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FISH PARASITOLOGY - ORIGINAL PAPER

Distribution patterns of two species of *Corynosoma* (Acanthocephala: Polymorphidae) in fishes from Southwestern Atlantic

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Abstract

Corynosoma australe and *C. cetaceum* are the most frequently reported acanthocephalans in fish from the Argentine Sea, particularly in central and northern areas. Their definitive hosts are otariids and odontocete cetaceans, respectively. The low specificity of these larvae, in combination with high infective capability and long survival periods in fish, make them potentially good biological markers for stocks and other biological features of their fish hosts. In order to determine the distribution patterns of these species and their determining factors, a large dataset composed by newly collected fish samples, published and unpublished data from previous studies by the authors in the region were analysed in relation to host and environmental variables. The complete dataset comprised a total of 5084 fish, belonging to 29 species distributed in 21 families and 9 orders. Host size and trophic habits arose as the main determinants of abundance for both species of *Corynosoma*, showing higher abundances on larger fish and on higher trophic levels, as it is usual for trophically transmitted parasites. Biogeographic province and depth (indirectly representing the temperature of water) were the main drivers of the spatial distribution, displaying a latitudinal pattern associated to the temperature clines created by the interaction of Malvinas and Brazil currents, determining a decrease in abundance southwards and towards the deeper areas. No patterns were found regarding the distribution of definitive hosts. The knowledge of these distribution patterns of *Corynosoma* spp. in fish at regional scale, as well as of their causes, provides useful information to design management and conservation policies thus contributing to maintain the full and sustainable productivity of fisheries.

Keywords *Corynosoma australe* · *Corynosoma cetaceum* · Distribution · Fishes · Biological tags

Introduction

Polymorphid acanthocephalans of the genus *Corynosoma* Lühe, 1909 are common components of marine ecosystems, where they reproduce in fish-eating mammals and birds, using amphipods and fishes as intermediate and paratenic hosts, respectively (Aznar et al. 2006). In fishes from central and northern areas of the Argentine Sea, two species, *Corynosoma australe* Johnston, 1937 and *C. cetaceum* Johnston and Best, 1942, are frequently reported (Cantatore and Timi 2015). In this region, the definitive hosts of *C. australe* are the otariids *Arctocephalus australis* Zimmermann, 1783 and *Otaria flavescens* Shaw, 1800 (George-Nascimento and Marín 1992; Sardella et al. 2005; Aznar et al. 2004, 2012), whereas the main definitive hosts of *C. cetaceum* are odontocete cetaceans *Pontoporia blainvillei* (Gervais and D'Orbigny, 1844), *Delphinus delphis* Linnaeus, 1758, *Tursiops truncatus* (Montagu, 1821) and *Phocoena spinipinnis* (Burmeister, 1865) (Hernández-Orts et al. 2015). These two larval acanthocephalans have low host specificity, being widely distributed across fish species in the southern Southwest Atlantic (Sardella et al. 2005; Santos et al. 2008; Hernández-Orts et al. 2015).

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In the Argentine Sea, juvenile *Corynosoma* have been identified among the best biological tags in diverse studies on fish stock discrimination (Cantatore and Timi 2015; Alarcos et al. 2016; Canel et al. 2019). A precise assessment of resources abundance in space and time is a prerequisite for the implementation of management and control measures, to restore stocks and to maintain the full and sustainable productivity of fisheries (Begg and Waldman 1999). *Corynosoma australe* and *C. cetaceum* share a combination of desirable characteristics as biological tags that make them excellent candidates for further studies to distinguish fish stocks in the region. First, they appear as larval stages of long permanence in fishes (Lester and MacKenzie 2009). Second, they have low specificity, which makes them potential markers for any fishery resource and, third, they show recurrent distribution patterns in different fish species in the Argentine Sea, such as a decrease in parasite burdens with increasing latitude (Cantatore and Timi 2015). Both acanthocephalans have also contributed to the identification of zoogeographical regions in the Southwest Atlantic in multivariate analyses of fish parasite assemblages (Lanfranchi et al. 2016; Braicovich et al. 2017; Soares et al. 2018). Such distribution patterns are congruent with the environmental conditions of the study region, mostly related with the temperature cline characteristic of the region (decreasing southwards) (Hoffmann et al. 1997; Piola et al. 2010), although water temperature also decreases with depth at lower latitudes (Acha et al. 2004; Piola et al. 2010). However, a combination of several interacting variables, environmental and those related to the biology of the hosts, could affect the distribution of *Corynosoma* spp., as been recorded for other parasites in the region (Irigoitia et al. 2018). The identification of these variables, and the resulting distribution patterns of *Corynosoma* spp., will help improving the knowledge of host population structure for many valuable resources under exploitation, and will provide predictive power to their use as biological tags.

In this work, we analyse a large database composed by newly collected *Corynosoma* spp. from several fish species at different spatial scales, complemented by unpublished data from studies carried out previously and those published by the authors in the region. Therefore, the aim of this work is to determine the spatial distribution patterns of *Corynosoma* spp. across fish species in the Argentine Sea and their main drivers.

Materials and methods

General procedures

A total of 1675 fish belonging to 12 species, 10 families and 6 orders were examined for juvenile acanthocephalans (Table 1). This included 32 samples, of at least 20 specimens each, from different localities of the Argentine Sea, ranging from the Argentine-Uruguayan Common Fishing zone to central Patagonian waters (35.00–49.25° S), caught between 1990 and 2018. Fishes were either kept fresh or deep frozen in plastic bags at − 18 °C until examination. After thawing, each fish was measured for total length (TL), dissected and examined for parasites. Body cavity, musculature and viscera (stomach, intestine, liver, swim bladder, spleen, heart, gonads and mesenteries) were examined with the aid of a stereoscopic microscope. Juvenile acanthocephalans were recorded and identified.

Quantitative analyses

Prevalence and mean abundance for each parasite species in each sample were calculated following Bush et al. (1997). Data on prevalence and mean abundance of juvenile acanthocephalans in fishes from the region were obtained from the literature. These were restricted to those articles published by members of the research team to ensure taxonomic consistence (Table 2). This way, by adding 63 additional samples to the unpublished data, the analysed dataset was extended to 5084 fishes belonging to 29 species, 21 families and 9 orders (Electronic supplementary table). The presence of other long-lived larval parasites (anisakids and cestodes) in the samples was also recorded in order to comparatively analyse the host range of the most common parasites in the region.

Statistical analyses

The effect of six variables on the abundance of *C. australe* and *C. cetaceum* in the Southwest Atlantic was evaluated using Generalised Linear Mixed Models (GLMMs) using a Compound Poisson distribution with log link function. The selected variables were host total length (L), biogeographic province of origin (BP)—a factor with three levels: Argentine province, Ecotonal zone and Magellanic province, trophic level (TL), diet (D)—a factor with four levels: fish, fish and invertebrates, invertebrates and plankton—depth (DE) and habitat (H)—a factor with three levels: pelagic, demersal and benthic. These variables were treated as fixed effects while host species (HS) was incorporated as a random effect. Treating host species as random effect introduces a correlation structure between all observations from the same host species. Initial data exploration showed no correlation between the explanatory variables, which corresponds to the independent variables assumption (Zuur et al. 2009). For these analyses, migratory fish species alternating between different regions or masses of water were excluded to avoid misinterpretation of results by assigning to a given locality, parasite loads acquired in other region, with different environmental and ecological conditions. Species identified as migratory were *Engraulis anchoita* Hubbs and Marini, 1935, that

Table 1 Composition of samples of fish hosts in the Argentine Sea, along with data on parasite loads

Host species	NHE	L (cm)	BP	DE (m)	H	D	TL	*Corynosoma australe*		*Corynosoma cetaceum*	
								P	MA ± SD	P	MA ± SD
Anchoa marinii 1	136	9.8	A	10	Pel	P	3.4	0.0	0.0	0.0	0.0
Anchoa marinii 2	23	9.5	A	20	Pel	P	3.4	0.0	0.0	0.0	0.0
Bassanago albescens	27	65.3	A	200	Ben	I	3.9	22.2	0.3 ± 0.9	11.1	0.1 ± 0.3
Odontesthes argentinensis	26	29.1	A	10	Pel	P	3.7	80.8	7.0 ± 6.7	0.0	0.0
Odontesthes incisa	66	8.9	A	50	Pel	P	3.4	3.0	0.1 ± 0.6	0.0	0.0
Patagonotothem ramsayi	48	25.6	E	60	Dem	I	3.5	35.4	0.8 ± 1.5	0.0	0.0
Percophis brasiliensis 1	23	54.7	M	50	Dem	F	4.2	73.9	3.6 ± 4.5	0.0	0.0
Percophis brasiliensis 2	47	37.3	A	40	Dem	F	4.2	89.4	8.8 ± 12.7	59.6	1.9 ± 3.6
Pomatomus saltatrix	41	42.4	A	25	Pel	F	4.5	85.4	17.3 ± 39.2	12.2	0.2 ± 0.5
Cynoscion guatucupa 1	57	7.0	A	20	Dem	P	3.3	3.5	0.04 ± 0.2	0.0	0.0
Cynoscion guatucupa 2	61	45.5	A	20	Dem	FI	4.2	83.6	33.7 ± 98.2	52.5	3.03 ± 8.8
Cynoscion guatucupa 3	121	8.4	A	20	Dem	P	3.3	2.5	0.03 ± 0.2	0.0	0.0
Cynoscion guatucupa 4	25	44.3	A	115	Dem	FI	4.2	100	15.0 ± 13.3	24	0.48 ± 1.1
Cynoscion guatucupa 5	154	22.7	A	115	Dem	I	3.5	25.9	0.6 ± 1.3	5.2	0.05 ± 0.2
Cynoscion guatucupa 6	54	20.9	A	110	Dem	I	3.5	9.3	0.1 ± 0.3	0.0	0.0
Cynoscion guatucupa 7	37	46.8	A	20	Dem	FI	4.2	100	22.0 ± 20.4	37.8	0.62 ± 1.1
Cynoscion guatucupa 8	34	9.2	A	20	Dem	P	3.3	0.0	0.0	0.0	0.0
Cynoscion guatucupa 9	59	14.8	A	20	Dem	I	3.5	52.5	1.6 ± 2.4	10.2	0.1 ± 0.3
Cynoscion guatucupa 10	60	11.5	A	20	Dem	I	3.3	5.0	0.05 ± 0.2	1.7	0.02 ± 0.1
Cynoscion guatucupa 11	77	18.4	A	20	Dem	I	3.5	27.3	0.7 ± 1.5	12.9	0.2 ± 0.6
Cynoscion guatucupa 12	36	49.0	A	20	Dem	FI	4.2	100	86.1 ± 82.0	69.4	5.6 ± 8.8
Cynoscion guatucupa 13	55	35.2	A	20	Dem	FI	3.7	78.2	5.9 ± 16.6	0.0	0.0
Cynoscion guatucupa 14	70	21.4	A	20	Dem	I	3.5	35.7	0.8 ± 1.45	12.9	0.2 ± 0.5
Cynoscion guatucupa 15	20	34.8	A	20	Dem	FI	4.2	85	4.45	50	0.65
Pagrus pagrus	26	27.9	A	75	Dem	FI	3.9	84.6	29.8 ± 36.5	3.9	0.04 ± 0.2
Congiopodus peruvianus 1	30	21.8	M	157	Dem	I	3.3	0.0	0.0	0.0	0.0
Congiopodus peruvianus 2	26	24.9	M	114	Dem	I	3.3	0.0	0.0	0.0	0.0
Helicolenus lahillei 1	44	19.0	E	64	Ben	I	4.2	43.2	0.8 ± 1.2	0.0	0.0
Helicolenus lahillei 2	79	17.5	E	89	Ben	I	4.2	41.8	0.7 ± 1.1	0.0	0.0
Merluccius hubbsi 1	50	41.8	M	80	Dem	F	4.2	42.6	0.7 ± 1.3	0.0	0.0
Merluccius hubbsi 2	31	44.7	M	80	Dem	F	4.2	16.1	0.2 ± 0.4	0.0	0.0
Merluccius hubbsi 3	32	40.5	M	80	Dem	F	4.2	12.2	0.2 ± 0.5	0.0	0.0

NHE, number of hosts examined; *L*, total length; *PB*, biogeographic province (argentine (A), ecotonal (E), Magellanic (M)); *DE*, depth; *H*, habitat (pelagic (Pel), demersal (Dem), benthic (Ben)); *D*, diet (fish (F), fish and invertebrates (FI), invertebrates (I), plankton (P)); *TL*, trophic level; *P* prevalence; *MA* ± *SD*, mean abundance ± standard deviance

alternates between coastal and slope (subantarctic) waters (Angelescu 1982); *Trachurus lathami* Nichols, 1920, *Umbrina canosai*, Berg, 1895 and *Pomatomus saltatrix* Linnaeus, 1766 which migrate from southern Brazil during warmer seasons (Saccardo and Katsuragawa 1995; Haimovici and Krug 1996; Haimovici et al. 2006) and *Odontesthes smitti* that moves from north Patagonian gulfs to the north of the Argentine Sea during winter (Carballo et al. 2012).

Trophic level was obtained from Froese and Pauly (2018) for each host species. Data on biogeographic province (as latitude and longitude) and depth were recorded for those specimens caught during research cruises; in the case of commercial catches, the depth was estimated from the region of capture in a bathymetric map. For those samples composed by fish caught in more than one trawl at sites close to each other, averaged depth values were used. Data on host habitat and diet were obtained from Cousseau and Perrotta (2004).

For each parasite species—*C. australe* and *C. cetaceum*—a global model, containing all explanatory variables to be evaluated, and a set of alternative candidate models, considered a priori biologically meaningful, was selected among all

Table 2 Composition of samples of fish hosts in the Argentine Sea, along with data on parasite loads from previously published studies in the Southwestern Atlantic

Host species	NHE	Number	L (cm)	BP	DE (m)	H	D	TL	Source	*Corynosoma australe*		*Corynosoma cetaceum*	
										P	MA	P	MA
Engraulis anchoita	671	4	14.8–16.3	A-E	30–80	Pel	P	2.5	Timi (2003)	0.0–18.2	0.0–0.05	0.0	0.0
Conger orbignianus	50	1	80.7	A	70	Ben	F	3.7	Timi and Lanfranchi (2013)	86.0	95.4	44.0	1.1
Odontesthes smitti	177	5	21.7–28.3	E-A	10–30	Pel	P	3.6	Carballo et al. (2012)	3.0–54.0	0.03–1.1	0.0	0.0
Merluccius hubbsi	344	4	38.7–40.5	A-E-M	90–170	Dem	F	4.2	Sardella and Timi (2004)	0.0–27.3	0.0–1.4	0.0	0.0
Urophycis brasiliensis	62	1	36.6	A	30	Dem	I	3.9	Pereira et al. (2014)	83.9	6.6	43.6	1.6
Raneya brasiliensis	183	4	23.0–24.7	A-E	20–80	Dem	I	3.6	Vales et al. (2011)	86.7–100	5.1–73.5	0.0–3.9	0.0–0.04
Trachurus lathami	223	2	19.5–20.0	A	30–40	Pel	P	4	Braicovich et al. (2012)	88.5–91.0	8.4–8.9	9.0–9.7	0.3–0.1
Nemadactylus bergi	100	5	32.4–36.2	A	30	Dem	I	3.2	Rossin and Timi (2010)	93.8–100	12.0–25.5	2.9–18.8	0.03–0.2
Mullus argentinae	75	1	19.5	A	30	Ben	I	3.5	Lanfranchi et al. (2009)	38.7	0.67	4.00	0.05
Percophis brasiliensis	412	9	49.4–56.6	A-E-M	20–50	Dem	F	4.2	Braicovich and Timi (2008), Braicovich and Timi (2010) and Braicovich et al. (2017)	75.0–100	5.5–174.7	25.0–78.0	1.4–5.9
Pinguipes brasilianus	310	7	32.5–37.1	A-E	20–100	Dem	I	3.5	Timi et al. (2009)	50.0–100	1.6–34.1	0.0–6.7	0.0–0.1
Pseudopercis semifasciata	100	3	67.2–71.2	A-E	20–30	Dem	FI	3.9	Timi and Lanfranchi (2009a)	90.0–100	5.5–79.9	2.0–85.0	1.0–13.3
Dules auriga	178	6	10.7–13.3	A	20–60	Ben	I	3.7	Braicovich and Timi (2015)	60.0–98.1	1.8–8.3	0.0–6.7	0.0–0.1
Pagrus pagrus	38	1	39.1	A	80	Dem	FI	3.9	Soares et al. (2018)	100	200.1	0.0	0.0
Paralichthys isosceles	51	1	27.9	A	60	Ben	I	4	Alarcos and Timi (2012)	92.2	14.7	0.0	0.0
Paralichthys patagonicus	51	1	35.2	A	60	Ben	I	3.9	Alarcos and Timi (2012)	94.1	6.4	74.51	2.6
Xystreurys rasile	133	3	29.2–32.1	A	10–50	Ben	I	3.3	Alarcos and Timi (2013)	53.0–90.0	1.7–9.3	2.0–15.0	0.04–0.4
Prionotus nudigula	101	1	19.7	A	20	Dem	I	4.2	Timi and Lanfranchi (2009b)	85.1	9.2	10.9	0.1
Zenopsis conchifer	44	1	27.4	E	100	Ben	F	4.5	Lanfranchi et al. (2016)	20.4	1.5	2.3	0.02
Umbrina canosai	106	3	28.9–37.2	A	20–60	Dem	I	3.9	Canel et al. (2019)	100	70.9–368	22.2–35.9	0.4–1.7

NHE, number of hosts examined; *N*, number of samples; *L*, total length; *PB*, biogeographic province (argentine (Arg), ecotonal (Eco), Magellanic (Mag)); *DE*, depth; *H*, habitat (pelagic (Pel), demersal (Dem), benthic (Ben)); *D*, diet (fish (F), fish and invertebrates (FI), invertebrates (I), plankton (P)); *TL*, trophic level; *P*, prevalence; *MA*, mean abundance possible models. In both cases, the response variable was the mean abundance of parasites. The fit of each global model (one for *C. australe* and one for *C. cetaceum*) was assessed graphically through quantile-quantile plots and residuals versus fitted values plots.

The information theoretic (IT) model comparison method was used, in order to select the best model of each set which allows evaluating simultaneously several competing models (Burnham and Anderson 2002). To identify the best model, it is necessary to trade off model bias against model precision; this was achieved by using Akaike Information Criterion adjusted for small samples (AIC_c) (Symonds and Moussalli 2011). The models were ranked by AIC_c, and the model with the lowest AIC_c was considered the best from each set. Then, the Δ_i were computed as the difference between the best model and each of the candidate models and the Akaike's weight (w_i) was calculated to obtain the relative likelihood, of each fitted model, of being the best among the set of candidates (Johnson and Omland 2004).

In case the best model showed a high degree of uncertainty ($w_i < 0.9$), model averaging was performed on the subset of models whose accumulated weights summed 0.9. This was made in order to estimate the magnitude of the effect of each predictor in explaining the variation of the response. The parameter estimates (β), standard errors (SE) and confidence intervals (CI) were recalculated after averaging and new Akaike's weights (w'_i) were recomputed (Burnham and Anderson 2002; Symonds and Moussalli 2011).

The relative importance of each variable was estimated adding the recomputed Akaike weights of all the models where the variable of interest occurs (Burnham and Anderson 2002).

All the statistical analyses were performed with the statistical software R, version 3.5.1 (R Development Core Team; www.r-project.org/) using the package CPLM version 0.7-7 (Zhang 2013).

Results

General results

Juvenile of both species of *Corynosoma* were found free or encapsulated in the body cavity on most fish species, being *C. australe* occasionally found in stomach and intestine serosa of some host species. No parasites were found in musculature.

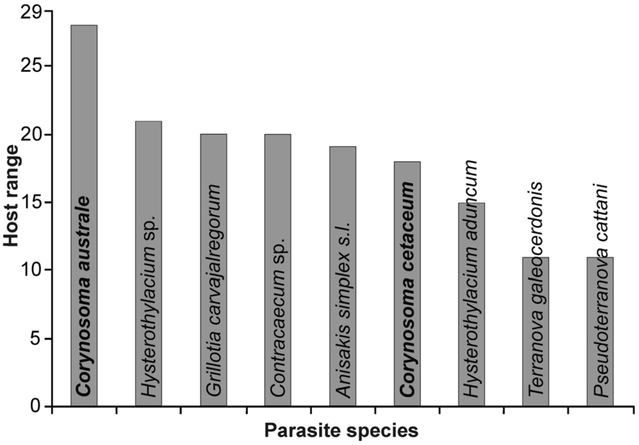


Fig. 1 Host range (number of host species) of long-lived and low specific larval parasites of fish (restricted to those with host range > 10 among the 29 considered fish species) in the Southwestern Atlantic

C. australe showed the highest host range among long-lived parasites of fishes in the study region (Fig. 1) parasitising 28 of the 29 fish species considered, excepting *Anchoa marinii* Hildebrand 1943. This species was also found in *Congiopodus peruvianus* (Cuvier, 1829) at very low abundance (a single worm in a single host) at two localities (41° 34′ S–58° 32′ W and 47° 13′ S–63° 15′ W) which were not included in the analyses due to the small sample size. On the other hand, the distribution of *C. cetaceum* was more restricted, being present in 18 of the considered host species (Fig. 1).

The prevalence of both species was variable across samples (Table 1); *C. australe* was absent only in samples of small coastal fishes (*A. marinii* and some juvenile of *Cynoscion guatucupa* (Cuvier, 1830)) and southern samples of

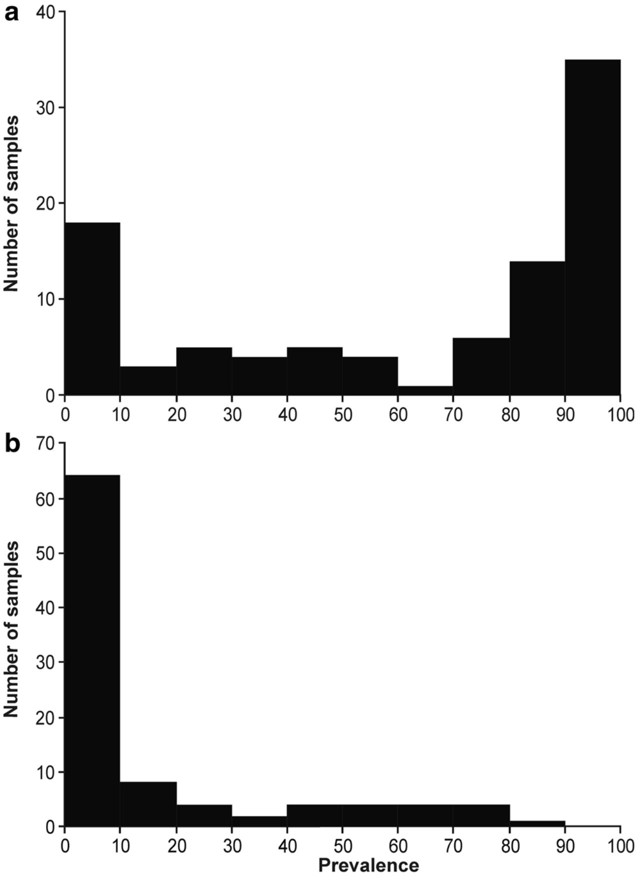


Fig. 2 Frequency of values of prevalence of *Corynosoma australe* (**a**) and *C. cetaceum* (**b**) across 95 fish samples in the Southwestern Atlantic

Merluccius hubbsi Marini, 1933 and *C. peruvianus*. Considering both, present (Table 1) and published (Table 2) data, this species was frequently present at high prevalence (Fig. 2a); whereas the prevalence of *C. cetaceum* was very low in a considerable proportion of the samples (Fig. 2b).

Corynosoma australe was present at low average abundance in most samples (Fig. 3a), although a group of them showed high values (60–200 parasites per fish) for this parameter, being represented by fish species (*Conger orbignyanus* Valenciennes, 1837, *C. guatucupa*, *Pagrus pagrus* Linnaeus, 1758, *Percophis brasiliensis* Quoy and Gaimard, 1825, *Pseudopercis semifasciata* (Cuvier, 1829), *Raneya brasiliensis* (Kaup, 1856) and *U. canosai*) with different habits, all from coastal waters in the northern region of the study area (Table 1). Finally, two samples of *U. canosai* harboured the higher values of mean abundance (297.0 and 368.6). *C. cetaceum* was comparatively much less abundant, with very low mean abundances prevailing across samples (Fig. 3b).

Distribution of *Corynosoma* spp.

Model validation plots showed no discrepancies from model theoretical assumptions (graphs not shown).

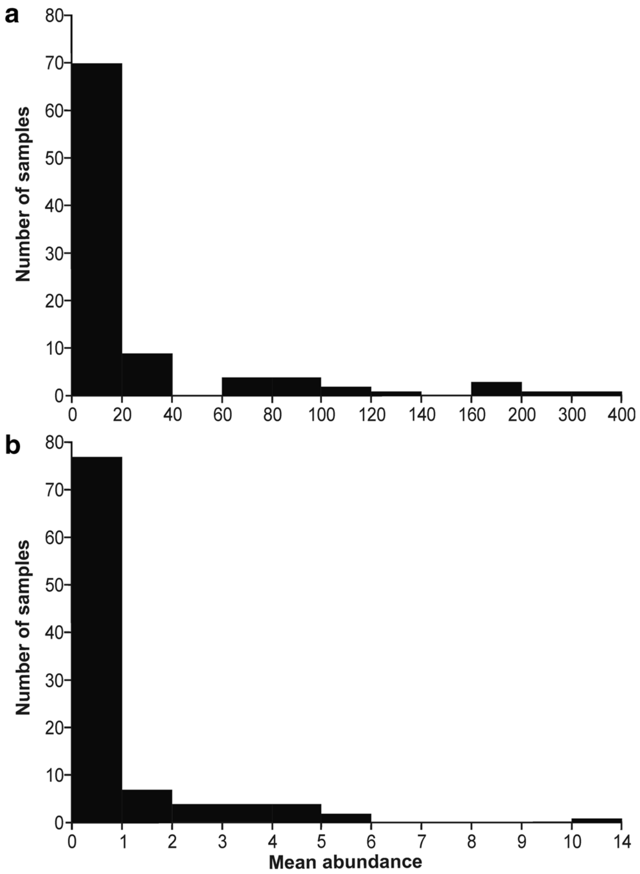


Fig. 3 Frequency of values of mean abundance of *Corynosoma australe* (**a**) and *C. cetaceum* (**b**) across 95 fish samples in the Southwestern Atlantic

Table 3 Alternative candidate GLMMs ranked according to their $\mathrm{AIC_c}$ to evaluate the effect of different predictor variables on the abundance of *Corynosoma australe* and *Corynosoma cetaceum*

Model	Predictors	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	$\mathrm{W_i}$
Corynosoma australe				
M3	*L + PB + DE + TL*	*507.4*	*0.00*	*0.719*
M4	*L + PB + DE + D*	*510*	*2.56*	*0.200*
MG	L + BP + DE + TL + D + H	512.4	4.98	0.060
M2	L + BP + TL	515.3	7.84	0.014
M1	L + BP + D	516.9	9.44	0.006
M7	L + BP	521.1	13.7	0.001
M15	BP + DE+ TL + D	525.6	18.19	0.00
M19	BP + DE + D + H	527.7	20.24	0.00
M6	BP + D	529.2	21.78	0.00
M9	L + D + DE	541.8	34.42	0.00
M16	L + DE + TL + D	542.5	35.05	0.00
M18	L + DE + TL + H	545.6	38.15	0.00
M5	L + D	559	51.62	0.00
M10	L + TL	559.5	52.1	0.00
M8	L	561.2	53.75	0.00
M13	D	567	59.59	0.00
M14	TL	576.8	69.37	0.00
M11	BP	580.8	73.4	0.00
M12	DE	598.1	90.68	0.00
M0	–	605.9	98.44	0.00
M17	H	606.9	99.22	0.00
Corynosoma cetaceum				
M4′	*L + BP + DE + D*	*117.2*	*0.00*	*0.651*
M3′	*L + BP + DE + TL*	*119.5*	*2.35*	*0.201*
MG′	*L + BP + DE + TL + D + H*	*120.5*	*3.39*	*0.120*
M15′	BP + DE + TL + D	124.1	6.97	0.020
M1′	L + BP + D	126.9	9.79	0.005
M2′	L + BP + TL	130.2	13.01	0.001
M19′	BP + DE + D + H	130.3	13.16	0.001
M6′	BP + D	130.9	13.79	0.001
M7′	L + BP	134.9	17.72	0.00
M9′	L + DE + D	138.8	21.69	0.00
M18′	L + DE + TL + H	139.0	21.81	0.00
M16′	L + DE + TL + D	139.7	22.52	0.00
M5′	L + D	148.6	31.50	0.00
M13′	D	151.4	34.23	0.00
M10′	L + TL	151.4	34.25	0.00
M8′	L	152.8	35.67	0.00
M14′	TL	157.1	39.94	0.00
M11′	BP	168.3	51.19	0.00
M12′	DE	176.8	59.62	0.00
M17′	H	178.3	61.12	0.00
M0′	–	180.1	62.98	0.00

Models used for averaging are set in italics

AIC_c, Akaike Information Criterion adjusted for small samples; ΔAIC_c, $\mathrm{AIC_c}$ (best)–$\mathrm{AIC_c}$(i); W_i, Akaike weight; *L*, host total length; *TL*, trophic level; *BP*, biogeographic province; *DE*, depth; *D*, diet; *H*, habitat

All models considered biologically meaningful for both *Corynosoma* species are shown in Table 3. In the case of *C. australe*, two models were well supported (accumulating a $w_i > 0.9$), consequently a model-averaging procedure was performed in order to estimate the relative importance of the variables included in those models (Fig. 4) and to estimate parameter coefficients and standard errors (Table 4). The same procedure was applied to *C. cetaceum*, but in this case, by averaging three models (accumulating $w_i > 0.9$) (Table 3). For both parasite species, the most relevant variables were host total length (L), biogeographic province (BP) and depth (DE) (Fig. 4). Parasite abundance increased with host length while it decreased in depth and towards southern waters (understood as Magellanic province) (Table 4). In addition, variables related to trophic aspects of the hosts were included in the best models, in the case of *C. australe* as trophic level (TL) and as diet (D) for *C. cetaceum*. Parasite abundance increased with higher trophic levels and for invertebrate eating hosts (Table 4). Host habitat showed minimum effect on the determination of the abundance since it was only present in one of the significant models for *C. cetaceum* (Fig. 4).

Table 4 Parameter estimates, standard errors (SE) and 95% confidence intervals (CI) of each predictor calculated after model averaging method on the abundance of *Corynosoma australe* and *Corynosoma cetaceum* in fishes from the Southwestern Atlantic

Parameter	Estimate	SE	CI
Corynosoma australe			
Intercept	− 6.62	4.02	(− 14.49, 1.25)
L	0.09	0.01	(0.06, 0.11)
TL	2.15	0.63	(0.91, 3.39)
BP (E)	− 1.82	0.33	(− 2.47, − 1.18)
BP (M)	− 3.56	0.58	(− 4.70, − 2.41)
DE	− 0.01	0.003	(− 0.02, − 0.005)
D (FI)	1.55	0.56	(0.45, 2.65)
D (F)	0.34	0.69	(− 1.03, 1.70)
D (P)	− 2.15	0.73	(− 3.58, − 0.72)
Corynosoma cetaceum			
Intercept	− 6.12	4.43	(− 14.8, 2.57)
L	0.06	0.02	(0.03, 0.09)
D (FI)	1.21	0.81	(− 0.38, 2.79)
D (F)	1.34	0.84	(− 0.31, 2.99)
D (P)	− 24.69	364.24	(− 739, 689)
BP (E)	− 1.59	0.49	(− 2.55, − 0.64)
BP (M)	− 26.09	366.81	(− 745, 693)
DE	− 0.02	0.01	(− 0.03, − 0.009)
TL	2.38	0.81	(0.79, 3.96)
H (DEM)	− 0.38	0.57	(− 1.51, 0.74)
H (PEL)	− 1.82	712.76	(− 1400, 1395)

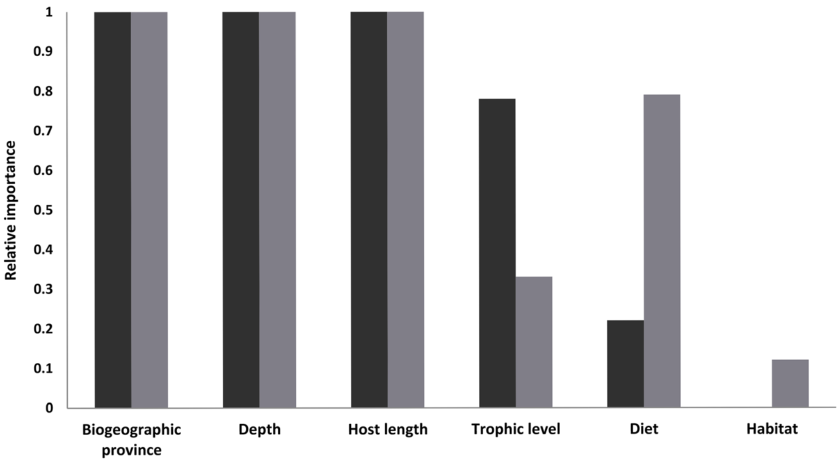
L, host total length; *TL*, trophic level; *BP*, biogeographic province (ecotonal (E), Magellanic (M)); *DE*, depth; *D*, diet (fish and invertebrates (FI), fish (F), plankton (P)); *H*, habitat (demersal (DEM), pelagic (PEL))

Discussion

Corynosoma australe showed a very broad spectrum of fish hosts in the region, in agreement with previous studies on this species (Timi et al. 2010; Hernández-Orts 2013; Cantatore and Timi 2015) as well as on other congeners from different regions (Zdzitowiecki 1978, 1996; Sinisalo and Valtonen 2003), being the most widely spread parasite across fish species in the Argentine Sea. On the other hand, *C. cetaceum* showed a more restricted distribution, which, however, is not due to a higher phylogenetic specificity since it was found in fish belonging to 7 orders. This narrower host range is probably a consequence of a different set of ecological filters related to the parasite life cycle, population attributes or transmission capabilities. Indeed, the lack of effect of the fish species as explanatory variable on the distribution of abundances of both helminth species is a further evidence of the low specificity of these parasites.

The differential distribution of both species is reflected also in quantitative grounds, being *C. australe* found at high prevalence and mean abundance in a considerable proportion of

Fig. 4 Relative importance of variables included in the model averaging for both *Corynosoma australe* (black bars) and *Corynosoma cetaceum* (grey bars)



samples, whereas *C. cetaceum* is much less prevalent and abundant. It is noteworthy that two samples of *U. canosai* harboured the most abundant infrapopulations of *C. australe*, being largely higher than any other species. The fact that *U. canosai* migrates from southern Brazilian waters (Haimovici et al. 2006), reaching the study zone during the warmer seasons, makes not possible to determine if these abundances are due to a specific behaviour of this host (perhaps a specialisation for preying on intermediate hosts of *C. australe*) or it reflects the structure of parasite populations from other latitudes. A combination of both factors can be also possible, since other fish with similar migratory behaviour, such as *T. lathami* and *P. saltatrix*, both pelagic (Saccardo and Katsuragawa 1995; Haimovici and Krug 1996), do not show parasite abundances notably higher than those of resident fishes.

Beyond the differences in parasite burdens displayed by both species, they share the same main determinants of their abundances: the host total length, biogeographic province of origin and depth. Regarding host length, cumulative patterns of parasite abundance as fish grow are commonly reported for trophically transmitted larval parasites (Dogiel et al. 1958; Poulin 2000, 2004; Poulin and Valtonen 2001; Timi et al. 2010; Valtonen et al. 2010; Timi and Lanfranchi 2013). Indeed, such ontogenetic changes have been previously demonstrated for *C. australe* in *P. brasiliensis* (Braicovich et al. 2016). These patterns are explained by the fact that larger hosts can ingest bigger quantities of food and display larger surface for parasites attachment, being able to sustain a greater absolute number that parasites than small ones (Guégan et al. 1992; Poulin 2000; Valtonen et al. 2010). Larger fish also can prey on larger food items, increasing the number of parasites acquired (Timi et al. 2010, 2011). All these processes, known at intraspecific level, can be extrapolated to interspecific level when unspecific parasites, such as *Corynosoma* spp., are considered. Additionally, for long-lived parasites, which remain for long periods or for the entire lifespan of their hosts, cumulative processes are expected to be more pronounced, because they depend not only on fish size, but also on age and longevity (Braicovich et al. 2016).

Concerning spatial variables, such as biogeographic province and depth, in the southern Southwest Atlantic, both region and depth are closely related to water temperature, due to the effect of subantarctic waters of the Malvinas current (cold and low-salinity water) flowing northwards along the continental slope and the Brazil current (warm and saline water) flowing from its origin in lower latitudes to near 38°S. Both currents determine temperature clines (decreasing southwards and with increasing depth) on shelf waters (Hoffmann et al. 1997; Acha et al. 2004; Piola et al. 2010) and contribute to delimit the two biogeographic provinces: the Argentinian and the Magellanic (Miloslavich et al. 2011). The ecotonal zone between both assemblages takes place around 43°-44° S, near Valdés Peninsula (Miloslavich et al. 2011). Water temperature, therefore, can have a direct effect on both acanthocephalans, whose development or transmission seems to be favoured in warmer environments. An indirect effect of temperature, through its influence on the distribution of different hosts involved in the life cycles of parasites is also possible. Unfortunately, the first intermediate hosts, known to be benthic amphipods for several species of *Corynosoma* (Zdzitowiecki and Presler 2001; Sinisalo and Valtonen 2003; Laskowski et al. 2010) are unknown in the region and no inferences can be made at this level of the life cycle.

Regarding definitive hosts, the distribution of *A. australis* and *O. flavescens* extends along all the study area, with higher concentrations of both species in Patagonian coasts (Crespo et al. 2015; Grandi et al. 2015) where *C. australe* is less abundant; consequently the density of sea lion populations is not a determinant of the observed clines in parasite abundance. On the other hand, the southern distribution limit of *P. blainvillei* is the San Matías Gulf (~ 42°S) in north Patagonian coasts (Crespo et al. 1998) and, although other known or potential cetacean hosts reach higher latitudes, *C. cetaceum* has been only recorded in the vicinity of San Matías Gulf, but not in southern regions (Hernández-Orts et al. 2015). This indicates that, variables other than availability of suitable definitive hosts also determine the distribution of *C. cetaceum.* Although vagility and migratory movements of some fish hosts may expand the distribution of both acanthocephalans, water temperature arose as the most probable driver of the distribution of both species, with *C. australe* displaying wider latitudinal and bathymetric ranges. High temperatures usually lead to an increase in the metabolic rates of ectothermic organisms (Schmidt-Nielsen 1997). According to it, several studies have reported a rise in parasite development rates with increasing temperatures in aquatic environments, especially for infective stages (e.g. Paull and Johnson 2011, 2014), such as it has been shown for cystacanths of polymorphid acanthocephalans in their amphipod host (Tokeson and Holmes 1982). Similar processes could be responsible of the apparent preference of both *Corynosoma* species for northern waters in the region. Warmer environments can lead to increasing levels of parasitism in two additional ways: affecting the ability of the infective stages to get to their host or affecting the capability of the host of resist the infection (Barber et al. 2016). Moreover, a modification in the metabolic rates of hosts due to the temperature shift may lead to a change in their rate of food consumption which can enhance exposure to trophically-transmitted parasites.

Depth itself is also recognised as a factor influencing the distribution of parasites with complex life cycle. In fact, parasite abundance declines with depth due to their dependence of the abundance of free-living fauna (Marcogliese 2002).

Many parasites with complex life cycles track food web interactions to propagate and maintain themselves in the marine realm (Marcogliese and Cone 1997). The results show that trophic habits are indeed a driving factor of *Corynosoma* spp. abundance, as trophic level and diet composition determine the range of prey a predator can consume, having a direct influence on the abundance and composition of parasite communities (George-Nascimento 1987; Marcogliese 2002; Chen et al. 2008). Also, Timi et al. (2010) demonstrated a strong influence of trophic level on the structure of parasite assemblages, including *C. australe* and *C. cetaceum*, of several fish species in the region, showing that the parasite abundance increases with trophic level.

Besides the relevance of the knowledge on the distribution of larval *Corynosoma* due to their value as tags of host population structure and zoogeography, another aspect to consider for the genus *Corynosoma* is their zoonotic potential, since human infestations have been occasionally recorded (Schmidt 1971; Takahashi et al. 2016; Fujita et al. 2016) besides infestation in birds and terrestrial mammals (Machado-Filho 1970; Schmidt 1971; Richardson and Cole 1997; Cabrera et al. 1999; Tantaleán et al. 2007; Hernández-Orts et al. 2017). High infective capability, long survival periods and low specificity make infestation by *Corynosoma* spp. a potential hazard for human health, transmissible by the consumption of raw or undercooked fish (Tantaleán et al. 2007; Fujita et al. 2016). Even though the risk of infestation seems to be low due to the microhabitat of the parasites, the high abundance in some fish species makes the contamination of fillets with infective stages probable. Therefore, a precise knowledge of the distribution across host species and localities acquires relevance.

In summary, ontogenetic, latitudinal and bathymetric effects over parasite abundance have been previously observed in several fish-parasite systems in the study area (Cantatore and Timi 2015; Braicovich et al. 2016; Irigoitia et al. 2018). However, the present findings show that host size and trophic habits are the main determinants of abundances for both species of *Corynosoma*, while biogeographic province of origin and depth (both indirectly representing the temperature of water) would be the main drivers of their spatial distribution. Knowing these host and environmental characteristics will allow to propose testable hypotheses on the burdens of *C. australe* and *C. cetaceum* to be found in any fish species inhabiting different regions of the Southwest Atlantic, as well as to better perform sampling designs to use parasite tags in further studies on host population structure and zoogeography.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical statement All fishes used in this work were obtained from commercial catches or research cruises. Therefore, no ethical statement is needed regarding use of animals for scientific purposes.

References

Acha EM, Mianzán HW, Guerrero RA, Favero M, Bava J (2004) Marine fronts at the continental shelves of austral South America physical and ecological process. J Mar Syst 44:83–105. https://doi.org/10.1016/j.jmarsys.2003.09.005

Alarcos AJ, Timi JT (2012) Parasite communities in three sympatric flounder species (Pleuronectiformes: Paralichthyidae): similar ecological filters driving toward repeatable assemblages. Parasitol Res 110:2155–2166. https://doi.org/10.1007/s00436-0112741-5

Alarcos AJ, Timi JT (2013) Stocks and seasonal migrations of the flounder *Xystreurys rasile* as indicated by its parasites. J Fish Biol 83: 531–534. https://doi.org/10.1111/jfb.12190

Alarcos AJ, Pereira AN, Taborda NL, Luque JL, Timi JT (2016) Parasitological evidence of stocks of *Paralichthys isosceles* (Pleuronectiformes: Paralichthyidae) at small and large geographical scales in south American Atlantic coasts. Fish Res 173:221–228. https://doi.org/10.1016/j.fishres.2015.07.018

Angelescu V (1982) Ecología trófica de la anchoíta del Mar Argentino (Engraulidae, *Engraulis anchoita*). Parte II. Alimentación, comportamiento y relaciones tróficas en el ecosistema. Contrib Inst Nac Invest Des Pesq, Mar del Plata

Aznar FJ, Cappozzo HL, Taddeo D, Montero FE, Raga JA (2004) Recruitment, population structure, and habitat selection of *Corynosoma australe* (Acanthocephala) in south American fur seals, *Arctocephalus australis*, from Uruguay. Can J Zool 82:726–733. https://doi.org/10.1139/Z04-044

Aznar FJ, Pérez-Ponce de León G, Raga JA (2006) Status of *Corynosoma* (Acanthocephala: Polymorphidae) based on anatomical, ecological, and phylogenetic evidence, with the erection of *Pseudocorynosoma* n. gen. J Parasitol 92:548–564. https://doi.org/10.1645/GE-715R.1

Aznar FJ, Hernández-Orts JS, Suárez AA, García-Varela M, Raga JA, Capozzo HL (2012) Assessing host-parasite specificity through coprological analysis: a case study with species of *Corynosoma* (Acanthocephala: Polymorphidae) from marine mammals. J Helminthol 86:156–164. https://doi.org/10.1017/S0022149X11000149

Barber I, Berkhout B, Ismail Z (2016) Climate change and the dynamics of multi-host parasite life cycles in aquatic ecosystems. Integr Comp Biol 56:561–572. https://doi.org/10.1093/icb/icw025

Begg GA, Waldman JR (1999) An holistic approach to fish stock identification. Fish Res 43: 35–44. https://doi.org/10.1016/S0165-7836(99)00065-X

Braicovich PE, Timi JT (2008) Parasites as biological tags for stock discrimination of the Brazilian flathead, *Percophis brasiliensis* in the south-west Atlantic. J Fish Biol 73:557–571. https://doi.org/10.1111/j.1095-8649.2008.01948.x

Braicovich PE, Timi JT (2010) Seasonal stability in parasite assemblages of the Brazilian flathead, *Percophis brasiliensis* (Perciformes: Percophidae): predictable tools for stock identification. Folia Parasitol 57:206–212. https://doi.org/10.14411/fp.2010.027

Braicovich PE, Timi JT (2015) Homogeneity of parasite assemblages of *Dules auriga* (Serranidae) in hydrographically heterogeneous sites. J Fish Biol 86:1363–1376. https://doi.org/10.1111/jfb.12648

Braicovich PE, Luque JL, Timi JT (2012) Geographical patterns of parasite infracommunities in the rough scad, *Trachurus lathami* Nichols off southwestern Atlantic Ocean. J Parasitol 98:768–771. https://doi.org/10.1645/GE-2950.1

Braicovich PE, Ieno EN, Sáez M, Despos J, Timi JT (2016) Assessing the role of host traits as drivers of the abundance of long-lived parasites in fish stock assessment studies. J Fish Biol 89:2419–2433. https://doi.org/10.1111/jfb.13127

Braicovich PE, Pantoja C, Pereira AN, Luque JL, Timi JT (2017) Parasites of the Brazilian flathead *Percophis brasiliensis* reflect West Atlantic biogeographic regions. Parasitology 144:169–178. https://doi.org/10.1017/S0031182016001050

Burnham KP, Anderson DR (2002) Model selection and multimodel inference, 2nd edn. Springer, New York

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 83:575–583. https://doi.org/10.2307/3284227

Cabrera R, Rojas R, Dávalos M (1999) *Corynosoma obtuscens* Lincicome, 1943 (Acanthocephala: Polymorphidae) en *Canis familiaris* de la ciudad de Chincha, Perú. Parasitol Día 23:58–61. https://doi.org/10.4067/S0716-07201999000100012

Canel D, Levy E, Soares IA, Braicovich PE, Haimovici M, Luque JL, Timi JT (2019) Stocks and migrations of the demersal fish *Umbrina canosai* (Sciaenidae) endemic from the subtropical and temperate southwestern Atlantic revealed by its parasites. Fish Res 173:221–228. https://doi.org/10.1016/j.fishres.2019.02.001

Cantatore DMP, Timi JT (2015) Marine parasites as biological tags in south American Atlantic waters, current status and perspectives. Parasitol 142:5–24. https://doi.org/10.1017/S0031182013002138

Carballo MC, Cremonte F, Navone GT, Timi JT (2012) Similarity in parasite community structure may be used to trace latitudinal migrations of *Odontesthes smitti* along Argentinean coasts. J Fish Biol 80:15–28. https://doi.org/10.1111/j.1095-8649.2011.03125.x

Chen HW, Liu WC, Davis AJ, Jordan F, Hwang MJ, Shao KT (2008) Network position of hosts in food webs and their parasite diversity. Oikos 117:1847–1855. https://doi.org/10.1111/j.1600-0706.2008.16607.x

Cousseau MB, Perrotta RG (2004) Peces marinos de Argentina: biología, distribución, pesca, 2nd edn. Publicaciones Especiales INIDEP, Mar del Plata

Crespo EA, Harris G, González R (1998) Group size and distributional range of the franciscana, *Pontoporia blainvillei*. Mar Mammal Sci 14:845–849

Crespo EA, Schiavini ACM, García NA, Franco-Trecu V, Goodall RNP, Rodríguez D, Stenghel Morgante J, De Oliveira LR (2015) Status, population trend and genetic structure of South American fur seals, *Arctocephalus australis*, in southwestern Atlantic waters. Mar Mammal Sci 31:866–890. https://doi.org/10.1111/mms.12199

Dogiel VA, Petrushevski GK, Polyanski YI (1958) Parasitology of fishes. Oliver and Boyd, London (translated from Russian by Kabata, Z. 1961)

Froese R, Pauly D (2018) FishBase. World Wide Web electronic publication. www.fishbase.org, version (06/2018). http://www.fishbase.org/search.php

Fujita T, Waga E, Kitaoka K, Imagawa T, Komatsu Y, Takanashi K, Anbo F, Anbo T, Katuki S, Ichihara S, Fujimori S, Morishima Y, Sugiyama H, Katahira H, Yamasaki H (2016) Human infection by acanthocephalan parasites belonging to the genus *Corynosoma* found from small bowel endoscopy. Parasitol Int 65:491–493. https://doi.org/10.1016/j.parint.2016.07.002

George-Nascimento M (1987) Ecological helminthology of wildlife animals hosts from South America: a literature review and search for patterns in marine food webs. Rev Chil Hist Nat 60:181–202

George-Nascimento M, Marín S (1992) Efecto de dos especies hospedadoras, el lobo fino austral *Arctocephalus australis* (Zimmerman) y el lobo marino común *Otaria byronia* (Blainville) (Carnivora; Otariidae), sobre la morfología y la fecundidad de *Corynosoma* sp. (Acanthocephala; Polymorphidae). Rev Chil Hist Nat 65:183–193

Grandi MF, Dans SL, Crespo EA (2015) The recovery process of a population is not always the same: the case of *Otaria flavescens*. Mar Biol Res 11:225–235. https://doi.org/10.1080/17451000.2014.932912

Guégan JF, Lambert A, Lévêque C, Combes C, Euzet L (1992) Can host body size explain the parasite species richness in tropical freshwater fishes? Oecologia 90:197–204. https://doi.org/10.1007/BF00317176

Haimovici M, Krug LC (1996) Life history and fisheries of the enchova, *Pomatomus saltatrix*, in southern Brazil. Mar Freshw Res 47:357–363. https://doi.org/10.1071/MF9960357

Haimovici M, Absalonsen L, Velasco G, Miranda LV (2006) Diagnóstico do estoque e orientações para o ordenamento da pesca de *Umbrina canosai* (Berg, 1985). In: Rossi-Wongtschowski CLDB, Ávila-da-Silva AO, Cergole MC (eds) Análise das Principais Pescarías Comerciais de Região Sudeste-Sul do Brasil: Dinâmica Populacional das Espécies em Exlotação II. São Paulo, pp 77–85

Hernández-Orts JS (2013) Taxonomy and ecology of metazoan parasites of otariids from Patagonia, Argentina: adult and infective stages. PhD thesis, University of Valencia, Valencia

Hernández-Orts JS, Paso Viola MN, García NA, Crespo EA, González R, García-Varela M, Kuchta R (2015) A checklist of the helminth parasites of marine mammals from Argentina. Zootaxa 3936:301–334. https://doi.org/10.11646/zootaxa.3936.3.1

Hernández-Orts JS, Brandão M, Georgieva S, Raga JA, Crespo EA, Luque JL, Aznar FJ (2017) From mammals back to birds: host-switch of the acanthocephalan *Corynosoma australe* from pinnipeds to the Magellanic penguin *Spheniscus magellanicus*. PLoS One 12:e0183809. https://doi.org/10.1371/journal.pone.0183809

Hoffmann J, Núñez M, Piccolo M (1997) Características climáticas del océano Atlántico sudoccidental. El Mar Argentino y sus Recursos Pesqueros Tomo I: Antecedentes históricos de las exploraciones en el mar y las características ambientales (ed Boschi E). Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, pp 163–193

Irigoitia MM, Braicovich PE, Lanfranchi AL, Farber MD, Timi JT (2018) Distribution of anisakid nematodes parasitizing rajiform skates under commercial exploitation in the southwestern Atlantic. Int J Food Microbiol 267:20–28. https://doi.org/10.1016/j.ijfoodmicro.2017.12.009

Johnson JB, Omland KS (2004) Model selection in ecology andevolution. Trends Ecol Evol 19:101–108. https://doi.org/10.1016/j.tree.2003.10.013

Lanfranchi AL, Rossin MA, Timi JT (2009) Parasite infracommunities of a specialized marine fish species in a compound community dominated by generalist parasites. J Helminthol 83:373–378. https://doi.org/10.1017/S0022149X09390069

Lanfranchi AL, Braicovich PE, Cantatore DMP, Alarcos AJ, Luque JL, Timi JT (2016) Ecotonal marine regions—ecotonal parasite communities: helminth assemblages in the convergence of masses of water in the southwestern Atlantic Ocean. Int J Parasitol 46:809–818. https://doi.org/10.1016/j.ijpara.2016.07.004

Laskowski Z, Witold Jeżewski W, Zdzitowiecki K (2010) New data on the occurrence of Acanthocephala in Antarctic Amphipoda. Acta Parasitol 55:161–166. https://doi.org/10.2478/s11686-010-0022-6

Lester RJG, MacKenzie K (2009) The use and abuse of parasites as stock markers for fish. Fish Res 97:1–2. https://doi.org/10.1016/j.fishres.2008.12.016

Machado-Filho DA (1970) Nova espécie do gênero *Corynosoma* Lühe, 1904 (Acanthocephala, Echinorhynchidea). Rev Bras Biol 30:377–379

Marcogliese DJ (2002) Food webs and the transmission of parasites to marine fish. Parasitology 124:83–99. https://doi.org/10.1017/S003118200200149X

Marcogliese DJ, Cone DK (1997) Food webs: a plea for parasites. Trends Ecol Evol 12:320–325. https://doi.org/10.1016/S0169-5347(97)01080-X

Miloslavich P, Klein E, Díaz JM, Hernández CE, Bigatti G, Campos L, Artigas F, Castillo J, Penchaszadeh PE, Neill PE, Carranza A, Retana MV, Díaz de Astarloa JM, Lewis M, Yorio P, Piriz ML, Rodríguez D, Yoneshigue-Valentin Y, Gamboa L, Martín A (2011) Marine biodiversity in the Atlantic and Pacific coasts of South America: knowledge and gaps. PLoS One 6:e14631

Paull SH, Johnson PTJ (2011) High temperature enhances host pathology in a snail-trematode system: possible consequences of climate change for the emergence of disease. Freshw Biol 56:767–778. https://doi.org/10.1111/j.1365-2427.2010.02547.x

Paull SH, Johnson PTJ (2014) Experimental warming drives a seasonal shift in the timing of host-parasite dynamics with consequences for disease risk. Ecol Lett 17:445–453. https://doi.org/10.1111/ele.12244

Pereira AN, Pantoja C, Luque JL, Timi JT (2014) Parasites of *Urophycis brasiliensis* (Gadiformes: Phycidae) as indicators of marine ecoregions in coastal areas of the south American Atlantic. Parasitol Res 113:4281–4292. https://doi.org/10.1007/s00436-014-4106-3

Piola AR, Martínez Avellaneda N, Guerrero RA, Jardón FP, Palma ED, Romero SI (2010) Malvinas-slope water intrusions on the northern Patagonia continental shelf. Ocean Sci 6:345–359. https://doi.org/10.5194/os-6-345-2010

Poulin R (2000) Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes. J Fish Biol 56:123–137. https://doi.org/10.1111/j.1095-8649.2000.tb02090.x

Poulin R (2004) Macroecological patterns of species richness in parasite assemblages. Basic Appl Ecol 5:423–434. https://doi.org/10.1016/j.baae.2004.08.003

Poulin R, Valtonen ET (2001) Nested assemblages resulting from host size variation: the case of endoparasite communities in fish hosts. Int J Parasitol 31:1194–1204. https://doi.org/10.1016/S0020-7519(01)00262-4

Richardson DJ, Cole RA (1997) Acanthocephala of the bald eagle (*Haliaeetus leucocephalus*) in North America. J Parasitol 83:540–541. https://doi.org/10.2307/3284428

Rossin MA, Timi JT (2010) Parasite assemblages of *Nemadactylus bergi* (Pisces: Latridae): the role of larval stages in the short-scale predictability. Parasitol Res 107:1373–1379. https://doi.org/10.1007/s00436-010-2011-y

Saccardo SA, Katsuragawa M (1995) Biology of the rough scad *Trachurus lathami*, on the southeastern coast of Brazil. Sci Mar 59:265–277

Santos CP, Gibson DI, Tavares LER, Luque JL (2008) Checklist of Acanthocephala associated with the fishes of Brazil. Zootaxa 1938:1–22. https://doi.org/10.5281/zenodo.184999

Sardella NH, Timi JT (2004) Parasites of argentine hake in the Argentine Sea: population and infracommunity structure as evidences for host stock discrimination. J Fish Biol 65:1472–1488. https://doi.org/10.1111/j.1095-8649.2004.00572.x

Sardella NH, Mattiucci S, Timi JT, Bastida R, Rodríguez D, Nascetti G (2005) *Corynosoma australe* Johnston, 1937 and *C. cetaceum* Johnston and Best, 1942 (Acanthocephala: Polymorphidae) from marine mammals and fish in Argentinean waters: genetic differentiation and taxonomic status. Syst Parasitol 61:143–156. https://doi.org/10.1007/s11230-005-3131-0

Schmidt GA (1971) Acanthocephalan infections of man, with two new records. J Parasitol 57:582–584. https://doi.org/10.2307/3277920

Schmidt-Nielsen K (1997) Animal physiology: adaptation and environment. Cambridge University Press, Cambridge

Sinisalo T, Valtonen ET (2003) *Corynosoma* acanthocephalans in their paratenic fish hosts in the northern Baltic Sea. Parasite 10:227–233. https://doi.org/10.1051/parasite/2003103227

Soares IA, Lanfranchi AL, Luque JL, Haimovici M, Timi JT (2018) Are different parasite guilds of *Pagrus pagrus* equally suitable sources of information on host zoogeography? Parasitol Res 117:1865–1875. https://doi.org/10.1007/s00436-018-5878-7

Symonds MR, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65:13–21. https://doi.org/10.1007/s00265-010-1037-6

Takahashi K, Ito T, Sato T, Goto M, Kawamoto T, Fujinaga A, Yanagawa N, Saito Y, Nakao M, Hasegawa H, Fujiya M (2016) Infection with fully mature *Corynosoma* cf. *validum* causes ulcers in the human small intestine. Clin. J Gastroenterol 9:114–117. https://doi.org/10.1007/s12328-016-0646-7

Tantaleán M, Mendoza L, Riofrío F (2007) The Andean fox, *Pseudalopes culpaeus*, a new host for *Corynosoma obtuscens* (Acanthocephala) in Peru. Rev Peru Biol 14:51–52. https://doi.org/10.15381/rpb.v14i1.1757

Timi JT (2003) Parasites of argentine anchovy in the south-west Atlantic: latitudinal patterns and their use for discrimination of host populations. J Fish Biol 63:90–107. https://doi.org/10.1046/j.1095-8649.2003.00131.x

Timi JT, Lanfranchi AL (2009a) The metazoan parasite communities of the Argentinean sandperch *Pseudopercis semifasciata* (Pisces: Perciformes) and their use to elucidate the stock structure of the host. Parasitology 136:1209–1219. https://doi.org/10.1017/S0031182009990503

Timi JT, Lanfranchi AL (2009b) The importance of the compound community on the parasite infracommunity structure in a small benthic fish. Parasitol Res 104:295–302. https://doi.org/10.1002/s00436-008-1191-1

Timi JT, Lanfranchi AL (2013) Ontogenetic changes in heterogeneity of parasite communities of fish: disentangling the relative role of compositional versus abundance variability. Parasitology 140:309–317. https://doi.org/10.1017/S0031182012001606

Timi JT, Lanfranchi AL, Etchegoin JA (2009) Seasonal stability and spatial variability of parasites in Brazilian sandperch from the northern Argentine Sea: evidence for stock discrimination. J Fish Biol 74:1206–1225. https://doi.org/10.1111/j.1095-8649.2009.02190.x

Timi JT, Luque JL, Poulin R (2010) Host ontogeny and the temporal decay of similarity in parasite communities of marine fish. Int J Parasitol 40:963–968. https://doi.org/10.1016/j.ijpara.2010.02.005

Timi JT, Rossin MA, Alarcos AJ, Braicovich PE, Cantatore DMP, Lanfranchi AL (2011) Fish trophic level and the similarity of larval parasite assemblages. Int J Parasitol 41:309–316. https://doi.org/10.1016/j.ijpara.2010.10.002

Tokeson JPE, Holmes JC (1982) The effects of temperature and oxygen on the development of *Polymorphus marilis* (Acanthocephala) in *Gammarus lacustris* (Amphipoda). J Parasitol 68:112–119. https://doi.org/10.2307/3281332

Vales DG, García NA, Crespo EA, Timi JT (2011) Parasites of a marine benthic fish in the southwestern Atlantic: searching for geographical recurrent patterns of community structure. Parasitol Res 108:261–272. https://doi.org/10.1007/s00436-010-2052-2

Valtonen ET, Marcogliese DJ, Julkunen M (2010) Vertebrate diets derived from trophically transmitted fish parasites in the Bothnian Bay. Oecologia 162:139–152. https://doi.org/10.1007/s00442-009-1451-5

Zdzitowiecki K (1978) On the occurrence of juvenile acanthocephalans of the genus *Corynosoma* Lühe, 1904 in fishes from South Georgia and South Shetland Islands (the Antarctic). Acta Ichthyol Piscat 8:111–127

Zdzitowiecki K (1996) Acanthocephala in fish in the Weddell Sea. Acta Parasitol 41:199–203

Zdzitowiecki K, Presler P (2001) Occurrence of Acanthocephala in intermediate hosts, Amphipoda, in Admiralty Bay, South Shetland Islands, Antarctica. Pol Polar Res 22:205–212

Zhang Y (2013) Likelihood-based and Bayesian methods fot Tweedie compound Poisson linear mixed models. Stat Comput 23:743–757

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer-Verlag, New York