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Endoparasite fauna of five Gadiformes fish species from the coast of Chile: host ecology versus phylogeny

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Abstract

The aims of the present study were to compare, using multivariate analyses, the degree of similarity of the endoparasite fauna of five fish species belonging to the order Gadiformes: *Merluccius gayi*, *Merluccius australis*, *Macruronus magellanicus* (Gadoidei) and *Micromesistius australis* and *Nezumia pulchella* (Macrouroidei), from the southern and central Chilean coast, and to evaluate whether the composition of the endoparasite fauna was determined by phylogenetic or ecological relationships. We employed our database of *Merluccius australis*, *M. magellanicus* and *Micromesistius australis*, which was complemented with published information for *M. magellanicus*, *Merluccius australis*, *Micromesistius australis*, *M. gayi* and *N. pulchella*. A higher number of endoparasite species was recorded for *Merluccius australis*, *Micromesistius australis* and *M. magellanicus*, namely *Anisakis* sp. and *Hepatoxylon trichiuri*, which is the most prevalent parasite among these hosts. *Aporocotyle wilhelmi* and *Hysterothylacium* sp. were detected only in *M. gayi*, whereas *Lepidapedon* sp. was found exclusively in *N. pulchella*. These results suggest that fish ecology rather than host phylogeny was the most important factor for the determination of similarity in parasite composition. This result could be explained by the similar trophic patterns of hosts and by the predominance of generalist larval species among these fish parasite communities.

Introduction

The composition of parasite communities is affected by, among other factors, the result of the interactions between their evolutionary history and the ecological characteristics of the hosts (Poulin, 1995). During their evolutionary history, hosts lose and/or acquire parasites due to the speciation of native parasites or the acquisition of new parasite species from other hosts (Poulin & Rohde, 1997). The ecological characteristics associated with the host, such as diet, habitat and niche position, have a great influence on the composition and structure of the parasite communities (Esch *et al.*, 1990; Poulin, 1995). Moreover, host geographic range is a main factor affecting the interchanges of parasite species that are phylogenetically related (Poulin & Morand, 1999; González & Oliva, 2006). Similarly, it has been demonstrated that depth and temperature both affect the parasite communities of fish (Rohde *et al.*, 1995; Oliva *et al.*, 2004).

Studies of parasite communities that do not account for phylogeny may provide inaccurate results (Brooks, 1980). Studies that analyse the determinants of parasite communities of related hosts show that phylogenetic relationships can confuse the real relationships between host ecology and community parasite richness (Poulin & Rohde, 1997). However, few studies have evaluated the importance of ecological and phylogenetic factors of the host simultaneously as determinants of parasite communities (Bush *et al.*, 1990; Poulin, 1996, 2010; Muñoz *et al.*, 2006), and those studies have provided contradictory results concerning the relationship between parasitological descriptors and ecological variables and/or host

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phylogeny. Therefore, additional studies are needed to determine whether these trends in the determination of parasite communities are consistent when the ecology and phylogeny of the host are considered.

The aims of the present study were to compare, using multivariate analyses, the degree of similarity of the endoparasite fauna of five fish species belonging to the order Gadiformes: three representatives of the suborder Gadoidei (*Merluccius gayi*, *Merluccius australis* (Merlucciidae), *Macruronus magellanicus* (Macrouronidae)) and two representatives of the suborder Macrouroidei (*Nezumia pulchella* (Macrouridae) and *Micromesistius australis* (Gadidae)), and to evaluate whether endoparasite compositions were mainly influenced by phylogenetic or by ecological relationships (e.g. niche dimensions such as diet, depth, latitude or habitat). Two host species (*M. gayi* and *N. pulchella*) share latitudinal and bathymetric distributions along the northern Chilean coast, whereas the other three host species (*Merluccius australis*, *M. magellanicus* and *Micromesistius australis*) are distributed along the central-southern Chilean coast (Froese & Pauly, 2010). As stated by Lillo *et al.* (2005) and Saavedra *et al.* (2006), these species share similar trophic patterns.

Materials and methods

We used our own database comprising *M. magellanicus*, *Merluccius australis* and *Micromesistius australis*, which were caught in 2006 by an industrial fishery from southern Chile (44°S and 45°S). Additionally, our database was complemented with published information for *M. magellanicus*, *Merluccius australis*, *Micromesistius australis*, *M. gayi* and *N. pulchella* (table 1). The latitudinal and bathymetric ranges and sizes for each species are presented in table 2.

For each parasite species, the prevalence and mean intensity of infection were calculated according to Bush *et al.* (1997). Cluster analyses (based on the Bray–Curtis similarity and simple linkage algorithm) were used to determine whether the endoparasite composition (prevalence and intensity of infection) among host species was similar. Correspondence analyses were then employed to evaluate the host–parasite associations. All multivariate analyses were performed using Statistica 6.0 software (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

The host species *N. pulchella* showed the narrowest latitudinal range, whereas *Merluccius australis*, *M. magellanicus* and *Micromesistius australis* demonstrated overlapping latitudinal distributions (table 2). Twenty endoparasite species were detected in the studied hosts. Of these species, seven were in the larval stages, and several parasite species were common among the host species. The larval parasites *Anisakis* sp. and *Hepatoxylon trichiuri* demonstrated a higher prevalence of infection in *Merluccius australis*, *Micromesistius australis* and *M. magellanicus* (table 1). There was no relationship between the sample size and parasite richness ($r^2 = 0.107$, $P > 0.20$).

The cluster analysis based on parasite prevalence (fig. 1) included *Micromesistius australis* and *M. magellanicus* in a clade with 50% similarity; *Merluccius australis* was included in this clade with a similarity of 49% and *M. gayi* with a similarity of 36%. Finally, *N. pulchella* demonstrated a parasite similarity of only 23% with the other four host species. The cluster analysis based on the mean intensity of infection (fig. 2) revealed the same pattern.

Table 1. Prevalence (P) and mean intensity of infection (MI) of endoparasites of five Gadiformes fish species off the Chilean coast.

	Merluccius australis		*Merluccius gayi*		*Macruronus magellanicus*		*Micromesistius australis*		*Nezumia pulchella*	
Parasite species	P	MI	P	MI	P	MI	P	MI	P	MI
Aporocotyle wilhelmi	–	–	11.6	1.5	–	–	–	–	–	–
Aporocotyle australis	21.9	3.5	–	–	–	–	–	–	–	–
Derogenes varicus	8.3	1.6	–	–	5.3	4.1	8.1	1.4	–	–
Elytrophalloides oatesi	–	–	–	–	25.3	8	–	–	–	–
Gonocerca phycidis	–	–	–	–	10.7	2.2	–	–	–	–
Hemiuridae gen sp.	–	–	–	–	–	–	29.5	3.5	–	–
Lepidapedon sp.	–	–	–	–	–	–	–	–	4.5	2.7
Anisakis sp.*	80.5	200.9	62	4.3	94.2	7.6	88.7	18.3	6	0.8
Ascarophis sp.	9.7	8.1	–	–	7	14.3	59.7	9.4	–	–
Pseudoterranova sp.*	17.7	5.6	34.7	5.1	1.1	1	4.9	1.3	3	0.5
Contracaecum sp.*	45.1	31.5	5.8	1.6	0.5	1	32.8	3.4	6	0.8
Hysterothylacium sp.*	–	–	33.1	1.8	–	–	–	–	–	–
Hysterothylacium aduncum	72.9	2.7	–	–	1.1	2.5	22.7	2.5	16.4	1.2
Cucullanus sp.	–	–	–	–	88.1	23.2	1.6	0.8	–	–
Corynosoma sp.*	52.3	1.4	6.6	3.9	2.1	1	9.8	1	16.4	1.3
Pseudophyllidea gen sp.	47.1	0.5	–	–	1.6	1	–	–	–	–
*Hepatoxylon trichiuri**	65.1	8.5	5.8	1.6	65.7	3.6	45.9	8.4	–	–
Clestobotrium crassiceps	94.3	5.4	40.5	4.8	0.5	1	1.6	1	–	–
*Grillotia heptanchi**	52.8	0.5	–	–	–	–	–	–	–	–
Diphyllobotrium sp.	–	–	–	–	–	–	4.9	1	–	–

* Larval stages.

Table 2. Number of analysed fish (n), fish size range (mean ± SD), latitudinal range and bathymetric range in gadiform fish species from Chile.

Species	n	Fish size (cm)	(Mean ± SD)	Latitudinal range	Bathymetric range (m)*
Merluccius australis (1)	18	61–102	(87.6 ± 11)	44°57′–45°11′S	60–800
Merluccius australis (2)	100	58–98	(79 ± 8.72)	43°36′–43°40′S	60–800
Merluccius australis (3)	663	40–97.1	(68 ± 10.4)	45°34′–53°91′S	60–800
Merluccius australis (4)	59	60–110	(75 ± 12.6)	52°57′–53°56′S	60–800
Merluccius gayi (5)	121	30–60	(45.4 ± 10.1)	35°02′–40°01′S	50–500
Macruronus magellanicus (1)	20	41–87	(65.1 ± 12.1)	44°57′–45°11′S	30–500
Macruronus magellanicus (6)	166	40–91	(64.1 ± 9.83)	36°40′–36°42′S	30–500
Micromesistius australis (1)	20	39–50	(43.1 ± 3)	44°57′–45°11′S	200–400
Micromesistius australis (7)	41	26–57	(44 ± 7.95)	47°02′–53°04′S	200–400
Nezumia pulchella (8)	67	20–38.3	(28.2 ± 4.7)	26°03′–28°09′S	250–960

Sources: (1) This study; (2) Fernández (1985); (3) George-Nascimento & Arancibia (1994); (4) González (2005) ; (5) George-Nascimento (1996); (6) Oliva (2001); (7) Niklitschek *et al.* (2009); (8) Salinas *et al.* (2008).
* From Froese & Pauly (2010).

The correspondence analysis based on prevalence (fig. 3) demonstrated significant differences in endoparasite composition among the host species ($\chi^2 = 630.07$, df = 76, $P < 0.001$); 66.5% of the variation was explained by the first two dimensions (39% and 27.5% for the first and second dimensions, respectively). Most parasites were associated with *Merluccius australis* and *Micromesistius australis*. However, *Aporocotyle wilhelmi* and *Hysterothylacium* sp. were strongly associated with *M. gayi*. Similarly, *Elytrophalloides oatesi*, *Gonocerca phycidis* and *Cucullanus* sp. were only associated with *M. magellanicus*, whereas *Lepidapedon* sp. was present only in *N. pulchella* (fig. 3).

The correspondence analysis based on the mean intensity of infection (fig. 4) also showed significant differences in endoparasite composition among the host species ($\chi^2 = 1812.1$, df = 76, $P < 0.001$); 68% of the variation was explained by the first two dimensions (38.6% and 29.7% for the first and second dimensions, respectively). Several endoparasites were associated with *Merluccius australis*, *Micromesistius australis*, *M. magellanicus* and *M. gayi* (fig. 4).

Discussion

Several studies have evaluated the role of ecological factors (e.g. niche dimensions such as diet, depth, latitude and habitat) on the structure and parasite richness of fishes (Aldana *et al.*, 2002; Muñoz *et al.*, 2002). However, studies investigating the relationship between parasite descriptors and ecological variables of the host, in particular those including phylogeny, are scarce (Poulin & Rohde, 1997; Morand *et al.*, 2000; Muñoz *et al.*, 2006). Specifically, the endoparasite communities of fishes can be determined by the feeding habits of the host (for instance, specialist versus generalist predators), changes in their ontogenetic feeding, and the availability of different prey (intermediary hosts) in a given environment (Poulin, 1995). The host species *Micromesistius australis* and *M. magellanicus*, which belong to different suborders in the Gadiformes, show greater similarity in their endoparasite compositions, which can be best explained by their similar trophic patterns instead of by phylogeny. *Micromesistius australis*, *M. magellanicus* and *Merluccius australis* are related trophically, because they feed mainly on the same species of myctophid fish (e.g. *Lampanyctus* sp.) and crustacean (*Pasiphaea doffleini*) (Lillo *et al.*, 2004, 2005; Saavedra *et al.*, 2006). This similarity in diet agrees well with the similarity of the endoparasite fauna of *Micromesistius australis* and *M. magellanicus*, which in turn is supported by cluster and correspondence analyses (figs 1–4), emphasizing the higher prevalence of *H. trichiuri* and *Anisakis* sp. in these three host fishes. The latter parasite can be transmitted to *Merluccius australis* via the ingestion of juveniles of *M. magellanicus*, their main prey (Lillo *et al.*, 2005), which is an intermediate host of *Anisakis* sp. (Riffo & George-Nascimento, 1992). The infection of *Micromesistius australis* by *Anisakis* sp. could be explained by the consumption of intermediate hosts (Crustacea) (Sakanari & McKerrow, 1989). The cestode *H. trichiuri* is a common parasite of merluccid fish (Mladineo, 2006). This cestode can infect all three hosts through the ingestion of larval stages harboured by crustaceans (Vásquez-López *et al.*, 2001). The similar trophic patterns of two Gadoidei (*Merluccius australis*, *M. magellanicus*) and one Macrouroidei (*Micromesistius australis*) are caused by their spatial overlap (both latitudinal and bathymetric). In contrast, the distribution of *M. gayi* overlaps those of the other three species only within a narrow latitudinal range, 28°S–47°S

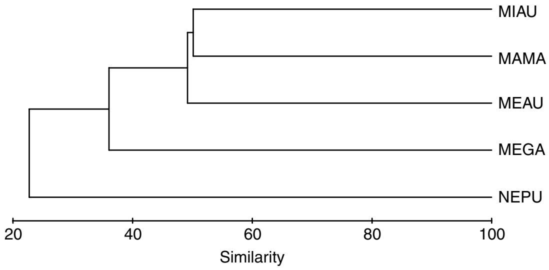

Fig. 1. Cluster analyses based on prevalence of infection of endoparasite fauna of five Gadiformes species. Code for host species: *Nezumia pulchella* (NEPU), *Merluccius gayi* (MEGA), *Merluccius australis* (MEAU), *Micromesistius australis* (MIAU) and *Macruronus magellanicus* (MAMA).

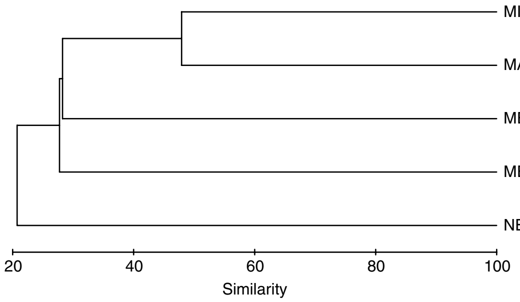

Fig. 2. Cluster analyses based on mean intensities of infection of endoparasite fauna of five Gadiformes species. Code for species as in fig. 1.

(Aguayo, 1995); this host species demonstrates distinct feeding habits, with its most important prey being the crustaceans *Pterygosquilla armata*, *Pleuroncodes monodon*, *Cerviminuda johni* and *Euphausia mucronata*, the fishes *Engraulis ringens* and *Strangomera bentincki* and other *M. gayi* (Arancibia & Fuentealba, 1993). On the other hand, *N. pulchella* overlaps with *M. gayi* both latitudinally and bathymetrically between 20°S and 33°S (Sielfeld & Vargas, 1996). This spatial overlap is not reflected in the parasite composition of these two fish species, as shown by cluster and correspondence analyses (figs 3 and 4). The lack of similarity between endoparasite fauna of *N. pulchella* and *M. gayi* could be explained by the digenean *Aporocotyle wilhelmi*, which is a parasite specific to *M. gayi* (Villalba & Fernández, 1986). However, the most important endoparasite species of *N. pulchella* (Macrouridae) is the digenean *Lepidapedon* sp., which is a common parasite of Gadiformes species (Bray & des Clers, 1992).

The phylogenetic information provided by comparative analysis avoids confusing effects among analysed ecological variables (Harvey & Pagel, 1991). Phylogenetic effects could be hidden by ecological effects, except in the presence of strong host ecological effects and high probabilities of acquiring or losing parasites, or in the case of marked changes in ecological characteristics during speciation events (Vickery & Poulin, 1998). According to Morand *et al.* (2000), host phylogenetic relationships have a strong influence on patterns of parasite richness. However, a consistent pattern explaining the variations in endoparasite composition and richness among fish species of Labridae (Cheiliniae) has not been observed, unless the species are phylogenetically related and present very similar diets and body sizes (Muñoz *et al.*, 2006). These observations suggest that the phylogenetic relationships of hosts do not have a significant effect on the structure of their parasite communities, and thus, the mixed effects of host descriptors (diet, weight) and phylogeny are the main contributors to endoparasite composition. Recently, Poulin (2010) suggested that similarity of parasite fauna decreases with the phylogenetic distance of the host species. In the present study, the results of multivariate analyses (figs 1–4) supported the observation that the fish species most closely related phylogenetically (*Merluccius gayi* and *Merluccius australis*) did not show greater parasite fauna similarities. In a similar way, the two species belonging to the suborder Macrouroidei (*M. magellanicus* and *N. pulchella*), as defined by Roa-Varón & Ortí (2009), show the higher divergence in the composition of their parasite fauna. Moreover, our results suggest that the most closely related parasite fauna is shared by *Micromesistius australis* and *M. magellanicus* – species that belong to different suborders in the Gadiformes. Those findings might be explained by the latitudinal/bathymetric

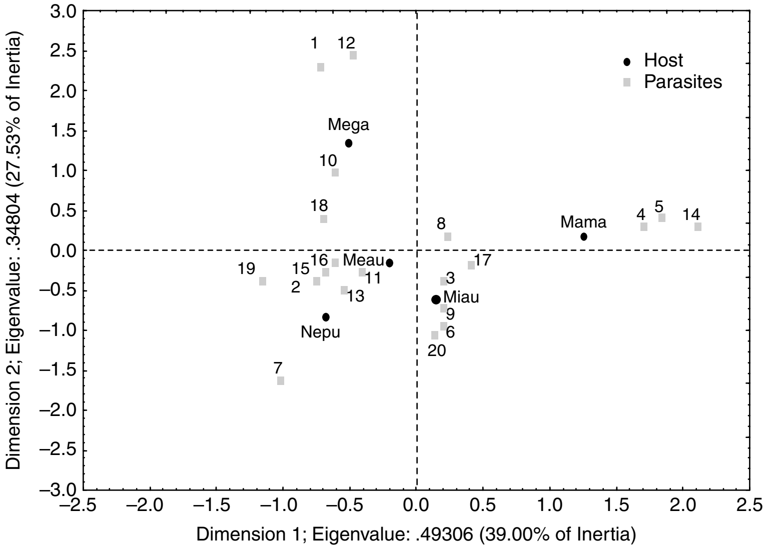

Fig. 3. Correspondence analysis based on prevalence of infection: *Nezumia pulchella* (Nepu), *Merluccius gayi* (Mega), *Merluccius australis* (Meau), *Micromesistius australis* (Miau) and *Macruronus magellanicus* (Mama). 1, *Aporocotyle wilhelmi*; 2, *Aporocotyle australis*; 3, *Derogenes varicus*; 4, *Elytrophalloides oatesi*; 5, *Gonocerca phycidis*; 6, Hemiuridae gen sp.; 7, *Lepidapedon* sp.; 8, *Anisakis* sp.; 9, *Ascarophis* sp.; 10, *Pseudoterranova* sp.; 11, *Contracaecum* sp.; 12, *Hysterothylacium* sp.; 13, *Hysterothylacium aduncum*; 14, *Cucullanus* sp.; 15, *Corynosoma* sp.; 16, Pseudophyllidea gen sp.; 17: *Hepatoxylon trichiuri*; 18, *Clestobothrium crassiceps*; 19, *Grillotia heptanchi*; 20, *Diphyllobothrium* sp.

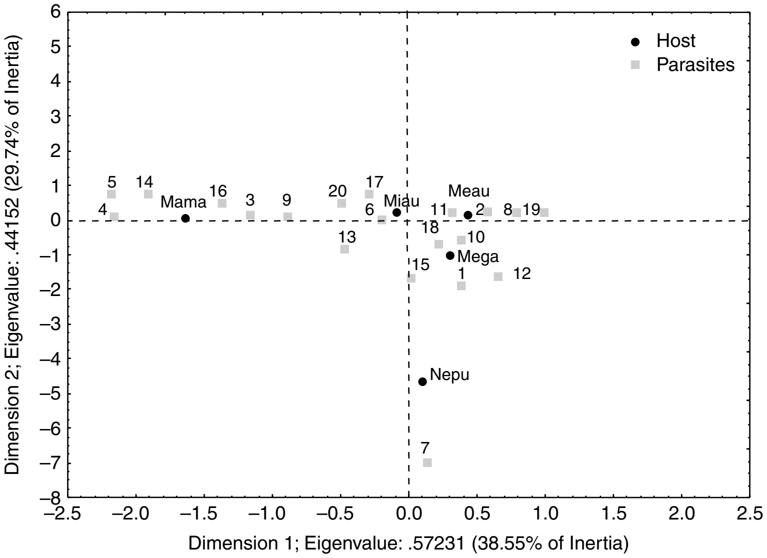

Fig. 4. Correspondence analyses based on mean intensity of infection. Code for host species and parasite species as in fig. 3.

segregation of these species and, consequently, the differential prey availabilities, indicating that the composition of the endoparasite fauna is mainly influenced by feeding habits (predator–prey relationships).

In summary, among the Gadiformes species studied herein, the high degree of endoparasite similarity was determined principally by their ecological characteristics (trophic overlap); consequently, phylogenetic relationships could play a secondary role in the determination of their endoparasite fauna. Nevertheless, and similarly to the results reported by Muñoz *et al.* (2006), the Gadiformes fish species described herein harbour mainly generalist endoparasites (*Anisakis* sp., *H. trichiuri*, *Derogenes varicus*), which infect several demersal fishes (*Genypterus* spp., *Dissostichus eleginoides*, *Hippoglossina macrops*, among others) (George-Nascimento & Huet, 1984; Oliva *et al.*, 2004, 2008). In addition, there is a possibility that our results could be biased, because generalist larval species such as *H. trichiuri*, *Anisakis* sp. and *Pseudoterranova* sp. could be different species that are morphologically similar, a finding that has been demonstrated genetically for some anisakid species (Mattiucci & Nascetti, 2007). Therefore, molecular studies may be necessary to identify such species and to evaluate conclusively the effects of ecological and phylogenetic factors on the composition of endoparasite communities in Gadiformes fish species.

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