## Similarity and structure of the ectoparasite communities of rockfish species from the southern Chilean coast in a temporal scale

## M. T. GONZÁLEZ<sup>1,2\*</sup> and M. E. OLIVA<sup>1</sup>

<sup>1</sup>Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta. Casilla 170-Antofagasta, Chile <sup>2</sup>Instituto de Ecología y Evolución, Universidad Austral de Chile. Casilla 567-Valdivia, Chile

(Received 2 March 2006; revised 19 March 2006; accepted 19 March 2006; first published online 6 June 2006)

#### SUMMARY

The understanding of the patterns and processes underlying the structure of parasite communities has progressed significantly in the last years; however, much of the evidence available to date on parasite community comes from unconfirmed studies. In this study the ectoparasite communities of 2 related rockfishes, *Sebastes capensis* and *Helicolenus lengerichi*, from the southern Chilean coast (ca.  $40^{\circ}$ S) were examined to determine whether their specific compositions are similar, structured in non-random ways, and repeatable among years. From 2001 to 2004, 189 specimens of *S. capensis* and 101 of *H. lengerichi* were examined, 10 and 9 parasite species were recorded in *S. capensis* and *H. lengerichi*, respectively. Component ectoparasite communities of these hosts were taxonomically similar (60%), but the abundances and prevalences of their parasites differed significantly among years and between hosts. The most prevalent species were *Lepeophtheirus chilensis*, and *Microcotyle* sp. for *S. capensis*, and *Microcotyle* sp., *Juanetia continentalis*, and *Interniloculus chilensis* for *H. lengerichi*. Infracommunities of *S. capensis* showed higher species richness and parasite numbers than those of *H. lengerichi*. The similarity among infracommunities (measured as parasite abundance) varied significantly among years both within and between hosts. Despite this, temporal nestedness patterns were observed in infracommunities of these hosts, suggesting that their ectoparasite communities are structured and might be predictable in time, at least in the southern Chilean coast where they share the same habitat.

Key words: infracommunity, structure, nestedness, similarity, Sebastes capensis, Helicolenus lengerichi, southern Pacific.

#### INTRODUCTION

The parasite communities of fishes at infra, component and compound community levels (as defined by Bush *et al.* 1997) are affected by host and parasite phylogeny, historical ecological associations, and current ecological factors such as diet, habitat or niche overlap (Esch *et al.* 1990; Poulin, 1995). Thus, for example, host size or host age, schooling behaviour, and ecological overlap with other host species are factors affecting the parasite infracommunity structure of the hosts (Nelson and Dick, 2002). Likewise, the environmental characteristics such as latitude, temperature and depth can affect the parasite communities of fishes (Rohde *et al.* 1995; Oliva *et al.* 2004).

In the last decade, knowledge of the patterns and processes underlying the structure of parasite communities has progressed significantly (Sousa, 1994; Poulin, 1996, 2001). However, much of the evidence available to date on parasite community comes from unconfirmed studies on either temporal or spatial scales (Poulin and Valtonen, 2002). Therefore, the potential temporal variations in community structure remain an unresolved issue. Recently, some studies have analysed the structure of parasite communities in the same host, considering the variability in time and/or space (Carney and Dick, 2000; Poulin and Valtonen, 2002; Timi and Poulin, 2003; Vidal-Martinez and Poulin, 2003, Zelmer *et al.* 2004; González and Poulin, 2005). Those studies have yielded contradictory results; therefore, additional investigations are required to determine whether the observed patterns are consistent on a temporal scale.

Nested subset analyses are valuable descriptive tools for revealing ecologically meaningful nonrandom patterns, and are useful exploratory tools for suggesting mechanisms that may structure a particular community (Worthen, 1996). A nested pattern has been defined as a departure from a random association of species in which species that compose a depauperate island community constitute a proper subset of those species inhabiting richer islands (Patterson and Atmar, 1986). Nestedness has been well documented for parasites and has been used extensively to test for non-random patterns

*Parasitology* (2006), **133**, 335–343. © 2006 Cambridge University Press doi:10.1017/S0031182006000370 Printed in the United Kingdom

<sup>\*</sup> Corresponding author: Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta. Casilla 170-Antofagasta, Chile. Tel: +56 55 637404. Fax: +56 55 637804. E-mail: mtgonzalez@uantof.cl

among species assemblages (Simková *et al.* 2001; Timi and Poulin, 2003; Zelmer *et al.* 2004; González and Poulin, 2005). Nestedness analyses can be used to assess the predictability of the parasite community structure in both space and time (Poulin and Valtonen, 2002).

In this study we examined the ectoparasite fauna of 2 related fish hosts (Sebastes capensis and Helicolenus lengerichi) from the southern Chilean coast to compare, through multivariate analyses, the degree of similarity of the ectoparasite fauna of these fish hosts at both component and infracommunity levels. Then, we determined, based on nested subset analyses, whether their ectoparasite infracommunities are structured. Lastly, we examined the temporal repeatability of ectoparasite community structure in these fish hosts. The scorpaenids, S. capensis and *H. lengerichi*, are the only species belonging to these genera found along the southeastern Pacific coast (Kong, 1985; Eschmeyer, 2000). These species are morphologically similar, but their bathymetric ranges differ. S. capensis inhabits shallow waters, from depths of 20 m to 150 m, and H. lengerichi inhabits deeper waters, between 50 m and 300 m in depth (Pequeño, 2000). Taking into account the characteristic of these hosts, it is hypothesized that similarity and structure, if any, of their ectoparasite communities can be expected as a consequence of their close phylogenetic relationship and habitat (bathymetric) overlap.

### MATERIALS AND METHODS

From October to December 2001 and November to December 2002, and in April 2003 and September 2004, 189 specimens of *S. capensis* and 101 specimens of *H. lengerichi*, were examined. Fishes were captured as by-catch in the ray (*Dipturus chilensis*) fishery during 2001, 2002 and 2004; and by hand line during 2003 from Valdivia ( $40^{\circ}$ S). The fishes were captured from 40 m to 250 m depth.

Fishes were transported to the laboratory, identified according to Eschmeyer (2000), and by their otolith morphology. The fish were measured (total length (TL), precision 0.5 cm), and sexed macroscopically. The skin, fins, eyes, mouth, and gills were examined for parasites. The collection of parasites followed the traditional parasitological techniques outlined by Pritchard and Kruse (1982). The parasites were fixed in alcohol (70%), and identified using specialized literature (see González and Acuña, 1998).

For each parasite species, abundance and prevalence were estimated according to the protocol of Bush *et al.* (1997). Parasite richness (number of parasite species per host) and the similarity index of Bray Curtis (following log (n+1) transformation of mean abundance data) were calculated at infraand component levels, respectively. Due to the non-normal distribution of the data, non-parametric tests were used (Zar, 1999). For each host fish, the sizes of the examined specimens and species richness per host among different sampling years were compared using the Kruskal-Wallis test. Spearman correlations ( $r_s$ ) were used to evaluate the association between fish size and species richness, and between fish size and abundances of each parasite species.

At the infracommunity level, patterns of similarity in ectoparasite fauna composition, both among years and between hosts, were investigated with multivariate discriminant analyses, using  $\log (n+1)$ transformed abundance data for each parasite species. At the component community level, correspondence analyses were used to evaluate the association between all of the parasite species and the year of sampling (Digby and Kempton, 1987). The analyses were performed using the software Statistica 6.0.

Nested subset analyses were carried out for ectoparasite infracommunities for each fish host in the different years. The matrix "temperature" (T) proposed by Atmar and Patterson (1993) was calculated, using the Nestedness Temperature Calculator Program (NTCP, Atmar and Patterson, 1995). For each community of parasites, the observed matrix temperature was compared with the T values of 1000 randomly generated presence-absence matrices produced with Monte-Carlo simulations. The statistical probability of the observed pattern was given by the proportion of simulated T values that were lower than or equal to the observed T value and was used as a measure of the departure from the structure expected under random assembly (Guégan and Hugueny, 1994). A P value <0.05 indicates communities that are significantly nested, whereas P values > 0.95 characterize significantly anti-nested patterns (Vidal-Martinez and Poulin, 2003).

#### RESULTS

### Parasite community of Sebastes capensis

A total of 10 ectoparasite species was recovered from this host. During the years 2001, 2002 and 2003, 95%, 98% and 100% of the fish, respectively, were parasitized by at least 1 parasite species. The species richness per host varied between 1 and 7 species  $(X=3\cdot0; \text{ s.D.}=1\cdot34)$ . The most prevalent parasite species were *Microcotyle* sp. and *Lepeophtheirus chilensis* through all these years (Table 1). None of the abundances of ectoparasite species were significantly correlated with fish size (P > 0.05 for all species).

The size of *S. capensis* varied between 20 cm and 41 cm TL during the years of sampling (Fig. 1). Significant differences in fish sizes among years were recorded ( $H_{(2, 189)}=100.69$ ; P<0.001). Also, there were significant differences in the parasite species

Table	1. Mean	abundances	and preva	lence (%)	of the	ectoparasites	recorded on	Sebastes	capensis
from '	Valdivia (	$40^{\circ}{ m S}$ ) during	the years	2001, 200	2 and 2	2003			

(S = skin, G = gill, M = mouth.)

	Year				
Species	2001	2002	2003		
Monogenea					
Udonella australis (S)	0.09(8.2)	0.03(3.3)	1.52 (40.3)		
Interniloculus chilensis (G)	0.41(13.1)	0.90(21.3)	0.48(31.3)		
Neobenedenia melleni (S)	0.09(8.2)	1.63(0.03)	0.10(10.4)		
Microcotyle sp. (G)	3.62 (60.6)	4.55 (78.7)	5.56 (95.5)		
Copepoda					
Caligus cheilodactylus (S)	0.31 (24.6)	0.21 (14.8)	2.21 (85.1)		
Lepeophtheirus chilensis (S)	1.13(52.5)	1.60(60.6)	2.10 (77.6)		
Trifur sp. (M)	0.09(6.5)	0.0(0.0)	0.03(1.5)		
Juanetia continentales (G)	0.05 (3.2)	0.06 (1.6)	0.0(0.0)		
Isopoda					
Ĝnathia sp. (S)	5.13 (73.7)	1.18 (62.3)	0.10 (10.4)		
Piscicolidae					
Piscicolidae gen.sp. (S)	0.31 (18.0)	0.04 (3.3)	0.16 (13.4)		
Total no. of parasites	712	574	836		
No. of fish examined	61	61	67		
Species richness	10	9	9		



Fig. 1. Distribution of fish size of *Sebastes capensis* and *Helicolenus lengerichi* during sampling years.

richness per host among years (H<sub>(2,189)</sub>=24.90; P < 0.001). The ectoparasite species richness per host was significantly correlated with host size during 2003 (r<sub>s</sub>=0.32; P=0.007; n=67), but there was no correlation between species richness per host and fish size during 2001 (r<sub>s</sub>=-0.07; P=0.55; n=61) and 2002 (r<sub>s</sub>=-0.15; P=0.23; n=61).

## Parasite community of Helicolenus lengerichi

A total of 9 ectoparasite species was recorded in *H. lengerichi*. During 2001, 2002 and 2004, 100%, 81%, and 100% respectively, of the specimens of this host were parasitized by at least 1 parasite species. The species richness per host varied between 1 and 5 species (X=2.0; s.D. = 1.24). The most prevalent parasite species were *Microcotyle* sp. (*Microcotyle* specimens from both hosts belong to the same undescribed species), *Juanetia continentalis*, and *Interniloculus chilensis* (Table 2). In this host, the abundances of *Gnathia* sp. ( $r_s=0.207$ ; P=0.03; n=101), *Microcotyle* sp. ( $r_s=0.214$ ; P=0.03; n=101) and *I. chilensis* ( $r_s=0.218$ ; P=0.02; n=101) were significantly correlated with fish size.

The sizes of *H. lengerichi* varied between 21·2 cm and 39·7 cm during the studied years (Fig. 1). There was no significant difference in fish sizes between years of sampling ( $H_{(2,101)} = 4.835$ ; P = 0.089). There were significant differences in the parasite species richness per host between years ( $H_{(2,101)} = 27.18$ ; P < 0.001). The ectoparasite species richness per host was significantly correlated with host size during 2002 (r = 0.34; P = 0.009; n = 56), but there was no correlation between species richness per host and fish

## M. T. González and M. E. Oliva

Table 2. Mean abundances and prevalence (%) of the ectoparasites recorded on *Helicolenus lengerichi* from the Valdivia coast (40°S) during the years 2001, 2002 and 2004

(S = skin, G = gill, M = mouth.)

	Year				
Species	2001	2002	2004		
Monogenea					
Udonella australis (S)	0.10 (10.0)	0.02(1.8)	0.00(0.0)		
Interniloculus chilensis (G)	2.30(40.0)	0.98(25.0)	24.48 (85.0)		
Microcotyle sp. 1 (G)	4.60 (90.0)	0.93 (41.1)	2.48 (84.0)		
Copepoda					
Ĉaligus cheilodactylus (S)	0.15(5.0)	0.0(0.0)	0.0(0.0)		
Lepeophtheirus chilensis (S)	0.40(20.0)	0.02(1.8)	0.0(0.0)		
Trifur sp. (M)	0.20(15.0)	0.0(0.0)	0.0(0.0)		
Juanetia continentales (G)	1.35 (40.0)	0.68 (39.3)	0.44 (32.0)		
Isopoda					
Ĝnathia sp. (S)	0.80 (30.0)	0.23 (17.9)	1.00 (44.0)		
Piscicolidae					
Piscicolidae gen.sp. (S)	0.40 (25.0)	0.32 (23.2)	0.16 (12.0)		
Total no. of parasites	712	574	714		
No. of fish examined	20	56	25		
Species richness	9	7	5		



Fig. 2. Discriminant analysis for infracommunities of *Sebsates capensis* during years 2001, 2002 and 2003 using abundances of all parasites recovered during each year of sampling.

size during 2001 (r = 0.40; P = 0.08; n = 20) or during 2004 (r<sub>s</sub> = 0.33; P = 0.10; n = 25).

# Similarity of the ectoparasite community within and between fish hosts

The infracommunities of *S. capensis* harboured higher total numbers of parasite individuals (U=6,459; P<0.001), and showed higher species richness (U=5,777; P<0.001) than the infracommunities of *H. lengerichi*. The similarity between infracommunities within the same host among years, and between infracommunities of both hosts (considering all study periods) were evaluated using multivariate discriminant analyses. In addition to abundance (previously  $\log(n+1)$  transformed),



Fig. 3. Discriminant analysis for infracommunities of *Helicolenus lengerichi* during years 2001, 2002 and 2004 using abundances of all parasites recovered during each year of sampling.

the year and host size were also considered as potential explanatory variables. The infracommunities of S. capensis showed significant differences in parasite abundances among years ( $F_{(20, 354)} = 25.40$ ; P < 0.0001; Wilks' Lambda = 0.168) (Fig. 2). Eightythree percent of infracommunities of this host were correctly assigned in each sampling year. The discriminant variables (those with highest F- to remove) were abundances of Gnathia sp. and C. cheilodactylus, and fish size. Likewise, the infracommunities of H. lengerichi showed significant differences in parasite abundances among years  $(F_{(12, 186)} = 9.94; P < 0.0001; Wilks' Lambda = 0.361)$ (Fig. 3). Seventy-four percent of infracommunities of this host were correctly assigned at each sampling year. The discriminant variables were the



Fig. 4. Multiple correspondence analysis for the parasite component communities of *Sebastes capensis* and *Helicolenus lengerichi* using prevalence of all parasites recovered during each year of sampling.

abundances of *I. chilensis* and *Microcotyle* sp. The multivariate discriminant analysis considering the variables: host species, host size and the abundances  $(\log(n+1) \text{ transformed})$  of each of the parasite species showed significant differences between infracommunities of each host species ( $F_{(12,277)} = 28.438$ ; P < 0.0002; Wilks' Lambda = 0.448). Overall, 89% of the infracommunities were correctly assigned to their respective hosts. The discriminant variables corresponded to those parasite species whose abundances and prevalences are significantly different between fish hosts:  $\mathcal{J}$ . *continentalis*, *I. chilensis*, and *L. chilensis* (see Tables 1 and 2).

At the component community (CC) level, S. capensis and H. lengerichi shared 60% of their parasites. The Bray-Curtis index of similarity of CC composition among years varied between 60% and 81% for S. capensis, and between 63% and 74% for H. lengerichi. Of the shared ectoparasite species 3 are specific to these scorpaeniformes: the copepod J. continentalis, and the monogeneans I. chilensis and Microcotyle sp. The correspondence analyses considering all parasite species (10 and 9 species, respectively) showed that in both hosts there were significant differences among years in their parasite prevalences (S. capensis:  $X^2 = 178.88$ ; D.F. = 18, P < 0.001; H. lengerichi:  $X^2 = 117.26$ , D.F. = 16, P < 0.0010.001). In S. capensis the differences were produced by the samples of 2003. In this year U. australis and C. cheilodactylus were most prevalent. In the case of H. lengerichi, the difference resulted mainly from the high prevalence of I. chilensis during 2004 (Fig. 4). Likewise, multiple correspondence analyses for component communities of each host considering all parasite prevalences and sampling years showed significant differences between hosts: *S. capensis* was strongly associated with the parasites *L. chilensis*, *C. cheilodactylus*, *N. melleni* and *U. australis*, while *H. lengerichi* was associated with their specific parasites: *I. chilensis* and *J. continentalis* (Fig. 4). Thus, although the taxonomic composition of parasites was similar during the studied years, the most prevalent species changed over time.

#### Temporal nestedness analyses for each fish host

Significant nestedness was found in the ectoparasite infracommunities of *S. capensis* and *H. lengerichi* during all years of sampling (Table 3), indicating that common species are found in infracommunities of varying richness, but rare species mainly occur in more diverse infracommunities, and that the ectoparasite community structure departs from randomness through all years of sampling.

#### DISCUSSION

To describe and explain patterns of community structure is one of the central themes in ecology and in fish parasite communities remain an unresolved issue. In this context, the temporal predictability of the parasite communities in fish has not been extensively evaluated because almost all studies are carried out in a short period of time (Poulin and Morand, 2000; Poulin and Valtonen, 2002). Some studies of parasite communities on a temporal scale

Table 3. Summary of the results of nestedness analyses within each ectoparasite component community of *Sebastes capensis* and *Helicolenus lengerichi* from the Valdivia coast (40°S) for different years

(P < 0.05 indicates nested communities. Average = mean of 1000 simulations matrix, and (S.D.) = standard deviation.)

Year	Matrix Fill	Matrix T	Average (s.d.)	P
Sebas	tes cabensis			
2001	26.1%	$20.17^{\circ}$	53·11° (5·2°)	<0.0001
2002	30.0%	$13.01^{\circ}$	$55.13^{\circ}(5.4^{\circ})$	<0.0001
2003	23.1%	18·99°	52·10° (4·8°)	<0.0001
Helico	olenus lengerich	hi		
2001	30.0%	$19.72^{\circ}$	46·04° (8·25°)	<0.0007
2002	27.3%	$33.47^{\circ}$	46·56° (7·23°)	<0.0352
2004	52.0%	$17.98^{\circ}$	$41.16^{\circ} (7.64^{\circ})$	<0.0012

have evaluated the similarity of infracommunities in terms of parasite abundances, prevalences and species richness, mainly focusing upon the endohelminth fauna of the hosts (e.g. Balboa and George-Nascimento, 1998; Garcías et al. 2001, Karvonen et al. 2005, but see Bagge et al. 2004). The endohelminth communities of fish can be determined by the feeding habits of the hosts (e.g. specialist versus generalist predators) and their ontogenetic changes, as well as by the availability of different prey species (intermediate hosts) in a given environment (Poulin, 1995), but the transmission of ectoparasites is not affected by such factors. The ectoparasite communities are affected by host habitat, host behaviour (e.g. migratory or sedentary habits), host density, and by environmental characteristics (e.g. depth and temperature) (Poulin, 1995; Oliva et al. 2004). Fish ectoparasite infracommunities represent colonization-dominated systems (Rohde et al. 1995). In this study, although the temporal scale might still be restricted, the ectoparasite composition of S. capensis and H. lengerichi showed between 60 and 80% of taxonomic similarity among years respectively, but significant differences were evident in the abundances and prevalences of their ectoparasite species. For S. capensis, the differences in these community descriptors can be explained either because in 2003, fish were captured in shallow water (25 m) and/or in early Autumn, whereas the rest of the samples were captured in Spring. The copepods L. chilensis and C. cheilodactylus and their hyperparasite U. australis can be most abundant in shallow water as these ectoparasites are also commonly present in other littoral fishes (González and Poulin, 2005). Additionally, seasonal variations in the abundances and prevalences of copepods of these genera have been reported (Boxshall, 1974; Schram et al. 1998). In the case of *H. lengerichi* the high intensity of infection of I. chilensis during samples of 2004 is responsible for the differences observed among

years. Therefore, parasite abundance is not a useful tool to predict fish infracommunities due to their variability.

In spite of the above-mentioned difficulties, during all the years of study a nestedness pattern was observed in infracommunities of both hosts; that is, rare species mainly occur in more diverse infracommunities, which suggests that the ectoparasite communities of these hosts are structured and might be predictable in terms of specific composition. Rohde et al. (1998) concluded that parasite assemblages in marine fish were commonly unstructured and unpredictable. However, other studies have shown that an increase in parasite species richness did not occur at random but followed a predictable pattern of parasite infracommunity structure (Guégan and Hugueny, 1994; González and Poulin, 2005). Rohde et al. (1998) indicated that nested patterns in fish parasite assemblages have been found only because fish samples include both juvenile and adult hosts, and considered that a nested pattern is merely a consequence of an increased parasite diversity associated with ontogeny of the host. Our data include only adult fish, avoiding the influence of host ontogeny suggested by Rohde et al. (1998). The analysis of parasite communities considering fish of different developmental stages is likely to generate apparent nestedness because of differential colonization probabilities among parasites (Poulin and Valtonen, 2001; Vidal-Martinez and Poulin, 2003). This assumption can be applied to ectoparasite infracommunities because larger fish present more space to be colonized by new ectoparasite species (Poulin, 1995). In this study, a significant correlation between fish size and species richness was observed only for S. capensis during 2003 and H. lengerichi during 2002. Species richness was not correlated with fish size during the other studied years; in these years the examined fish were larger and covered a wider host range size. However, these infracommunities were not the richest. Therefore, in these hosts, larger fish do not harbour infracommunities richer than those of smaller fish, and the observed nested patterns are not influenced by fish size.

The nestedness in ectoparasite communities of marine fish has been explained as a consequence of epidemiological processes that in turn depend of the demographic characteristics of each parasite species in an assemblage (Morand *et al.* 2002). Thus, a nested pattern can be the result of different factors that affect the probability of a given host being infested by a particular parasite. In this sense, host biology may be a key determinant of parasite infracommunity structure (Zelmer and Arai, 2004; González and Poulin, 2005). The rockfish *S. capensis* is an abundant and sedentary species, without migratory movements, inhabiting the rocky subtidal zone, where it waits motionless in order to capture prey (Moreno, 1981; Barrientos et al. 2006). Individual fish (between 20 cm and 35 cm TL) should occupy a similar and restricted habitat, ensuring the recruitment of the same parasite species in individual hosts of these sizes. Thus, the gregarious and sedentary habits of this fish species (added to their abundance) should favour a richer and predictable ectoparasite community structure, through direct contact between individual hosts. On the other hand, H. lengerichi is a fish species distributed across a broader depth range (from 50 m to 300 m depth), which could allow wide-ranging movements of individual fish. So, it is also likely that larger fish occupy a different habitat (deeper water) than smaller fish (Massutí et al. 2001). This differential use of habitat could affect the colonization rate of ectoparasites in this host and generate the observed nested patterns (Guégan and Hugueny, 1994).

Exchanges of parasite species may occur over evolutionary time between phylogenetically related host species, and therefore related hosts living in the same geographical area could harbour richer parasite communities, sharing similar parasites (Kennedy and Bush, 1994). At the component community level, the ectoparasite taxonomic composition of S. capensis along the southern Chilean coast is similar to those recorded along the northern (González and Acuña, 1998), and central Chilean coasts (González and Poulin, 2005). Fish from the southern coast, inhabiting deeper waters, harbour only 1 additional (although rare) parasite species, the copepod Juanetia continentalis, a species originally described from H. lengerichi (Villalba and Fernández, 1985). However, the species richness of the infracommunities of S. capensis on the southern Chilean coast is higher than those recorded on the northern and central Chilean coasts. Similarly, the parasite species richness of H. lengerichi on the southern coast is higher than those recorded from central Chile (George-Nascimento and Iriarte, 1989). On the southern coast ( $40^{\circ}$ S), at the component community level these rockfish species share between 60 and 80% of their ectoparasite species. Then, the higher species richness per host and similarity in the ectoparasite faunas of both host species in this geographical area might be explained because the habitats of S. capensis and H. lengerichi overlap between 50 m and 150 m in depth, which makes possible the interchange of specific ectoparasites (e.g. Microcotyle sp., I. chilensis, J. continentalis) as well as generalist species (e.g. L. chilensis, C. cheilodactylus, Gnathia sp.) between these rockfish hosts. Additionally, S. capensis inhabits the rocky-littoral zone with diverse fish species (e.g. Prolatilus jugularis, Eleginops maclovinus, Cheilodactylus variegatus, Chromis crusma) that also harbour the copepods C. cheilodactylus and L. chilensis (Fernández and Villalba, 1986), thus facilitating the exchange of these caligid parasites between these fish hosts. On the contrary, *H. lengerichi* inhabits the deeper water, near the bottom (demersal), where a higher diversity of fish species is present (e.g. *Merluccius* spp., *Genypterus* spp.) (Pequeño, 2000). It is well known that these fish host harbour specific ectoparasite species that are not found in Scorpaenids. Therefore, for *H. lengerichi* the exchange of ectoparasite species among different fish hosts does not play an important role in the composition or species richness of their ectoparasite community.

According to Kennedy and Bush (1994), generalist parasite species should reduce the predictability of the parasite community of a host species, whereas host-specific parasites should produce predictable parasite communities. Host specificity determines whether a parasite is able to colonize a host and therefore may be a factor influencing the nestedness structure in parasite communities (Matejusová et al. 2000). This argument is supported for parasite infracommunities of H. lengerichi whose specific parasites were predominant during all the years of study. However, it is equally possible that generalist parasites can be evenly distributed between ranges of host species producing predictable parasite communities both within and between these hosts. This seems be the case for S. capensis where both specific and generalist parasites were equally present during the whole period of study. Thus, independent of the degree of specificity of their ectoparasites, the consistent temporal nested patterns observed in their infracommunities support the hypothesis that the ectoparasite communities of these rockfishes are structured and, therefore, might be predictable over time, at least in the southern Chilean coast where they share the same habitat.

We thank Professor Robert Poulin of the University of Otago for his comments and criticism. Thanks also to Julio Lamilla and Roberto Licandeo of the Zoology Department of Universidad Austral de Chile for their help with the collection of fish samples from the ray Fishery. This study was funded by fellowships CONICYT AT-4040092 and D.I.D. of the Universidad Austral of Chile granted to the principal author.

#### REFERENCES

- Atmar, W. and Patterson, B. D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* **96**, 373–382.
- Atmar, W. and Patterson, B. D. (1995). The nestedness temperature calculator: a visual basic program, including 294 presence-absence matrices. AICS Research, Inc., University Park, NM and The Field Museum, Chicago, II. http://www.aics-research.com/ nestedness/tempcalc.html.
- Bagge, A. M., Poulin, R. and Valtonen, A. T. (2004). Fish population size, and not density, as the determining factor of parasite infection: a case study. *Parasitology* 128, 305–311.
- **Balboa, L. and George-Nascimento, M.** (1998). Variaciones ontogeneticas y entre años en las

infracomunidades de parásitos metazoos de dos especies de peces marinos de Chile. *Revista Chilena de Historia Natural* **71**, 27–37.

**Barrientos, C., González, M. T. and Moreno, C. A.** (2006). Feeding pattern of the rockfish, *Sebastes capensis*, along its geographic range of distribution in South America. *Fishery Bulletin* (in the Press).

**Boxshall, G. A.** (1974). The population dynamics of *Lepeophtheirus pectoralis* (Müller): seasonal variation in abundance and age structure. *Parasitology* **69**, 361–371.

Bush, A. O., Lafferty, K. D., Lotz, J. M. and Shostak, A. W. (1997). Parasitology meets ecology in its own terms: Margolis *et al.* revisited. *Journal of Parasitology* 83, 575–583.

Carney, J. P. and Dick T. A. (2000). Helminth communities of yellow perch, *Perca flavescens* (Mitchill): determinants of pattern. *Canadian Journal of Zoology* 78, 538–555.

**Digby, P. G. and Kempton, R. A.** (1987). *Multivariate Analysis of Ecological Communities*. Chapman and Hall, New York.

Esch, G. W., Bush, A. O. and Aho, J. M. (1990). Parasite Communities: Patterns and Process. Chapman and Hall, London.

Eschmeyer, E. (2000). http://www.fishbase.org/

Fernández, J. and Villalba, C. (1986). Contribución al conocimiento del género Caligus Müller, 1785 (Copepoda: Siphonostomatoida) en Chile. *Gayana Zoologia* 50, 37–62.

Garcías, F., Mendoza, R. and George-Nascimento, M. (2001). Variación entre años de las infracomunidades de parásitos metazoos de la corvina *Cilus gilberti* (Pisces: Sciaenidae) en Chile. *Revista Chilena de Historia Natural* 74, 833–840.

George-Nascimento, M. and Iriarte, J. (1989). Las infracomunidades de parásitos metazoos del chancharro Helicolenus lengerichi Norman, 1937 (Pisces: Scorpaenidae): un ensamble no interactivo. *Revista Chilena de Historia Natural* 62, 217–227.

González, M. T. and Acuña, E. (1998). Metazoan parasites of the red rockfish *Sebastes capensis* off northern Chile. *Journal of Parasitology* 84, 783–788.

**González, M. T. and Poulin, R.** (2005). Spatial and temporal predictability of the parasite community structure of a benthic marine fish along its distributional range. *International Journal for Parasitology* **35**, 1369–1377.

**Guégan, J. F. and Hugueny, B. A.** (1994). Nested parasite species subset patterns in tropical fish host as major determinant of parasite infracommunity structure. *Oecologia* **100**, 184–189.

Karvonen, A., Cheng, G. H. and Valtonen, E. T. (2005). Within-lake dynamics in the similarity of parasite assemblages of perch (*Perca fluviatilis*). *Parasitology* 131, 817–823.

Kennedy, C. R. and Bush, A. O. (1994). The relationship between pattern and scale in parasites communities: a stranger in a strange land. *Parasitology* **109**, 187–196.

Kong, I. (1985). Revisión de las especies chilenas de Sebastes (Osteichthyes, Scorpaeniformes, Scorpaenidae). *Estudios Oceanologicos* 4, 21–75.

Massutí, E., Moranta, J., Gil de Sola, L., Morales-Nin, B. and Prats, L. (2001). Distribution and population structure of the rockfish *Helicolenus dactylopterus*  (Pisces: Scorpaenidae) in the western Mediterranean. Journal of the Marine Biological Association of the United Kingdom **81**, 129–141.

- Matejusová, I., Morand, S. and Gelnar, M. (2000). Nestedness in assemblages of gyrodactylids (Monogenea: Gyrodactylidae) parasitizing two species of cyprinid-with reference to generalists and specialists. *International Journal for Parasitology* **30**, 1153–1158.
- Morand, S., Rohde, K. and Hayward, C. (2002). Order in ectoparasite communities of marine fish is explained by epidemiological processes. *Parasitology* (Suppl.) **124**, S57–S63.

Moreno, C. A. (1981). Desarrollo de los estudios sobre relaciones tróficas en peces del sublitoral rocoso antártico y subantártico de Chile. *Medio Ambiente (Chile)* 5, 161–174.

Nelson, P. and Dick, T. (2002). Factors shaping the parasite communities of trout-perch, *Percopsis omiscomaycus* Walbaum (Osteichthyes: Percopsidae), and the importance of scale. *Canadian Journal of Zoology* 80, 1986–1999.

Oliva, M., González, M. T. and Acuña, E. (2004). Metazoan parasite fauna as biological tag for the habitat of the Flounder, *Hippoglossina macrops* from Northern Chile, in a depth gradient. *Journal of Parasitology* **90**, 1374–1377.

Patterson, B. D. and Atmar, W. (1986). Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnaean Society* 28, 65–82.

**Pequeño, G.** (2000). Delimitaciones y relaciones biogeográficas de los peces del Pacifico suroriental. *Estudios Oceanologicos* **19**, 53–76.

Poulin, R. (1995). Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecological Monograph* 65, 283–302.

**Poulin, R.** (1996). Richness, nestedness, and randomness in parasite infracommunity structure. *Oecologia* **105**, 545–551.

Poulin, R. (2001). Interactions between species and the structure of helminth communities. *Parasitology* 122 (Suppl.), S3–S11.

Poulin, R. and Morand, S. (2000). The diversity of parasites. *The Quarterly Review of Biology* 75, 277–293.

**Poulin, R. and Valtonen, E. T.** (2001). Nested assemblages resulting from host size variation: the case of endoparasite communities in fish hosts. *International Journal for Parasitology* **31**, 1194–1204.

**Poulin, R. and Valtonen, E. T.** (2002). The predictability of helminth community structure in space: a comparison of fish populations from adjacent lakes. *International Journal for Parasitology* **32**, 1235–1243.

Pritchard, M. A. and Kruse, G. O. (1982). *The Collection and Preservation of Animal Parasites*. University of Nebraska Press, Lincoln, USA.

Rohde, K., Hayward, C. and Heap, M. (1995). Aspect of the ecology of metazoan ectoparasites of fishes. *International Journal for Parasitology* **25**, 945–970.

Rohde, K., Worthen, W. B., Heap, M., Hugueny, B. and Guégan, J. F. (1998). Nestedness in assemblages of metazoan ecto-and endoparasites of marine fish. *International Journal for Parasitology* 28, 543–549.

Schram, T. A., Knutsen, J. A., Heuch, P. A. and Mo, T. A. (1998). Seasonal occurrence of *Lepeophtheirus*  salmonis and Caligus elongatus (Copepoda: Caligidae) on sea trout (Salmo trutta), off southern Norway. ICES Journal of Marine Science 55, 163–175.

- Simková, A., Gelnar, M. and Morand, S. (2001). Order and disorder in ectoparasite communities: the case of congeneric gill monogeneans (*Dactylogyrus* spp.). *International Journal for Parasitology* **31**, 1205–1210.
- Sousa, W. P. (1994). Patterns and processes in communities of helminth parasites. *Trends in Ecology* and Evolution 9, 52–57.
- Timi, J. T. and Poulin, R. (2003). Parasite community structure within and across host populations of a marine pelagic fish: how repeatable is it? *International Journal for Parasitology* **33**, 1353–1362.
- Vidal-Martínez, V. and Poulin, R. (2003). Spatial and temporal repeatability in parasite community structure of tropical fish hosts. *Parasitology* **127**, 387–398.

- Villalba, C. and Fernández, J. (1985). Contribución al conocimiento de la familia Chondracanthidae en Chile (Copepoda: Poecilostomatoida) *Gayana, Zoology* 49, 31–58.
- Worthern, W. D. (1996). Community composition and nested-subset analyses: basic descriptors for community ecology. *Oikos* **76**, 417–426.
- Zar, J. (1999). *Biostatistical Analysis*. 4th Edn. Prentice-Hall Inc., New Jersey.
- Zelmer, D. and Arai, H. (2004). Development of nestedness: host biology as a Community process in parasite infracommunities of Yellow Perch (*Perca flavescens* (Mitchill)) from Garner Lake, Alberta.
   Journal of Parasitology 90, 435–436.
- Zelmer, D., Paredes-Calderón, L., León-Règagnon,
  V. and García-Prieto, L. (2004). Nestedness in colonization-dominated systems: helminth infracommunities of *Rana vaillanti* Brocchi (Anura: Ranidae) in Los Tuxtlas, Veracruz, Mexico. Journal of Parasitology 90, 705–710.