needed to identify them with more precision using morphological and molecular information. However, molecular analyses have not yet improved the precision of the taxonomic identification of baleen whale parasites because molecular scatology techniques so far only reach taxonomy at the phylum level (Acanthocephala) [20, 37, 38]. This lack of information contrasts with the comparatively large taxonomic knowledge of helminth parasites that infect domestic animals.

Studies on parasitism in free-ranging animals through feces analysis vary widely in their sample size and are typically not linked to known biological features of the sampled individuals [20, 36–38, 50, 53]. We explored the possible effect of sex, sexual maturity and female reproductive status on parasite egg load for the first time in any cetacean species worldwide. However, our relatively large blue whale sample size integrated over 18 years (1996–2014) did not show

significant differences in any of the intraspecific comparisons. Therefore, we rejected the hypothesis of differences in egg parasite load as a function of host sex, age or reproductive status. This conclusion implies that all blue whales were parasitized and showed statistically similar helminth egg intensities, independently of their sex, reproductive status or sexual maturity. This likely also applies to fin whale, but is not statistically tested due to the lack of linked feces/individual fin whale information. We initially expected significant sex and size differences because some parasitological studies on terrestrial mammals, with considerably smaller body and shorter life span than baleen whales, showed that the males or lactating female's condition could be predisposing factors that increase parasite loads [13, 45, 64, 87, 93].

The McMaster technique, with various modifications, has been widely used in small ruminants, several exotic species, and humans [10]. Fin whales had significant lower mean EPG counts (252 eggs/g, range = 100–1300 eggs/g) than the blue whales (443 egg/g, range = 100–1400 eggs/g) (Mann–Whitney test $U = 372$, $p = 0.0001$). The mean and maximum EPG count found in both baleen whale species were smaller than the wide range of EPG counts observed in wild donkeys (100–9200 eggs/g) [88] and wild boar (1450–102,000 eggs/g) [36]. It is expected that a portion of the individuals in a population have a high parasite load [62]. In chimpanzees, only 4% of the individuals showed high EPG counts. After resampling, outliers appeared only once in multiple consecutive samples from a single individual [50]. The same phenomenon occurred in our study where 13 blue whale individuals had EPG counts higher than the upper standard deviation (14.8%; outliers > 761 eggs/g) (Table 2). Several of these individuals were resampled, but most showed intensity values near the population mean. Thus, only five out of 44 feces from resampled blue whale individuals had EPG above one standard deviation (Table 2). This observational evidence suggests that, despite the fact that all blue whales were parasitized (100% prevalence), the "wormy animal" status was a low frequency condition (< 11%). Only two fin whale individuals had higher EPG values than the upper standard deviation (10.5%; outliers > 579 eggs/g); a similar proportion of those observed in blue whales.

The EPG variability observed in the feces of different blue and fin whale individuals could be attributed to several factors, some of them frequently found in other mammals. These include the following: depression of the immune system [42], hormonal fluctuations [44, 45, 65] and factors related to prey, such as abundance and patchy distribution of parasites among euphausiid swarms [32–34, 63]. The fecundity rate of helminths and intestinal transit times of the host also can influence the egg intensities [6, 89]. This should be evaluated in both baleen whale species. There was no significant variation in blue whale EPG counts in consecutive fecal samples collected from the same individual during the same day. This agrees with results from feces of elephants (*Elephas maximus*) in semi-captivity [53]. We found no significant difference in intra or inter-annual re-sampling events of the same blue whale individual. For example, two blue whale individuals (ID-124 and ID-12) were resampled several times without variations in EPG counts (Table 2). Therefore, observed egg intensities could be considered "normal" helminth egg load.

In view of the complexity of assessing cetacean health, the mean egg parasite intensity, along with other health parameters such as pathogen load in exhaled breath condensate [2], UV effect on skin [57] and general stress using glucocorticoids concentration in feces [85] will be useful complementary approaches for monitoring the general health of blue and fin whales.

Conclusions

This study is the first quantitative assessment of parasite loads in free-ranging cetaceans in the world and introduces a new baseline for monitoring health of blue whales and fin whales. Blue whale individuals sampled in the Gulf of California during winter showed 100% prevalence of helminth eggs in their feces and showed similar helminth egg intensity independently of sex, age class, reproductive status and at several time scales (same day, same year and between years). This evidence suggests that blue whales are permanently parasitized with helminths compared to the low population prevalence (61%) and intensities and higher diversity of helminths in fin whales, perhaps related with distinct feeding habits. Adults of Acanthocephala *Bolbosoma* spp. and eggs of Trematoda, Nematoda and Cestoda were the taxonomic groups found in the fecal samples of both baleen whale species. Future molecular analyses will hopefully increase our knowledge and precision about parasite diversity, intensity and prevalence in these baleen whales, although three previous molecular studies have not been taxonomically precise as the morphologic identifications carried out in the present study.

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