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Spatial and temporal predictability of the parasite community structure of a benthic marine fish along its distributional range

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Abstract

The search for consistent patterns of organisation in parasite communities remains a central theme in parasite community ecology. However, to date, much evidence comes from studies without replication in both space and time; when replicate communities are examined, repeatable patterns are rarely observed. Here we determine, using nested subset analyses, whether the infracommunities of ectoparasites and endoparasites of a benthic marine fish (*Sebastes capensis*) show non-random structure. Then we examine the spatial repeatability of parasite community structure across the host's distribution in the southern Pacific, and the temporal repeatability of ectoparasite community structure from one locality. In total, 537 fish were captured from different latitudes (between 11°S and 52°S) along the Pacific coast of South America; a further 122 specimens were captured in two other years from one of the sampling localities, Valdivia (40°S). In spite of variation in fish sizes among samples, fish size generally did not correlate with either ecto- or endoparasite species richness. The ecto- and endoparasite species richness of the component communities were also not correlated with fish sample size across the nine localities. Significant nested patterns were found in the ectoparasite communities of *S. capensis* at all eight localities, except at latitude 52°S. Significant nested patterns were also found in the endoparasite infracommunities of *S. capensis* at seven of the nine localities, the exceptions being those from latitudes 11°S and 20°S. On a temporal scale, significant nestedness was observed in the ectoparasite infracommunities of *S. capensis* during each of the 3 years of sampling at Valdivia. In general, the same parasite species are responsible for the repeatability of nested patterns, though their importance varies among localities. The spatial and temporal predictability of the parasite community structure in *S. capensis* may be associated with the fish's benthic habitat and territorial behavior, suggesting that host biology may be a key determinant of the structure of parasite communities.

Keywords: Infracommunity structure; Nestedness subset analyses; *Sebastes capensis*; Southeastern Pacific

1. Introduction

The search for consistent non-random patterns in the structure of parasite communities represents a central theme in parasite community ecology. In the past decade, our understanding of the patterns and processes underlying the structure of parasite communities has made much progress (e.g. Esch et al., 1990; Sousa, 1994; Rohde et al., 1995; Poulin, 1996, 1998, 2001). However, much of the evidence available to date derives from studies without replication in both space and time. Therefore, the potential spatial and temporal variation in community structure, as well the detection of short-term or local processes, are usually ignored (Poulin and Valtonen, 2002). Only recently have a few studies focused on the analyses of the structure of parasite communities into the same host species either across localities or over time (Carney and Dick, 2000; Poulin and Valtonen, 2002; Goüy de Bellocq et al., 2003; Timi and Poulin, 2003; Vidal-Martinez and Poulin, 2003; Calvete et al., 2004; Zelmer et al., 2004). Those studies have produced contradictory results. In some host species, the structure of parasite communities is repeatable in both space and time, i.e. it is the same in different localities or years; in others, it is highly variable and unpredictable. Therefore, additional investigations are

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required to determine what factors influence the consistency of observed patterns in parasite community structure at temporal and spatial scales.

Structured communities can be described by a departure from randomness, where an assemblage of species is significantly more ordered than would be expected by chance. To test whether communities are significantly structured, pattern-based null models are often formulated and compared with real communities (Gotelli, 2000; Poulin, 2001). One null model that has been used extensively to detect community structure is species nestedness (Atmar and Patterson, 1993). Nested subset analyses are a useful exploratory tool for suggesting mechanisms that may structure a particular community (Worthen, 1996). Nested patterns were originally thought to develop through ordered extinction (Patterson and Atmar, 1986) but have subsequently been shown to arise via colonisation as well (Simberloff and Martin, 1991; Rohde et al., 1998). Although nestedness can evolve through both colonisation and extinction processes, its existence suggests a higher-level order that delineate predictability of the community structure.

In parasite communities, a nested subset pattern occurs when the parasite species found in depauperate infracommunities represent non-random subsets of progressively richer ones (Rohde et al., 1998; Poulin and Valtonen, 2001). Nestedness has been well documented for parasites and has been used extensively to test for non-random patterns among species assemblages (Guégan and Hugueny, 1994; Poulin and Valtonen, 2001; Simková et al., 2001; Goüy de Bellocq et al., 2003; Fellis et al., 2003; Timi and Poulin, 2003; Zelmer et al., 2004). In addition, nested subset analyses can be used to assess the repeatability of community structure in both space and time (Poulin and Valtonen, 2002; Vidal-Martínez and Poulin, 2003).

In this study we first determine, using nested subset analyses, whether the infracommunities of ecto- and endoparasites of a benthic marine fish (*Sebastes capensis*) are structured non-randomly. Then we examine the spatial repeatability of parasite community structure across of the host's latitudinal distribution in the southern Pacific (along the South American coast), and we also examine the temporal repeatability of ectoparasite community structure across different years at one locality. The red rockfish, *S. capensis,* is distributed along the southeastern Pacific coast from 10°S to 53°S. This fish lives associated with the cold waters of the Humboldt Current System, and southward of 43°S, it lives in the fjord areas of Chile (Kong, 1985). *Sebastes capensis* is one of the most abundant species along the Chilean coast. It is a sedentary species, ovoviviparous, without schooling behaviour, that inhabits in the rocky subtidal zone (Pequeño, 2000); it is an ambush predator, whose diet is restricted mainly to crustaceans (Ojeda and Fariña, 1996). The low mobility and restricted diet of this host species are factors that may generate stability and predictability in parasite community structure in both space and time, by contributing to regular and stable colonisation rates by different parasite species.

2. Materials and methods

The fish were captured from the following localities along the southeastern Pacific: Huacho (11°S) on the Peruvian coast; Iquique (20°S), Antofagasta (23°11′S), Coquimbo (29°58′S), Valparaíso (32°54′S), Talcahuano (36°44′S), Valdivia (39°45′S), Aysen Fjord (45°34′S) and Punta Arenas (52°S) along the Chilean coast (Fig. 1).

From April to September 2003 and from April to August 2004, 537 fish were captured either by hand line, or speared by divers, or else they were acquired from local fishermen who caught them with spinners. Also, from October to December 2001, and from November to December 2002, 122 specimens of *S. capensis* were captured as by-catch in the ray (*Dipturus chilensis*) fishery in the vicinity of Valdivia (39°45′S). Fish identification was confirmed using the otolith morphology and taxonomic characteristics outlined by Eschmeyer (1998). The captured fish were placed in individual bags. No ectoparasites were recorded on the fish from Peru. Thus, only 487 specimens were included in the spatial analyses of ectoparasite communities. Temporal analyses of parasite community structure were performed only for ectoparasites infracommunities, as data on endoparasites were not recorded in 2001 and 2002.

Following capture, the fish were transferred from the sampling locality to the laboratory, and were frozen until analysis. The total length (TL) of each fish was measured (±1 cm) prior to dissection. Ectoparasites and endoparasites were collected using traditional parasitological techniques (Pritchard and Kruse, 1982). The collected parasites were sorted, counted and preserved in 70% alcohol for future identification. Techniques from the specialised literature was used to identify parasite species (see González and Acuña, 1998).

Due to the non-normality of fish size data in the samples, the Kruskal–Wallis test was used to compare fish sizes from different localities and among different sampling years (Zar, 1996). Box-plots were used to show the distribution of fish-size data. In these graphs, range refers to the minimum and maximum values encompassing 95% of the data, and outliers refer to those values located outside of this 95% data range. For each parasite species, mean abundance (= number of parasites of a given species per host examined, including both infected and uninfected hosts) and prevalence (= percentage of hosts infected by a particular species of parasite) were estimated according to Bush et al. (1997). Parasite species richness for each individual host (number of ectoparasite or endoparasites species present in each infracommunity) was calculated for each locality. The Spearman rank correlation (r_s) was used to evaluate the association between the species richness per host and fish size for ectoparasites and endoparasites separately.

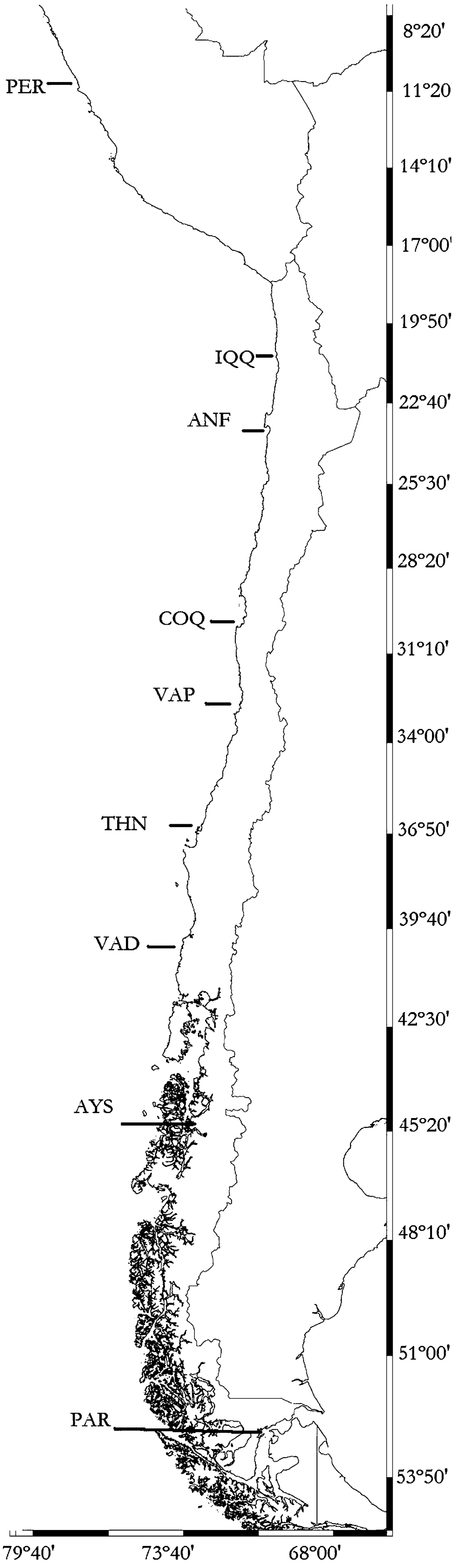

Fig. 1. Sampling localities for red rockfish *Sebastes capensis* along the Southern Pacific coast of South America. PER, Huacho (11° S); IQQ, Iquique (20° S); ANF, Antofagasta (24° S); COQ, Coquimbo (30° S); VAP, Valparaíso (33° S); THN, Talcahuano (36° S); VAD, Valdivia (40° S); AYS, Aysen channels (45° S); PAR, Punta Arenas (52° S).

The same analysis was used to evaluate the possible correlation between sample size and component community species richness across all localities and among years of sampling.

All parasite species found in a fish are probably not a true community because the life strategies of ectoparasites and endoparasites are different. Thus, nested subset analyses were carried out separately for ectoparasites and endoparasites. The matrix 'temperature' (T) proposed by Atmar and Patterson (1993) was used to assess nestedness; the matrices consisted of parasite species versus individual host for each locality, and parasite species versus individual host for each year of sampling. Matrix temperature 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; Hugueny and Guégan, 1997). A $P < 0.05$ indicates communities that are significantly nested, whereas $P > 0.95$ characterise significantly anti-nested patterns (Poulin and Valtonen, 2001; Vidal-Martinez and Poulin, 2003).

3. Results

3.1. Spatial analyses

The sizes of specimens of *S. capensis* ranged between 17 and 36 cm in total length. Significant differences in fish sizes were evident among sampled localities (Kruskal–Wallis, $H_{(8537)} = 256.71$; $P < 0.001$), the fish being smallest in Huacho (11°S) and largest in Punta Arenas (52°S) (Fig. 2).

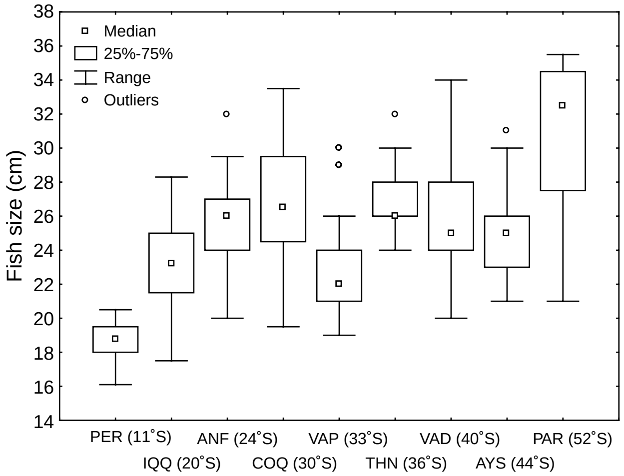

Fig. 2. Size distribution of examined specimens of *Sebastes capensis* from different localities (latitudes). Abbreviations of locality name are as in Fig. 1.

The ectoparasite species richness per host ($r_s=0.132$; $P<0.05$) and endoparasite species richness per host ($r_s=0.270$; $P<0.001$) were correlated with fish size when all localities were pooled. However, when Spearman correlations were performed for each locality separately, the ectoparasite species richness was only correlated with fish size in Valdivia (40°S) ($r=0.322$; $P=0.007$; $n=67$) and Aysén channels (45°S) ($r_s=0.24$; $P=0.03$; $n=79$), and endoparasite species richness was negatively correlated with fish size in Iquique (20°S) ($r_s=-0.37$; $P=0.005$; $n=55$), and positively in Talcahuano (36°S) ($r_s=0.252$; $P=0.033$; $n=71$). The ectoparasite species richness ($r_s=0.09$; $P>0.05$) and endoparasite species richness ($r_s=0.314$; $P>0.05$) of component communities were not correlated with fish sample size across the nine localities.

Ninety-four percent of the specimens of *S. capensis* were parasitised by at least one ectoparasite species, while an 84% of fish were parasitised by at least one endoparasite species. A total of 14 ectoparasite species and 25 endoparasite species were recovered from the pooled samples. The commonest ectoparasite species distributed along the Pacific coast were the larval isopod, *Gnathia* sp.; the monogeneans, *Microcotyle* sp., and *Interniloculus chilensis* and the copepods, *Caligus cheilodactylus* and *Lepeophtheirus chilensis* (Table 1). The commonest endoparasite species were the nematodes, *Ascarophis sebastodis*, and *Anisakis* sp.; the larval acantocephalan *Corynosoma australe*; and the digenean, *Pseudopecoelus* sp. (Table 2). The number of fish analysed, species richness, prevalence and mean abundance of the ectoparasites and endoparasites per locality are given in Tables 1 and 2, respectively.

In the spatial comparisons across localities, significant nestedness was found in the ectoparasite infracommunities of *S. capensis* at seven of the eight studied localities (Table 3). Only fishes from Punta Arenas, the southernmost locality (52°S), did not show nestedness patterns. In this locality, the examined fish were larger than in the other sites. However, in this locality, the richness of species per host was not correlated with host size ($r=0.01$; $P=0.93$; $n=37$). Significant nestedness was also found in the endoparasite infracommunities of *S. capensis* at seven of the nine localities (Table 4). In this case, there was no evidence of nestedness in the endoparasite

Table 1
Mean abundances and prevalence (%) of the ectoparasites recorded in *Sebastes capensis* from different localities along the southeastern Pacific

Species	IQQ	ANF	COQ	VAL	THN	VAD	AYS	PAR
Udonella australis			0.16 (13.1)	0.04 (2.0)	1.79 (42.3)	1.52 (40.3)		
Interniloculus chilensis		1.19 (13.4)	62.56 (67.2)	0.20 (8.0)	0.13 (5.6)	0.48 (31.3)	0.13 (5.1)	0.05 (5.4)
Neobenedenia melleni	0.09 (9.1)	0.10 (9.0)	0.18 (18.0)	0.04 (4.0)	0.30 (23.9)	0.10 (10.5)	0.05 (5.1)	
Capsalidae					0.03 (2.80)			
Microcotyle sp.1	10.07 (5.5)	1.03 (34.3)	0.26 (24.6)	0.98 (34.0)	16.28 (94.4)	5.57 (95.5)	1.47 (58.2)	0.62 (18.9)
Microcotyle sp.2					0.10 (7.0)	0.19 (6.0)		
Ancyrocephalidae gen.sp.							0.52 (30.4)	0.08 (5.4)
Caligus cheilodactylus	4.55 (98.2)	0.69 (28.4)	0.05 (4.90)	0.50 (26.0)	1.03 (52.1)	2.21 (85.1)	0.53 (36.7)	0.05 (5.4)
Lepeophtheirus chilensis	0.36 (29.1)	0.18 (13.4)	23.26 (100)	10.34 (88.0)	20.03 (95.8)	2.10 (77.6)	0.48 (31.6)	
Trifur sp.		0.10 (7.5)				0.03 (1.5)	0.01 (1.3)	0.11 (5.4)
Gnathia sp.		0.01 (1.5)	55.62 (100)	2.90 (62.0)	0.08 (5.6)	0.10 (10.4)	1.05 (62.0)	7.86 (67.6)
Cirolana sp.			0.30 (18.0)	0.02 (2.0)	0.03 (2.8)			
Rocinela sp.		0.01 (1.5)						
Piscicolidae gen.sp.			0.02 (1.6)		0.21 (11.3)	0.16 (13.4)		
Total no. parasites	279	223	8688	751	2840	836	335	325
No. fish examined	55	67	61	50	71	67	79	37
Species/locality	4	8	9	8	11	10	8	6

IQQ, Iquique (20° S); ANF, Antofagasta (24° S); COQ, Coquimbo (30° S); VAL, Valparaíso (33° S); THN, Talcahuano (36° S); VAD, Valdivia (40° S); AYS, Aysén channels (45° S); PAR, Punta Arenas (52° S).

Table 2
Mean abundances and prevalence (%) of the endoparasites recorded in *Sebastes capensis* from different localities along the southeastern Pacific

Species	PER	IQQ	ANF	COQ	VAL	THN	VAD	AYS	PAR
Ascarophis sebastodis	0.62 (24.0)	2.40 (65.5)	1.98 (29.9)	1.36 (34.4)	0.52 (34.0)	7.42 (94.4)	0.64 (38.8)	0.34 (22.8)	1.54 (35.1)
Cucullanus sp.				0.02 (1.6)			0.02 (1.5)	0.09 (8.9)	0.22 (10.8)
Anisakis sp.			0.10 (7.5)	0.28 (18.0)	0.12 (6.0)	0.79 (35.2)	1.02 (38.8)	1.24 (38.0)	3.54 (86.5)
Hystherothylacium sp.							0.38 (29.9)	0.53 (24.1)	1.62 (56.8)
Nematoda sp.1			0.06 (6.0)						
Nematoda sp.2						0.03 (2.8)			
Nematoda sp.3							0.31 (13.4)		
Corysnosoma australe	0.50 (26.0)	3.31 (65.5)	10.73 (56.7)	0.72 (34.4)	0.16 (10.0)	4.73 (74.6)	0.82 (47.8)		0.46 (18.9)
Lecithochirium genypteri				0.25 (14.8)	0.12 (10.0)				
Lecithochirium sp.								0.19 (7.6)	
Lecithastheridae sp.1			0.02 (1.5)						
Lecithastheridae sp.2					0.06 (4.0)				
Lecithastheridae sp.3						0.04 (4.2)			
Hemiuridae						0.09 (8.5)	1.12 (53.7)		
Helicometrina nimia	0.12 (8.0)		0.27 (10.4)						
Pseudopecoelus sp.	0.10 (10.0)	0.52 (34.5)	1.70 (47.8)	0.72 (27.9)	0.72 (32.0)			0.01 (1.3)	
Psettarium sp.				0.18 (19.7)	0.02 (2.0)		0.12 (9.0)		1.81 (29.7)
Zoogonidae						0.01 (1.4)	0.59 (35.8)		
Digenea sp.1									0.11 (10.8)
Digenea sp.2									0.03 (2.7)
Diphyllobotrium sp.									0.03 (2.7)
Diphyllidea sp.1				0.02 (1.6)					
Diphyllidea sp.2							0.02 (1.5)		
Hepatoxylon trichiuri						0.02 (1.5)			
Scolex pleuronectis						0.01 (1.4)	0.06 (4.5)		
Total no. parasites	67	343	996	216	86	933	345	193	347
No. analysed fish	50	55	67	61	50	71	67	79	37
Species/locality	4	3	7	8	7	9	13	6	10

PER, Huacho (11° S), IQQ, Iquique (20° S); ANF, Antofagasta (24° S); COQ, Coquimbo (30° S); VAL, Valparaíso (33° S); THN, Talcahuano (36° S); VAD, Valdivia (40° S); AYS, Aysén channels (45° S); PAR, Punta Arenas (52° S).

infracommunities from Huacho (11°S) and Iquique (20°S), the two northernmost localities. The examined fish from those two localities were smaller that in the other localities (Fig. 2). The endoparasite species richness was correlated, though negatively, with fish size only in Iquique (20°S).

3.2. Temporal analyses

The fish sizes of *S. capensis* varied between 20 and 41 cm TL during the sampling years (Fig. 3). Significant differences in the fish sizes among years of sampling were

Table 3
Summary of the results of nestedness analyses within each ectoparasite component community of *Sebastes capensis* across its latitudinal distribution

Locality	Matrix fill (%)	Matrix *T* (°)	Average (SD)	*P*
IQQ (20°S)	35.4	5.40	44.6° (8.0°)	<0.0001
ANF (24°S)	21.5	25.37	41.7° (7.3°)	0.01
COQ (30°S)	29.3	8.35	51.3° (5.7°)	<0.0001
VAP (33°S)	30.0	7.61	51.5° (6.6°)	<0.0001
THN (36°S)	32.7	13.82	59.0° (4.5°)	<0.0001
VAD (40°S)	37.1	13.41	58.4° (4.4°)	<0.0001
AYS (45°S)	31.5	18.86	54.1° (5.4°)	<0.0001
PAR (52°S)	18.5	27.07	35.5° (7.8°)	0.14

$P<0.05$ indicates nested communities; $P>0.05$ indicates randomly-structured communities. Average = mean of 1000 simulated matrices, and SD.

recorded ($H_{(2189)}=100.69$; $P<0.001$). The ectoparasite species richness per host was significantly correlated with host size during 2002 ($r=-0.27$; $P=0.03$; $n=61$), and during 2003 ($r=0.322$; $P=0.007$; $n=67$), but there was no correlation between species richness per host and fish size during 2001 ($r=-0.09$; $P=0.46$; $n=61$). In this year, the analysed fish were larger and the size range was wider (Fig. 3). The sample size was similar during these years and the species richness also was similar among years (Table 5).

During the years 2001, 2002 and 2003, 95, 98 and 100% of the fish, respectively, were parasitised by at least one parasite species. The most prevalent parasite species were *Gnathia* sp., *Microcotyle* sp. and *L. chilensis* through all three years (Table 5).

Significant nestedness was found in the ectoparasite infracommunities of *S. capensis* during the 3 years of sampling (Table 6), indicating that the rare species mainly occur in the most diverse infracommunities, and that the ectoparasite community structure departed from randomness in all years of sampling.

Table 4
Summary of the results of nestedness analyses within each endoparasite component community of *Sebastes capensis* across its latitudinal distribution

Locality	Matrix fill (%)	Matrix *T* (°)	Average (SD)	*P*
PER (11°S)	32.6	53.04	40.3° (10.7°)	0.84
IQQ (20°S)	53.0	40.04	33.1° (6.9°)	0.81
ANF (24°S)	25.4	22.22	46.2° (7.0°)	<0.0001
COQ (30°S)	23.7	29.60	43.6° (7.0°)	0.02
VAP (33°S)	21.4	21.69	37.8° (7.7°)	0.01
THN (36°S)	25.2	7.93	50.3° (5.4°)	<0.0001
VAD (40°S)	23.1	18.99	52.1° (4.8°)	<0.0001
AYS (45°S)	25.9	18.51	45.8° (7.7°)	<0.0001
PAR (52°S)	25.6	21.29	47.8° (6.7°)	<0.0001

$P<0.05$ indicates nested communities; $P>0.05$ indicates randomly-structured communities. Average = mean of 1000 simulated matrices, and SD.

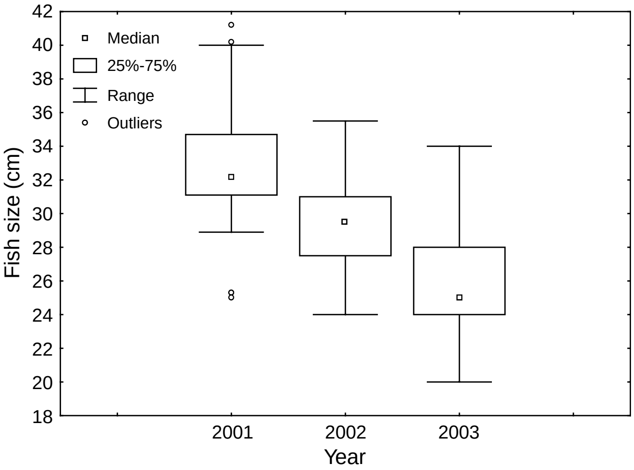

Fig. 3. Size distribution of examined specimens of *Sebastes capensis* from Valdivia (40° S) during the years 2001, 2002 and 2003.

4. Discussion

Both the ectoparasite and endoparasite infracommunity structure of *S. capensis* show nested patterns that are consistent across almost all studied localities. Likewise, the ectoparasite infracommunity structure of this host shows a consistent nested pattern across years in the same locality. These results contrast with previous spatial and temporal analyses of the parasite community structure in freshwater fishes (Carney and Dick, 2000; Poulin and Valtonen, 2002; Vidal-Martínez and Poulin, 2003), and the marine pelagic fish, *Engraulis anchoita* (Timi and Poulin, 2003). In previously studied fish hosts, the nested patterns have shown very little consistency in either space or time. The lack of repeatability of the nestedness patterns in those fishes might be attributed to the variability of the environments they inhabit. Carney and Dick (2000) and Poulin and Valtonen (2002) studied perch inhabiting cold temperate lakes where surface water freezes during winter.

Table 5
Mean abundances and prevalence (%) of the ectoparasites recorded in *Sebastes capensis* from Valdivia (40° S) during the years 2001, 2002 and 2003

Species	year 2001	2002	2003
Udonella australis	0.09 (8.2)	0.03 (3.3)	1.52 (40.3)
Interniloculus chilensis	0.41 (13.1)	0.90 (21.3)	0.48 (31.3)
Neobenedenia melleni	0.09 (8.2)	1.63 (0.03)	0.10 (10.4)
Microcotyle sp. 1	3.62 (60.6)	4.55 (78.7)	5.56 (95.5)
Microcotyle sp. 2			0.19 (6.0)
Ancyrocephalidae gen.sp.	0.04 (4.9)	0.77 (42.6)	
Caligus cheilodactylus	0.31 (24.6)	0.21 (14.8)	2.21 (85.1)
Lepeophtheirus chilensis	1.13 (52.5)	1.60 (60.6)	2.10 (77.6)
Trifur sp.	0.09 (6.5)		0.03 (1.5)
Juanetia continentalis	0.05 (3.2)	0.06 (1.6)	
Gnathia sp.	5.13 (73.7)	1.18 (62.3)	0.10 (10.4)
Piscicolidae gen.sp.	0.31 (18.0)	0.04 (3.3)	0.16 (13.4)
Total no. parasites	712	574	836
No. fish examined	61	61	67
Species richness	11	10	10

Table 6
Summary of the results of nestedness analyses within each ectoparasite component community of *Sebastes capensis* from Valdivia (40° S) for different years

Year	Matrix fill (%)	Matrix *T* (°)	Average (SD)	*P*
2001	26.1	20.17	53.11° (5.2°)	<0.0001
2002	30.0	13.01	55.13° (5.4°)	<0.0001
2003	23.1	18.99	52.10° (4.8°)	<0.0001

$P<0.05$ indicates nested communities; $P>0.05$ indicates randomly-structured communities. Average = mean of 1000 simulated matrices, and SD.

The pronounced temporal changes in those lakes possibly affect the structure of their faunas, as well as regulating temporal changes in the presence of intermediate hosts and thus the colonisation of helminth parasites. The pelagic fish, *E. anchoita,* inhabits the top 30 m of the water column, and undergoes extensive migrations. Therefore, the causes of differences in nestedness patterns among anchovy populations might be related to the predominant environmental conditions in the regions inhabited by each host population (Timi and Poulin, 2003). In contrast, *S. capensis* is a sedentary fish, without migratory movements, closely associated with the rocky subtidal zone. This fish host does not undergo significant ontogenetic changes in diet (González and Acuña, 1998; unpublished data), and fish between 20 and 30 cm TL occupy a similar habitat, thus facilitating the recruitment of the same parasite species among individual hosts. Thus, the spatial and temporal predictability of the parasite community structure of *S. capensis* may result from its habitat and territorial behavior, and/or from its restricted diet.

Rohde et al. (1998), in an extensive survey, showed that only one-third of ectoparasite assemblages studied were nested, concluding that parasite assemblages in marine fish were commonly unstructured and unpredictable, at least in terms of hierarchical species assembly rules. However, other studies have shown that an increase in parasite species richness among individual fish hosts did not occur at random but followed a predictable pattern of parasite infracommunity structure (Guégan and Hugueny, 1994). Rohde et al. (1998) pointed out that nested patterns in fish parasite assemblages have been found only because fish samples include both juvenile and adult hosts. The analysis of parasite communities still in development is likely to generate apparent nestedness because of differential colonisation probabilities among parasites (Poulin and Valtonen, 2001; Vidal-Martinez and Poulin, 2003). This assumption applies to endoparasite infracommunities, because larger (and older) fish have higher feeding rates and undergo ontogenetic changes in their diet, thus promoting the differential colonisation of endoparasite species. A similar scenario can apply to ectoparasite infracommunities, because larger fish offer more surface area for colonisation by new ectoparasite species. However, in most component communities of *S. capensis* the species richness per host was not correlated with fish size. Therefore, the nested pattern found within the parasite component communities of this host is not a consequence of the size structure of the examined fish.

Despite the consistency in the spatial nested patterns among the ectoparasite infracommunities of *S. capensis*, random assembly patterns were found in the ectoparasite infracommunity structure from Punta Arenas (52°S), where the examined fish were the largest. The random structure found in the fish from this locality might result from larger and older fish having developed immunity to the infestations, and/or also from larger fishes showing greater individual movement and inhabiting different habitats (depths), which could contribute to the loss of past infestations and random rates of new infestations. This suggestion is plausible because larger fish live in deeper water (Pequeño, 2000). Additionally, the low water temperature (between 7 and 8 °C during months of sampling) at this latitude might affect the developmental time of the parasites, mainly caligids copepods (González and Carvajal, 2003), which would result in low species richness, low abundances and low prevalences of these ectoparasites.

Random assembly patterns were also found in the endoparasite infracommunities from Huacho (11°S) and Iquique (20°S). Typically, within the same fish population, larger fish harbour richer endoparasite infracommunities because these fish have a higher feeding rate and also because larger fish have been accumulating larval parasites for a longer time than small fish. Thus, larger fish sample the available endoparasite species at a higher rate and have done so for longer than small fish; and in that case small fish harbour only the common endoparasites (Poulin and Valtonen, 2001). This may occur in the endoparasite infracommunities of *S. capensis* from Huacho (11°S). Endoparasite infracommunities in this locality showed no nested patterns, indicating that the community is assembled randomly. All examined fish from this northern locality were small with a narrow size range (16–20 cm TL), and the prevalence of endoparasite species was low (Table 2). It is probable that the smaller (and younger) fish do not harbour structured parasite communities because the parasites have recently been colonising these individual hosts, and therefore, the parasite community is only beginning to develop. On the other hand, Poulin and Valtonen (2002) demonstrated that as the prevalence or mean intensity of parasites increase in a fish population, the likelihood that the parasite infracommunities are nested also increases. Thus, the random pattern found in fish from Huacho might be explained by both the sizes of examined fish and low parasite prevalences. It would be necessary to examine larger specimens (comparable with the other localities) in order to conclude whether the parasite community in this locality is structured or not.

The other locality that showed no nested pattern among endoparasite infracommunities was Iquique (20°S). The nestedness analysis is sensitive to species richness, and component communities harbouring less than three species are not appropriate for this type of analysis (Poulin and Valtonen, 2001). At the component community level, only three endoparasite species were recorded in Iquique and 85% of infracommunities harboured only one or two species. Thus, a methodological artefact could be generating the random pattern found in the endoparasite community of this locality. It is important to note that a nested pattern was found in endoparasite infracommunities from Valparaiso (33°S). In Valparaiso, the sizes of examined fish were similar to those from Iquique, but both the infracommunity species richness and component species richness were higher (seven species). Thus, the predominance of species-poor infracommunities at Iquique is most likely responsible for the observed random pattern in this locality. This low local diversity in Iquique might result from a low availability of prey.

The endoparasite infracommunities of Huacho (11°S) and Iquique (20°S) and ectoparasite infracommunities of Punta Arenas (52°S) showed random patterns. These localities form the boundary of the geographical range of *S. capensis* on the Pacific coast; they also belong to different biogeographical areas (Briggs, 1974). When localities are close to each other, fish are exposed to the same local pool of parasites and therefore similar and repeatable patterns of community structure are expected. This assumption is supported by the observed decay of similarity over geographical distance among parasite communities of *S. capensis* along their latitudinal range on the Pacific coast (Oliva and González, 2005). The distance among localities was also an important factor affecting the parasite species composition and thus nestedness and repeatability in the tropical fish studied by Vidal-Martinez and Poulin (2003). In this context, the different oceanographic characteristics that might affect the distribution of ectoparasites, and the absence of intermediate hosts that in turn affect the distribution of endoparasite species, could account for the random patterns observed in the parasite communities of marginal localities.

In conclusion, nested patterns in the parasite community structure of *S. capensis* appear to be a true, repeatable and general pattern across large spatial scales and not influenced by fish size examined. Nestedness is produced mainly by a few widespread and locally prevalent parasite species, although their importance varies among localities. Nevertheless, the nested pattern may disappear in the margins of the distributional range of this host as a consequence of the limitations imposed by the environment on parasite distributions. In the case of the temporal analysis, the nested pattern among ectoparasite infracommunities also proved to be consistent in the studied locality. This indicates that in general the parasite community structure of *S. capensis* departs from randomness in a constant manner, and might therefore be predictable in both space and time, along the host's distributional range on the south-eastern Pacific coast.

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