ONTOGENETIC VARIATION IN PARASITE INFRACOMMUNITIES OF THE CLINGFISH *SICYASES SANGUINEUS* (PISCES: GOBIESOCIDAE)

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ABSTRACT: This study analyzed the variation of the parasite infracommunities and their relationship with the diet and spatial distribution of the clingfish *Sicyases sanguineus* during its ontogeny. In total, 154 clingfish were collected from the intertidal and the upper subtidal zone of Pacific Ocean along the central Chilean coast. A wide range in body length (1.4–34.5 cm) was observed, including juvenile and adult specimens. Eleven parasite species were found in the clingfish, i.e., 2 Copepoda, 2 Hirudinea, 1 Monogenea, 5 Digenea, and 1 Cestoda. The prevalence, total abundance, Brillouin's diversity index, and the infracommunity species richness increased with fish body length. The parasite communities, the diet, and the spatial distribution changed during clingfish ontogeny, specifically between juveniles (<20 cm body length [BL]) and adults (>20 cm BL). When fish reached a 20-cm BL, a considerable increment in abundance and species richness of parasites was observed; this coincided with an increase in the number of prey items in the diet and with a change of the fish from the intertidal into the subtidal zone. Therefore, the ontogeny of *S. sanguineus* is important for the variation of parasite infracommunities, which also was associated with dietary and spatial distribution shifts of this fish.

Parasite infracommunities, which refer to populations of parasites in an individual host organism (Bush et al., 1997), are variable over time and space for several reasons. One source of such variability is the parasite's habitat, which may, in part, correspond to the host body. This habitat usually changes in size and physiology over time due to growth and reproduction. Each ontogenetic variation in host organisms could possibly affect, in different ways, the composition, abundance, richness, and prevalence within parasite infracommunities (Timi et al., 2010).

Normally, host ontogeny is associated with changes in body size (length or weight). Thus, an examination of a wide range of host body sizes, consisting of different developmental stages, can provide different parasite species and its variation through host body size and ontogeny. Many studies have demonstrated that abundance, prevalence, and species richness of parasite infracommunities increase with host body size (e.g., Geets et al., 1997; Lo et al., 1998; Amundsen et al., 2003; Violante-González et al., 2010). In general, a larger fish is more likely to be sexually mature and more likely to have been exposed to parasites for a longer time, thereby increasing the probability of larger infrapopulation sizes and greater infracommunity diversity of parasites. Accordingly, larger fish may have more, or different, parasite species than smaller fish (Ryce et al., 2004; Zapata et al., 2006). Finally, piscine hosts frequently change their behavior and habitat preferences during the aging process. In fact, many fish species shift their diet and habitat requirement at different phases of their lives (e.g., Labropoulou et al., 1997; Morato et al., 2000; Gning et al., 2008; Lecchini and Poignocec, 2009). Collectively, these changes can strongly affect the composition, abundance, and species richness of parasites.

The clingfish *Sicyases sanguineus* (Müller and Troschel, 1843) is an interesting species in which to investigate the significance of host ontogeny on parasite infracommunities, because it undergoes a dietary shift during maturation (Cancino and Castilla, 1988). Moreover, the changes in the diet of the clingfish are associated with its habitat. *Sicyases sanguineus* is a common species that inhabits the middle and upper intertidal habitats along the rocky coast of South America, from southern Peru to southern Chile (Buen, 1960). This species has been described as a generalist consumer that will eat both animals and vegetation (Paine and Palmer, 1978; Cancino and Castilla, 1988). Individuals with a body length (BL) <15 cm are typically found in the high intertidal zone and feed mainly on algae, whereas the larger individuals, BL > 23 cm, are found in the low intertidal and subtidal zones and prey mainly on invertebrates, e.g., gastropods, bivalves, and crustaceans (Cancino and Castilla, 1988). These differences in distribution and diet among fishes of different sizes should have an effect on the parasite infracommunities of *S. sanguineus*, which we predict to change significantly in fishes with BL of approximately 20 cm. Therefore, the aims of the present study were to describe the parasite infracommunities of the clingfish and to analyze the change in clingfish diet and parasite infracommunities in relation to fish ontogeny.

MATERIALS AND METHODS

Specimens of the clingfish, *S. sanguineus*, were collected in central Chile, on the rocky intertidal zone from Las Cruces (33°29′S, 71°37′W) and in the intertidal and subtidal zones from Reñaca (32°57′S, 72°57′W), between August and November 2007 and in June 2008. Fish were collected by hand or by using nets in the intertidal rocky pools, and with a "chinguillo" (a mesh with a handle of 1.5–2.0 m in length) while fishing in the subtidal zone. In total, 154 specimens were collected. Fish were stored in plastic bags; ~90% of them were frozen at −10 C, the remainder was dissected while fresh. We measured the total length of fish body (BL) and the state of sexual maturity was determined by direct observation of the gonads. Juveniles have white, sometimes translucent small gonads, whereas adults have large gonads distinguished by color and structure. Male gonads are white and compact; seminiferous tubules can be visualized using microscopy. Female gonads are yellowish and oocytes are easily seen (Cerisola, 1984).

The skin, fins, mouth, and gill cavity were checked for ectoparasites. At necropsy, muscles, internal organs (digestive tract, liver, heart, kidney, and gonads), and the internal cavity were examined for endoparasites. The isolated parasites were preserved in 10% formalin, and the taxonomic identification was accomplished using Villalba and Fernández (1985), Oliva and Zegers (1988), Bray (2002), Gibson (2002), and Overstreet and Curran (2002).

Prevalence, mean abundance, mean total abundance, and mean infracommunity richness were calculated according to Bush et al. (1997). Brillouin's diversity index and the total prevalence were calculated according to Magurran (1988) and Muñoz et al. (2002), respectively.

To study the diet of the clingfish, the food content of digestive tract of 104 clingfish was analyzed. All food contents of each fish were washed, and prey items were separated and then preserved in 10% formalin.

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Identification of each food item was made to the lowest taxonomic level possible. We calculated the percentage frequency of occurrence (FO%) of each food item, defined as the percentage of guts containing certain food items in relation to the total number of guts with food contents (Hyslop, 1980).

To establish differences in parasites and diet during the ontogeny of *S. sanguineus*, the prevalence, mean total abundance, mean infracommunity richness, mean species diversity, component community richness (number of parasite species in all hosts) and the number of prey consumed were compared between specimens that were smaller (juveniles) and larger (adults) than 20 cm in length by using the Mann–Whitney U-test and 2×2 contingency table (Zar, 1996). To determine the importance of fish body length for total abundance, diversity, and richness of parasite infracommunities, and the number of prey items, Spearman correlations (r_s) between these variables were applied (Zar, 1996).

RESULTS

Of the total number of fish sampled, 36 were females, 24 males, and 95 juveniles. BL varied between 1.4 and 34.5 cm, for which 7 arbitrary BL ranges were generated (Table I). Eighty-seven percent of the fish sampled had at least 1 parasite species. In total, 902 parasite individuals, represented by 11 species (5 ectoparasites and 6 endoparasites), were present. The trematode *Proctoeces* sp. had the highest mean abundance (2.30 ± 9.16) and prevalence (46%) among endoparasites, whereas the copepod *Acanthochondria sicyasis* had the highest mean abundance (1.84 ± 5.59) and prevalence (20.3%) among ectoparasites.

Few parasite species were found in small fish ≤15 cm BL, with most parasites appearing in host fish between 15 and 20 cm BL, although abundances were low (Table I). More parasites in higher abundances or prevalence were found in fish >20 cm BL (Table I). The copepods *A. sicyasis* and *Lepeophtheirus* sp.; 1 leech (Pisicolidae sp. 1); and the trematodes *Proctoeces lintoni*, *Helicometrina nimia*, and *Lecithaster* sp. appeared in fish with a BL > 15 cm (Table I). Only *Proctoeces* sp. was found both in small and large fish and was the most prevalent and abundant in medium-sized fish (10- and 20-cm BL; Table I). The monogenean *Gyrodactylus* sp. was initially found mainly on small fish. However, this parasite was subsequently detected during a later stage of this research; it was presumably overlooked due to its small size (0.150 mm); hence, only prevalence was considered in the data analysis (Table I). Only 2 individuals of *Lepeophtheirus* sp. were found in 1 fish 27.7 cm in BL. Only 2 fishes harbored 1 leech each (Pisicolidae), and 1 individual with the larval stage of a pseudophyllidean in a small fish of 1.7-cm BL.

The mean total abundance, mean species richness, and mean diversity of parasite infracommunities were 14.9 ± 5.8, 1.0 ± 1.3, and 0.14 ± 0.30, respectively. These descriptors showed positive and significant relationships with body length of *S. sanguineus*: total abundance, $r_s = 0.708$, $P < 0.001$ and $r_s = 0.644$, $P < 0.001$ for ecto- and endoparasites, respectively (Fig. 1A); infracommunity species richness, $r_s = 0.706$, $P < 0.001$, $r_s = 0.638$, $P < 0.001$ for ecto- and endoparasites, respectively (Fig. 1B); and total diversity of parasites, $r_s = 0.675$, $P < 0.001$ (Fig. 1C). The breakpoints of total abundance, diversity and infracommunity species richness of parasites were in fish with a BL of 20 cm and are clearly seen in Figure 1.

After separating the sample into 2 groups according to size, BL <20 cm and BL > 20 cm, we found the component community richness was similar between both groups of fish. However, prevalence, mean abundance, mean diversity, and mean infra-community richness were significantly higher in clingfish larger

TABLE I. Mean abundance (A) and percentage of prevalence (P) of parasite from 7 body length groups (BL ranges, centimeters) of *Sicyases sanguineus*. N is number of fishes in each body length group; mean BL (SD) per each group.

BL range	<5.0 A	<5.0 P	5.1–10.0 A	5.1–10.0 P	10.1–15.0 A	10.1–15.0 P	15.1–20.0 A	15.1–20.0 P	20.1–25.0 A	20.1–25.0 P	25.1–30.0 A	25.1–30.0 P	30.1–35.0 A	30.1–35.0 P
Mean BL (SD)	2.23 (0.56)		8.40 (0.67)		13.04 (1.38)		17.87 (1.48)		22.13 (1.80)		26.92 (1.23)		31.81 (1.56)	
N	33		44		28		21		15		5		8	
Ectoparasite														
Piscicolidae gen sp. 1*					0.1	4	0.1	5	2.9	67	5.6	100	7.6	75
Piscicolidae gen sp. 2*							<0.1	5	0.1	13				
Acanthochondria sicyasis							0.3	19	4.6	93	14.0	100	17.1	100
Lepeophtheirus sp.											0.4	20		
Gyrodactylus sp.*		100†		33.3†		20.0†		0†		0†				
Endoparasite														
Helicometrina nimia							0.6	5	0.5	27	5.6	60	1.3	50
Proctoeces lintoni							<0.1	5	0.3	13	0.8	40	1.3	38
Proctoeces sp.*			0.6	39	3.1	82	3.4	86	8.1	47	4.4	40	2.9	50
Lecithaster sp.							0.1	5	4.2	27			0.3	13
Prosorhynchoides sp.*									0.7	13	0.4	40	1.3	25
Pseudophyllidea gen. sp.‡	<0.1	3												

* Undescribed species.
† Number of fish revised was 8, 9, 20, 3, and 2, respectively.
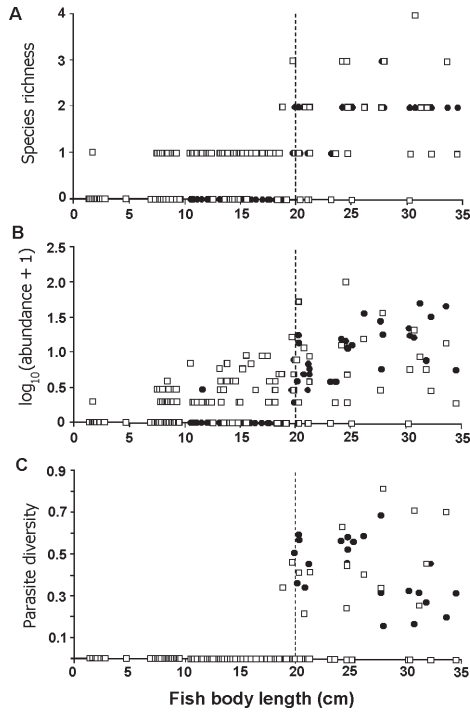‡ Larval stage.

FIGURE 1. (**A**) Species richness. (**B**) Total abundance. (**C**) Diversity of parasite infracommunities correlated to body length of *Sicyases sanguineus*. (●) Ectoparasites. (□) Endoparasites. Broken line sets at 20-cm fish BL, where parasite descriptors significantly increase.
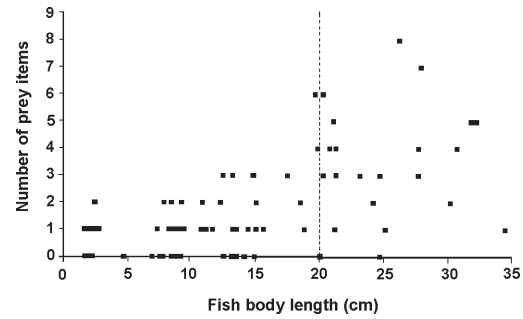

FIGURE 2. Relationship between the numbers of animal prey items in the gut and body length of *Sicyases sanguineus*. Broken line identifies 20-cm fish BL, where diet frequency significantly increases.

significantly correlated to the BL of fish ($r_s = 0.600$, $P < 0.001$; Fig. 2). When the clingfish reached 20 cm in BL, there was an apparent increase in food items (Table II); between 1.4- and 20-cm BL, the clingfish exhibited a maximum of 3 items, whereas in fish >20 cm in BL, there was a maximum of 8 items (Fig. 2). The total number of food items and species richness, diversity, and abundance of endoparasites were significantly correlated (n = 77; $r_s > 0.46$, $P < 0.01$ for the 3 descriptors).

DISCUSSION

Here, we have determined the importance of clingfish *S. sanguineus* ontogeny on the variation of parasite populations and communities. Larger adult fish had higher abundances and species richness of ecto- and endoparasites than smaller juvenile fish. As we predicted, there was a great change in parasite abundance and richness in fish >20 cm in BL. This can be associated with ontogenetic dietary changes that occurred ~20 cm in BL; clingfish grow and move from the intertidal to the rocky subtidal zone, where they reach sexual maturity and lay eggs on the rocks (Pérez, 1981; Cancino and Castilla, 1988). The increase in energy requirements due to growth and reproduction lead to an increase in the quantity, size, and diversity of prey consumed. Clingfish >20 cm in LB had more dietary items than smaller fish. This included a greater number of crustacean taxa that, in general, are the intermediate hosts for many endoparasitic species (Marcogliese, 1995; Cribb et al., 2003). Therefore, the increase of

than 20 cm than in fish smaller than 20 cm ($P < 0.001$ for all descriptors; Table II).

From 104 clingfish specimens, only 77 had identifiable food contents; 13 presented only macroalgae, 21 only invertebrates, and 43 possessed both macroalgae and invertebrates. The spectrum of animal prey was composed of 35 taxa, mainly molluscs and crustaceans (Appendix 1). The most frequent item was the mussel *Semimytilus algosus*. The smaller clingfishes (BL <5 cm) did not feed on molluscs, but they frequently preyed on small crustaceans. In larger clingfishes (BL > 15 cm), molluscs were more frequent food items than crustaceans. The frequency of occurrence of molluscs and crustaceans increased with body size (Table I). The number of food items found in *S. sanguineus* was

TABLE II. Parasite descriptors and host traits for 2 groups of *Sicyases sanguineus*: small clingfishes (BL < 20 cm) and large clingfishes (BL > 20 cm).

Variables	BL < 20 cm	BL > 20 cm
Parasites descriptors		
Prevalence (%)	46.4	100
Mean abundance ± SD	1.33 ± 2.44	25.38 ± 26.73
Mean infracommunity richness ± SD	0.54 ± 0.67	3.21 ± 1.37
Mean infracommunity diversity ± SD	0.02 ± 0.11	0.65 ± 0.34
Component community richness	8	9
Host traits		
All prey items ± SD	2.06 ± 1.52	4.28 ± 2.03
Invertebrates prey ± SD	1.01 ± 1.14	3.52 ± 2.04
Habitat	Intertidal: crevices in exposed rocks	Low intertidal and subtidal zones: on rocks exposed to waves
Maturity stage	Juveniles	Mature adults

the consumption of crustaceans would presumably increase the possibility of acquiring a higher number and greater diversity of parasites.

Ectoparasites also were more abundant and prevalent in clingfish >20 cm. When clingfish move to new habitats, they are of greater body size and present a larger "target" for the recruitment of bigger ectoparasites, such as the leeches and the copepod *A. sicyasis*. Furthermore, it is possible that the calmer physical conditions of the subtidal environment are better for the transmission and permanence of ectoparasites.

Variations in parasite communities have been observed in other temporal intertidal fish, i.e., *Bovichthys chilensis* and *Aphos porosus* (see Muñoz et al., 2002; Cortés and Muñoz, 2008). Similar to *S. sanguineus*, these 2 species also move to the subtidal zone at some point in their development. Generally, parasite richness in these fishes is positively correlated with body size and increases as they move from the intertidal to subtidal zones (Muñoz et al., 2002). It is also important to note that animal biodiversity of temperate subtidal and intertidal zones can be different (Kukliński and Barnes, 2008); thus, the diversity and richness of intermediate hosts strongly affect the composition of the parasite fauna of fish in both habitats.

Trematodes were common in *S. sanguineus*. Most of these parasites were present in clingfish larger than 15 cm, which is in accordance to the change in diet. Thus, *Helicometrina nimia* and *Lecithaster* sp. are transmitted to the definitive host by crustaceans, which are normally the second intermediate hosts for these trematodes (Cribb et al., 2003). The occurrence of these parasites can be explained by increased predation on crustaceans (Cirripedia and Decapoda) as the fish grow in size. The presence of *Prosorhynchoides* sp. in clingfish, however, is surprising because all known bucephalids are transmitted as metacercaria in the flesh of fish (Cribb et al., 2003; Pina et al., 2009). However, the clingfish's diet is not known to include fish (Paine and Palmer, 1978; Cancino and Castilla, 1988; Muñoz and Ojeda, 1997; this study). Either the assumed life cycle of this trematode species is incorrect, or the feeding habit of clingfish is misrepresented in the literature.

Proctoeces spp. were the most common trematodes of the clingfish. Species of *Proctoeces* use a bivalve as the first host and another mollusc as the second intermediate host (Bray, 1983; Cribb et al., 2003). *Proctoeces lintoni* was mostly present in large fish with a more carnivorous diet (Table I), whereas *Proctoeces* sp. was more abundant in smaller fish (5–10-cm BL) that mostly have a herbivorous diet. The presence of *Proctoeces* sp. in small fish could be possible if this trematode has a 2-host cycle in which the sporocysts and metacercarias are in a single bivalve species as reported for *Proctoeces maculatus* (Wardle, 1980). Alternatively, perhaps the cercariae are directly consumed by the definitive host as reported for some fellodistomid trematodes (Bray, 1988). These possibilities require further study. The presence of *P. lintoni* has been linked to ingestion of infected limpets (*Fissurella* spp.), which normally harbor this trematode in a so-called "non-encysted metacercaria" stage, and it has been assumed that the transmission of *P. lintoni* is via ingestion of limpets (George-Nascimento et al., 1998; Oliva and Huaquín, 2000). In the present study, *P. lintoni* appears in clingfish larger than 15 cm, which coincides with the presence of limpets in their diet (Table II). However, the average shell length of limpets found in the clingfish in the present study, 1.6 ± 0.2 cm (maximum shell length of

3.4 cm), was smaller in comparison with the shell lengths reported previously for limpets parasitized with *P. lintoni* (Oliva and Díaz, 1992; Oliva and Vásquez, 1999). Thus, the lengths of limpets preyed on by clingfish here and the limpets that are parasitized with *P. lintoni* in previous studies are inconsistent. It is possible that the transmission of *P. lintoni* to the clingfish here may imply another secondary intermediate host, possibly the gastropod *Concholepas concholepas* that also harbors sporocysts of an unidentified species of *Proctoeces* (Oliva et al., 1999). However, the length of the gastropods consumed and the minimal length reported for parasitized gastropods is inconsistent as well. Consequently, *Proctoeces* transmission may imply other molluscan species as intermediate host.

This is the first study to describe parasite infracommunities of the clingfish *S. sanguineus*. The parasite community was composed of a variety of species (Table I), several of which represent new records for this host and for Chile. For example, the leeches, the monogenean *Gyrodactylus* sp., and the trematode *Prosorhynchoides* sp. are new species records for Chile (cf., Muñoz and Olmos, 2007, 2008). We also demonstrate that the ontogeny of *S. sanguineus* is an important variable for the variation of parasite infracommunities, which is associated with dietary and spatial distribution changes of this fish, similar to other temporal intertidal fish species.

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APPENDIX 1. Dietary composition of *Sicyases sanguineus*. Percentage of frequency of occurrence of each prey item from 7 ranges of the fish BL (centimeters). n is number of specimens with food content.

BL ranges	<5.0	5.1–10.0	10.1–15.0	15.1–20.0	20.1–25.0	25.1–30.0	30.1–35.0
n	10	21	18	7	11	5	5
Food items							
MACROALGAE	10.0	85.7	100.0	71.4	63.6	20.0	100.0
MOLLUSCA							
Bivalvia							
Perumytilus purpuratus				42.9	18.2	20.0	40.0
Semimytilus algosus		4.8	11.1	28.6	72.7	80.0	80.0
Brachidontes granulatus		4.8					
Gastropoda							
Littorina araucana			16.7	14.3	27.3		
Scurria scurra				14.3			20.0
Concholepas concholepas					9.1	20.0	
Acanthina monodon				14.3		20.0	
Fissurella sp.				14.3	9.1	60.0	40.0
Muricoidea gen. sp.					9.1		
Trochacea gen. sp.						20.0	
Patelloidea gen. sp.		14.3	11.1	28.6	36.4	20.0	40.0
Crepiduloidae gen. sp.					9.1	20.0	
Columbellidae gen. sp.						20.0	
Polyplacophora gen sp.			5.6			20.0	
Cephalopoda				14.3			
CRUSTACEA							
Cirripedia							
Balanus laevis					9.1	40.0	
Balanus flusuculus			16.7	28.6	36.4	40.0	20.0
Chthamalus sp.					9.1		20.0
Verruca laevigatus							20.0
Unidentified specimens				14.3	9.1		40.0
Decapoda							
Acanthocyclus sp.							20.0
Pilumnoides purpuratus						20.0	
Pisoides edwarsi						20.0	
Unidentified specimens						20.0	
Isopoda					9.1		
Amphipoda	40.0	14.3	5.6				
Copepoda	40.0						
Unidentified crustaceans	10.0	4.8					
INSECTA							
Unidentified adult specimens		4.8	5.6				
Unidentified larvae 1	20.0	23.8	38.9	42.9			
Unidentified larvae 2			11.1				
ANNELIDA							
Polychaeta		4.8			27.3		
ECHINODERMATA							
Tetrapygus niger					9.1		
FORAMINIFERA						20.0	