

Metazoan Parasite Infracommunities of the Toadfish *Aphos porosus* (Pisces: Batrachoidiformes) in Central Chile: How Variable Are They over Time?

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ABSTRACT: The present study examines variation in parasite community characteristics of the toadfish *Aphos porosus* across sampling years. We analyzed and compared the species composition and numeric descriptors of the parasite infrapopulations and infracommunities in 101 fish collected during the springs of 1999, 2006, and 2007 from rocky intertidal ponds in El Tabo, central Chile. Parasites were found in 94.1% of specimens necropsied. In total 5,532 parasites were collected, representing 12 taxa, of which 7 were found in the 3 annual samples. The most prevalent and abundant parasites in the 3 sampling years were larval tetraphyllidean cestodes, followed by anisakid nematodes. The community descriptors of average richness and abundance varied significantly across the 3 yr, with the exception of parasite dominance. The parasite species composition and relative abundance showed low variability among years. A few parasite taxa (*Anisakis* sp., *Pseudoterranova* sp., tetraphyllideans, and *Clesthobothrium crassiceps*) dominated the infracommunities of the toadfish; however, tetraphyllideans were the parasites that greatly varied over time. Consequently the parasite infracommunities of the toadfish were variable among years, with a low variation in parasite composition, but large differences in the aggregate descriptors.

The distribution of parasite communities generally shows spatial and temporal variations (Esch and Fernández, 1993), which allow for investigators to determine whether or not a community, in terms of species richness, specific identity, and abundance of the parasite species, exhibits a predictable and repetitive structure over time and space. When the species composition, abundances, and prevalences of the parasite species differ significantly from what were statistically expected (Poulin, 1998), it is possible to investigate and associate biological factors and ecological processes (e.g., Rohde, 1993; Poulin, 1998) that structure such communities. Most species exhibit variability in community structure over time, but they do so in different degrees and depending on which descriptors have been considered (Micheli et al., 1999).

Determining how, and by how much, parasite communities change over time allows for understanding the natural variations that these communities experience and, with this, may generate basic knowledge to improve parasite prevention and control procedures for cultivated species. In Chile little research has addressed temporal variability of parasite infracommunities and the factors that explain the changes in the species composition and populations and communities descriptors over time (e.g., Balboa and George-Nascimento, 1998; Garcías et al., 2001; Díaz and George-Nascimento, 2002; González and Oliva, 2006). In general, it is possible to expect that parasite communities exhibit a low variation when they are coming from host individuals collected from a single locality and sampled in the same season over time. The present research was designed to determine if the parasite infracommunities of the toadfish *Aphos porosus* (Valenciennes, 1837) collected from rocky intertidal ponds of El Tabo (33°27'S, 71°38'W), in central Chile, vary significantly among sampling years.

Between October and November (during spring) in 1999, 2006, and 2007, 101 toadfish specimens were collected (see Table I for sample sizes per year). Most of the fish were frozen immediately, while others were dissected fresh. Metazoan ecto- and endoparasites were collected from each specimen following the methodology described by Díaz and George-Nascimento (2002). The anisakid nematodes were fixed in 70% alcohol, then cleared in glycerine to observe their internal structures; the other parasites collected were fixed in 10% formalin. Identity of the parasites was determined using Moore (1910), Schmidt (1970), Petrochencko (1971), and Oliva and Zegers (1988). Population and community descriptors of parasites in each sampling year were enumerated. The prevalence, abundance (Margolis et al., 1982), and relative abundance

(number of individual parasites of a determined species divided by the total number of parasites of each infracommunity) were obtained for each parasite species; infracommunity data included average of species richness, total abundance (Díaz and George-Nascimento, 2002), and Simpson's dominance (Magurran, 1988). Nonparametric analyses were applied, given that the data were not normally distributed (Zar, 1999). A significance level of $P < 0.05$ was used for statistical analyses.

Ninety-four percent ($n = 95$) of the hosts examined harbored at least 1 parasite taxon. In total, 5,532 parasites were collected; 12 taxa were identified, of which the majority were endoparasitic larvae. Five taxa were uncommon, i.e., infrequent or less abundant parasites, whereas 7 parasite taxa were found in all 3 yr of sampling (Table I). The tetraphyllidean cestodes, followed by the nematodes *Pseudoterranova* sp. and *Anisakis* sp., were the most prevalent and abundant parasites in all of the samples (Table I). The prevalence of each parasite taxon was compared between years using a 2×2 contingency table, and the statistical significance was evaluated with a Chi square test (Zar, 1999), whereas the average of parasite abundance was compared among years by a Kruskal-Wallis test. Annual variations were found in the prevalence of *Proctoeces lintoni*, *Nybelinia* sp., *Grillotia* sp., the tetraphyllidean larvae, and *Anisakis* sp. ($P < 0.04$ in all cases; Table I), and in the abundance of *Nybelinia* sp., tetraphyllidean cestodes, *Anisakis* sp., and *Pseudoterranova* sp. ($P < 0.007$ in all cases). In all comparisons the sample taken in 1999 differed from the fish captured in 2006 and 2007. Despite these differences, none of the years was dominated by any parasite in particular, given that the correspondence analysis between the sampling year and the infrapopulation parameters of parasites, i.e., prevalence, abundance, and relative abundance, were not related to one another ($P > 0.10$ in all cases).

All of the fish collected were adults, and their body lengths ranged between 18.0 and 32.8 cm (25.2 ± 4.1 cm), with significant differences among the samples (Kruskal-Wallis test, $H_{(2)} = 8.66$, $P = 0.01$); fish of shorter body length were obtained in 1999 (23.6 ± 2.8 cm) compared to those collected in the other samples (2006: 26.8 ± 3.9 cm; 2007: 25.1 ± 4.4 cm). With the aim of reducing the effect of this variable on the results, a sample of 77 toadfish was selected by excluding those fishes with the smallest (<20 cm) and the largest body lengths (>31 cm). The selected sample was composed of 22, 22, and 33 specimens for 1999, 2006, and 2007, respectively. The selected sample of fish did not show significant difference in the body lengths among years (Kruskal-Wallis test, $H_{(2)} = 5.57$, $P = 0.07$). Although female fishes were smaller than the males (Mann-Whitney, $U = 50$, $P < 0.001$), parasite infracommunity richness (Mann-Whitney, $U = 223.5$, $P = 0.71$) and total abundance ($U = 224.5$, $P = 0.72$) did not differ.

However, at the infracommunity level, richness and total abundance of parasites varied significantly between sampling years (Kruskal-Wallis test, $n = 77$, richness: $H_{(2)} = 17.11$, $P < 0.01$; total abundance: $H_{(2)} = 17.71$, $P < 0.01$). The sample from 1999 registered the lowest total infracommunity abundance and richness of parasites (Table I). Parasite dominance did not show significant differences across years (Kruskal-Wallis test, $n = 77$, $H_{(2)} = 5.15$, $P = 0.08$), as the average of this parameter varied between 0.67 ± 0.31 and 0.79 ± 0.30 .

The parasite species composition and the abundance of each species was analyzed through a non-metric multidimensional scaling (NMDS) with the software Primer-E (Clarke and Gorley, 2001). Previous to the application of this analysis, the data were organized in a similarity matrix that was calculated using the Bray-Curtis coefficient. Two analyses were performed, one for abundance (previously transformed to $\log_{10}[x + 1]$) and other for relative abundance of parasites, considering the parasitized fish only ($n = 95$), which includes the data that can be used in the NMDS. The adjustment of the analysis was evaluated by means of the Kruskal's stress test and was interpreted in accordance with Clarke and Warwick (2001). Subsequently the scores of the first and second dimensional axes, which generally show the largest variation between groups obtained from the NMDS for each host specimen per

TABLE I. Parasite taxa of the toadfish *A. porosus*: site of infection, total number of parasite individuals per taxa (N), prevalence (P, %), mean abundance (A), and standard deviation (SD) of parasites found in 101 toadfish collected in 1999, 2006, and 2007 from the intertidal rocky zone.

Parasite taxa*	Site†	1999 (n = 22)			2006 (n = 30)			2007 (n = 49)		
		N	P	A (SD)	N	P	A (SD)	N	P	A (SD)
Digenea	DT									
<i>Proctoeces lintoni</i> ¹					1	3.3	0.03 (0.18)	14	16.3	0.29 (1.04)
Cestoda										
<i>Nybelinia</i> sp. ^{1,2}	CC	2	9.1	0.09 (0.29)	3	6.7	0.10 (0.40)	38	34.7	0.78 (1.56)
<i>Grillotia</i> sp. ²	CC	1	4.6	0.05 (0.21)				7	14.3	0.14 (0.35)
Tetraphyllidea gen. sp. ¹	DT	140	59.1	6.36 (12.45)	1,920	80.0	64.00 (67.99)	2,795	87.8	57.04 (62.98)
<i>Clestopothrium crassiceps</i>	DT	5	13.6	0.23 (0.61)	9	23.3	0.30 (0.60)	182	32.6	3.71 (15.27)
Pseudophyllidea gen. sp.	CC							1	2.0	0.02 (0.14)
Acanthocephala										
<i>Corynosoma</i> sp.	CC	3	13.6	0.14 (0.35)	28	13.3	0.93 (4.38)	22	24.3	0.45 (1.06)
<i>Polymorphus</i> sp.	CC				1	3.3	0.03 (0.18)	2	4.1	0.04 (0.20)
Nematoda										
<i>Anisakis</i> sp. ^{1,2}	M, CC	2	4.6	0.09 (0.43)	10	23.3	0.33 (0.66)	81	63.3	1.65 (2.79)
<i>Pseudoterranova</i> sp.	M, CC	22	59.1	1.00 (1.23)	128	80.0	4.27 (5.48)	98	65.3	2.00 (2.53)
Spirurida gen. sp.	DT	2	4.6	0.09 (0.43)						
Hirudinea										
<i>Platybdella chilensis</i>	BS	3	13.6	0.14 (0.35)	4	10.0	0.13 (0.43)	8	14.3	0.16 (0.43)
Total sample (n = 101)										
Mean abundance ± SD			8.18 ± 12.88			70.13 ± 71.45			66.29 ± 69.47	
Richness of species ± SD			1.82 ± 1.01			2.40 ± 1.40			3.59 ± 1.51	
Selected sample (n = 77)										
Mean abundance ± SD			8.18 ± 12.88			51.45 ± 54.46			62.12 ± 63.64	
Richness of species ± SD			1.82 ± 1.01			2.05 ± 1.01			3.45 ± 1.60	

* Prevalence of parasite statistically different between years: (1) 1999 and 2007; (2) 2006 and 2007 (see text).

† Site of infection in the host: BS = body surface, CC = celomic cavity, DT = digestive tract, M = muscles.

year, were compared by means of a Kruskal-Wallis analysis (Zar, 1999). The relative abundance data had a better fit (stress = 0.07) than the abundance of parasites (stress = 0.22), because the similarity distances of data were more variable in the abundance of parasites. In fact, when the abundance was used, axis scores were significantly different among years for the first and second dimension (Kruskal-Wallis test, first axis: $K_{(2)} = 13.42$, $P = 0.001$; second axis: $K_{(2)} = 10.57$, $P = 0.005$). However, when the relative abundance of parasites was used, the 2 axis scores were not significantly different among years for the first and second dimension (Kruskal-Wallis test, first axis: $K_{(2)} = 5.46$, $P = 0.07$; second axis: $K_{(2)} = 2.56$, $P = 0.28$).

The parasite composition and NMDS scores, for the first-dimensional axis representing parasite abundances, are shown in Figure 1. The abundances and the position of each species of parasites are on the vertical axis against the horizontal axis represented by the host body length. The parasite species closer to the majority of the data were in most infracommunities. Therefore, a few parasite taxa can be considered as common (anisakid nematodes, *Nybelinia* sp., Tetraphyllidea, and *Corynosoma* sp.). The first-dimensional axis showed a great overlap between host specimens, so there were no differences between hosts of different body lengths (Fig. 1).

The use of different descriptors is necessary to analyze community variation because each of them give different information. In this context the parasite communities of the toadfish has low variation over time if we consider parasite composition (parasite identity), dominance of parasites (a few taxa were more abundant in all samples), and relative abundance (the proportion of parasite species was stable). Nevertheless, the same parasite communities of this fish can be determined as highly variable because the average abundance of some species, species richness, and total abundance of parasites differ greatly among years. These findings are not unusual because parasite communities that vary over time do so in species composition or in their aggregate parameters, but

not both (see Balboa and George-Nascimento, 1998; Bennet et al., 1998; Garcías et al., 2001; Díaz and George-Nascimento, 2002; Kennedy and Moriarty, 2002; González and Oliva, 2006; Campbell et al., 2007). Consequently those communities with low community variations over time are those with little variations in the species composition and in their community aggregate descriptors. In any event, those communities with dominant species seem to be more constant over time (e.g., Kennedy and Moriarty, 2002). However, parasite communities can be within a wide range of variation degrees in total abundance, prevalence, and species composition; it is difficult to determine when, or at what level, the parasite communities significantly change over time (e.g., Garcías et al., 2001; Díaz and George-Nascimento, 2002).

Based on this premise, Micheli et al. (1999) noted different results in community variability based on different descriptors (species composition, abundance, and relative abundance). Accordingly they proposed 4 categories for community variability, i.e., stasis, compensation, synchrony, and asynchrony. According to the characteristics of these categories, the parasite communities of the toadfish are variable over time and would be in the synchronic group because these communities had low compositional variation over time, but they showed great variation in average abundance of parasites among years. However, the relative abundance of each parasite species per fish sample kept a similar proportion (see Table I) that was also reflected in the low variation of the relative abundance of parasites across the 3 yr. The synchronic pattern of community variation can occur when species in that community are responding similarly to abiotic changes. Moreover, it may imply a positive relationship between species (Micheli et al., 1999), which is possible in parasite communities of fishes because there is much evidence regarding the lack of interspecific competition (e.g., Rohde, 1993; Poulin 1998).

In several studies regarding temporal variations of parasite infracommunities, it has been determined that differences in body size of hosts

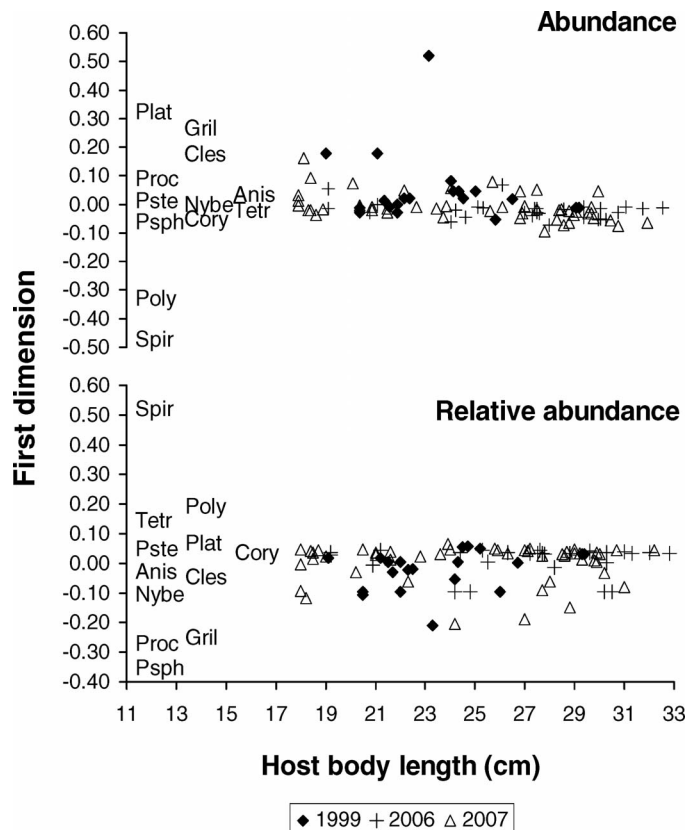


FIGURE 1. Relationship between the first compositional dimension axis of the NMMDS analysis, based on the abundance and relative parasite abundance of 95 infracommunities of *A. porosus* (parasitized only), and the host body length per sampling year. Parasite taxa listed in front of his position in the respective axes of NMMDS. Abbreviations are: Proc: *P. lintoni*; Nybe: *Nybelinia* sp.; Gril: *Grillotia* sp.; Tetr: Tetracyllidae; Cles: *C. crassiceps*; Psph: Pseudophyllidae; Cory: *Corynosoma* sp.; Poly: *Polymorphus* sp.; Anis: *Anisakis* sp.; Pste: *Pseudo-terranova* sp.; Spir: Spirurida gen. sp.; Plat: *P. chilensis*.

have been the main cause of variation (Garcías et al., 2001; Díaz and George-Nascimento, 2002). In the present study, however, host body size was not a determining factor (see Fig. 1), given that the infracommunity analysis was based on samples with similar host body lengths; variations in intrapopulations and infracommunities must be due to other causes. For example, it was determined that environmental variations, e.g., temperature, turbidity, salinity, sea level, and the presence of polluting agents, can increase or reduce the number of individuals in certain populations of parasites (Mikheev et al., 2000; Tucker et al., 2000; Hogue and Peng, 2003; Sures, 2005; Poulin and Mouritsen, 2006). In addition, hosts can also be affected by these factors, influencing their population size and susceptibility to certain parasite species. However, we are unable at present to identify the nature of those factors that may influence the variations found in the parasite infracommunities of *A. porosus*. Nevertheless, there have been several biotic and abiotic changes in the littoral zone of Chile. For the intertidal and shallow subtidal zones, species composition and physical conditions have been changing through spatial and temporal scales, with unpredictable within-year patterns (Thiel et al., 2007). Distribution and species interactions have not only been affected by oceanographic processes, but also by human activities, such as overfishing and pollution (Thiel et al., 2007). In fact, the demersal zone of central Chile, where the toadfish normally lives, has suffered great changes in the abundances of some fish species when overfishing became a serious problem in the 1990s (Sernapesca, 2005). Constant population declines by just a few species in an ecosystem can affect the abundances and interactions of other species over time. Con-

sequently several factors may have influenced the parasite fauna of the toadfish among years.

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