Effects of Human Exclusion on Parasitism in Intertidal Food Webs of Central Chile

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Abstract: *Numerous ecological studies have demonstrated the dramatic effects that humans have on coastal marine ecosystems. Consequently, marine reserves have been established to preserve biodiversity. Recent reviews show that this strategy has paid off because inside reserves, most species have rapidly increased in size and abundance. Even though these studies focused on free-living organisms and paid little attention to parasite populations, numerous authors support the hypothesis that parasitism levels could be good indicators of ecosystem stability. We examined harvesting effects on the dynamics of a parasitic trematode (*Proctoeces lintoni*) that completes its life cycle in intertidal mussels (*Perumytilus purpuratus*), keyhole limpets (*Fissurella crassa*), and clingfish (*Sicyases sanguineus*). All of these species are directly or indirectly affected by humans. Prevalence and abundance of the trematode* P. lintoni *in the three host species were compared in four study sites that differed in the intensity of human harvest. Parasitism infection in limpets and mussels was significantly higher in areas protected from human harvesting than in open-access areas, which suggests a significant change in parasite dynamics inside reserves. Yet the average parasitic biomass found in the gonads of* F. crassa *did not differ between protected and open-access areas. These results show, then, that the parasite system responded by increasing infection rates in marine protected areas without implication for reproductive success of the intermediate host. Our findings show that the indirect effects of harvesting by humans on the embedded parasite communities of littoral ecosystems require further scientific investigation.*

Key Words: *Fissurella crassa*, marine reserves, parasitism, *Proctoeces lintoni*, rocky intertidal environments

Efectos de Exclusión Humana sobre Parasitismo en Redes Tróficas Intermareales del Centro de Chile

Resumen: *Numerosos estudios ecológicos han demostrado los efectos dramáticos de la actividad humana sobre ecosistemas marinos costeros. Consecuentemente, se han establecido las reservas marinas para preservar la biodiversidad. Revisiones recientes muestran que esta estrategia es adecuada porque la mayoría de las especies dentro de las reservas han incrementado en tamaño y abundancia rápidamente. Aunque, estos estudios se han concentrado en organismos de vida libre y han puesto poca atención a poblaciones de parásitos, numerosos autores apoyan la hipótesis de que los niveles de parasitismo pueden ser buenos indicadores de la estabilidad del ecosistema. Examinamos los efectos de pesquería artesanal sobre la dinámica de un trematodo parásito (*Proctoeces lintoni*) que completa su ciclo de vida en mitíldos intermareales (*Perumytilus purpuratus*), lapas (*Fissurella crassa*) y Sicyases sanguineus, los cuales son afectados por humanos directa o indirectamente. La prevalencia y abundancia del trematodo* P. lintoni *en las tres especies de hospedadores fueron comparadas en cuatro sitios de estudio que difieren en la intensidad de recolecta por humanos. La infección parasitaria en lapas y mitíldos fue significativamente mayor en áreas protegidas que en áreas de libre acceso, lo que*

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sugiere un cambio significativo en la dinámica del parásito dentro de las reservas, pero, la biomasa promedio de parásitos en gónadas de F. crassa *no fue diferente entre áreas protegidas y de libre acceso. Por lo tanto, los resultados muestran que el sistema parásito respondió incrementando tasas de infección en áreas marinas protegidas sin consecuencias sobre el éxito reproductivo del ho spedador intermediario. Nuestros hallazgos muestran que se requiere más investigación científica de los efectos indirectos de los humanos sobre las comunidades de parásitos en ecosistemas litorales.*

Palabras Clave: *Fissurella crassa*, intermareal rocoso, parasitismo, *Proctoeces lintoni*, reservas marinas

Introduction

Humans are top predators in rocky intertidal and shallow subtidal environments along most coastal areas of the world (e.g., Moreno et al. 1984; Pinnegar et al. 2000; Shears & Babcock 2003). Many observations and experiments conducted in harvested and unharvested sites have furthered the identification of the critical ecological role humans play in coastal ecosystems (e.g., Moreno et al. 1986; Hockey 1994; Castilla 1999). By removing a large biomass of a wide variety of species, humans trigger direct and indirect modifications in the structure and functioning of rocky intertidal communities (e.g., Kingsford et al. 1991; Addessi 1994; Edgar & Barrett 1999).

Results of many studies conducted on the coast of central Chile illustrate large human effects on intertidal populations of invertebrates and algae (Castilla & Durán 1985; Oliva & Castilla 1986; Durán & Castilla 1989; Manríquez & Castilla 2001). In this system, the most far-reaching reported effects of humans occur through the harvest of the muricid gastropod *Concholepas concholepas* (Bruguière 1789; George-Nascimento & Quiroga 1983), known in Chile as *loco*. In the absence of harvesting, *locos* are capable of decimating beds of the competitively dominant mussel *Perumytilus purpuratus* (Castilla 1999; Navarrete & Castilla 2003). Human harvesting in the intertidal zone is also directed at herbivorous keyhole limpets (*Fissurella* spp.; Durán et al. 1987), which in turn has important effects on the abundance of several algal species (Oliva & Castilla 1986). Thus, remarkably different communities are found inside and outside marine protected areas (MPA) (Castilla 1999).

Numerous studies have focused on human effects on free-living organisms, but relatively few have looked at the consequences on the embedded parasite populations (Pimm et al. 1991). Indeed, parasitism is "a missing ingredient" (Morand & Gonzalez 1997) in ecological studies on food-web modification by humans. Models of parasite population dynamics show that changes in host densities and size structure produce different parasite transmission probabilities among hosts (Begon et al. 1996). Empirical evidence supports these model predictions. For instance, high concentrations of water birds, the final host of a digenean parasite, increase the prevalence of fluke larvae in the gastropod intermediate host (Bustnes et al. 2000). It is therefore possible that human activities in the littoral zone provide different conditions for completion of parasite life cycles. Our goal was to evaluate the indirect effects of human harvesting on the population of the parasite digenea *Proctoeces lintoni* in the rocky intertidal community of central Chile. We selected this parasite because humans have direct or indirect effects on populations of the three different hosts in its life cycle.

The first intermediate host is the mytilid mussel *P. purpuratus* (M.A., unpublished data), which can form extensive beds in the mid-intertidal zone along the coast of central Chile (Broitman et al. 2001). The parasite cercariae leave the mussel to infect and develop into a metacercaria stage in the gonads of the second intermediate host, keyhole limpets (*Fissurella* spp.; George-Nascimento & Quiroga 1983). Metacercaria of *P. lintoni* can exert large damage on limpet gonads, affecting the reproductive success of the host (Oliva & Diaz 1988; Oliva 1993; Oliva & Vega 1994; Sullivan et al. 1985). The clingfish *Sicyases sanguineus* consumes infected limpets and is the definitive host in which *P. lintoni* reaches sexual maturity (Osorio et al. 1986; Oliva 1993; George-Nascimento et al. 1998). *S. sanguineus* is a trophic generalist whose habitat and diet change according to size (Paine & Palmer 1978). Individuals smaller than 15 cm are frequently found grazing algae at the highest points in the intertidal zones. Only fish larger than 15 cm occurring in the low intertidal and subtidal zones consume a great variety of prey items including *Fissurella* spp. (Cancino & Castilla 1988), making these factors relevant to transmission of *P. lintoni*.

To evaluate the effects of human harvesting on the host-parasite system, we (1) quantified the differences in human activity among four study sites in central Chile; (2) evaluated effects of harvesting on the density and size structure of the three host species, *P. purpuratus*, *F. crassa*, and *S. sanguineus;* (3) determined the prevalence and abundance of *P. lintoni* in *P. purpuratus*, *F. crassa*, and *S. sanguineus* as indicators of changes in the dynamics of the host-parasite system; and (4) compared the parasitic biomass related to the gonadic weight of limpets among the four study sites to evaluate the impact of the parasite on limpet reproduction within the context of biological conservation.

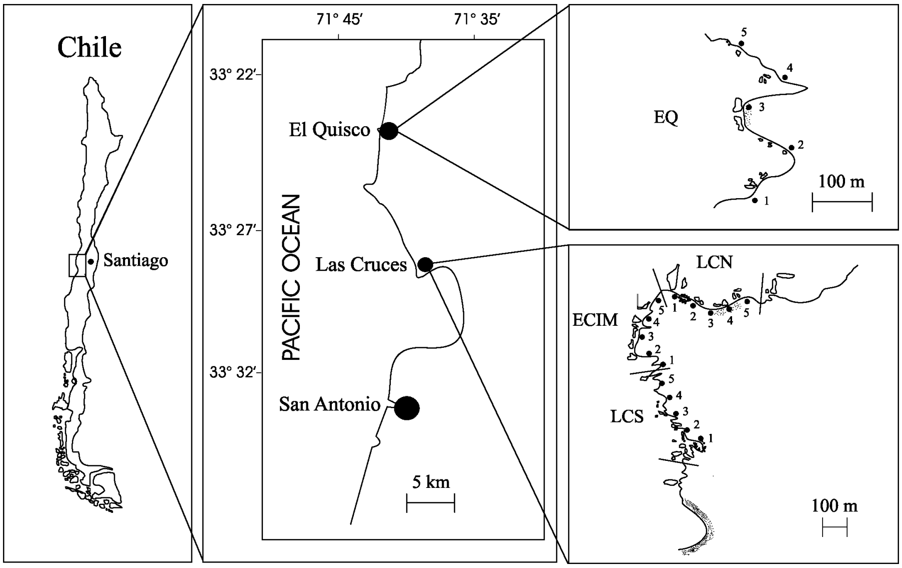

Figure 1. Location of study sites on the central coast of Chile indicating the position of the five observation points where humans and clingfish surveys were conducted.

Methods

Study Sites

The four areas we sampled on the central coast of Chile (Fig. 1) differed in intensity of human perturbation. The first site was a small marine reserve (Estación Costera de Investigaciones Marinas [ECIM]) of Pontificia Universidad Católica de Chile in Las Cruces (33° 31′ S, 71° 38′ W). The ECIM is a MPA that has been closed to the public, including fishers and tourists, since December 1982 (Castilla & Durán 1985; Durán et al. 1987). The second site was a management and exploitation area (MEA; Castilla 1994) at Caleta El Quisco (EQ; 33° 23′ S, 71° 42′ W), which is a restricted-access area used by small-scale fishers (Payne & Castilla 1994; Castilla et al. 1998). This site has a fisheries management program in place that regulates the amounts and sizes of invertebrates exploited. The third site was an open-access area adjacent to ECIM to the south (Las Cruces South [LCS]), and the fourth site was an open-access area to the north of ECIM (Las Cruces North [LCN]), where fishing and tourism activities are common and harvesting of invertebrates from the shore is intense and largely unregulated (Castilla & Durán 1985; Castilla & Bustamente 1989; Durán & Castilla 1989). The four study areas selected were along approximately 500 m of coastline, were directly exposed to waves, and had similar geological characteristics (Oliva & Castilla 1986).

Assessment of Human Perturbation

More people are present in coastal areas during the summer months (December to March). Las Cruces also receives large numbers of weekend vacationers because it is located approximately 2 hours from Santiago (Cornelius et al. 2001). We recorded the number of people observed at the intertidal and supralittoral zones of study sites twice a month during low tides from December 2001 through March 2002. Surveys were conducted during daylight hours along five 100-m stretches of coastline. The survey time within each area was standardized to a 30-minute walk. Human activity was expressed as the number of people per 100 m of shoreline counted in 30 minutes. To cover all sites within the same tide, we did not distinguish between people recreating or harvesting. Results from previous studies showed that people recreating represent 90% of all people observed at these sites (Durán et al. 1987; Cornelius et al. 2001).

Abundance and Size Structure of Host Community

Estimates of clingfish abundance were carried out each month (from December 2001 to March 2002) during low tides. We selected five observation points along the supralittoral zone of the four study sites (Fig. 1), from which we surveyed a delimited area of 100 m of coastline over 30 minutes. Because clingfish can detect moving objects over distances ranging from 10 to 15 m (Paine & Palmer 1978), observations were conducted from a distance of about 20 m with the aid of binoculars. We recorded the abundance of clingfish in crevices after observation of visible fish on the rock surface. Small clingfish (<5 cm) are very active on the rocks, but as they grow they tend to become sedentary (Cancino & Castilla 1988). Thus, the observation time was sufficient to obtain a reliable count.

Clingfish abundance was expressed as the number of individuals per 100 m of shoreline counted in 30 minutes. To estimate fish size, we affixed white plastic reference strips 8 cm long and 10 cm apart on rock walls where fish were usually observed. Specimens of *S. sanguineus* were assigned to one of four size classes (15–20 cm, 20–25 cm, 25–30 cm, and >30 cm) with the aid of these reference strips.

Although the pattern of abundance of limpets and mussels has been evaluated and published in detail in other studies (Oliva & Castilla 1986; Castilla 1999; Broitman et al. 2001), we conducted new surveys to obtain abundance data at the exact sites where parasite collections were taken. The abundance of *F. crassa* was quantified at the four study sites along horizontal 12-m transects laid down in the low and mid-intertidal zones of each study area. Twelve 50 × 50 cm quadrats were positioned at 1-m intervals along the transects, and the number and shell length of all *F. crassa* were recorded in each quadrat. Percent cover of the mussels *P. purpuratus* was estimated along the same transects, with 50 × 50 cm quadrats marked with 81 uniformly positioned intersection points.

Parasite Analysis

We collected 71 clingfish from ECIM (16 specimens), EQ (16 specimens), LCS (28 specimens), and LCN (11 specimens) that encompassed the size range observed in the field. We collected clingfish with a hook or a net attached to a 2-m pole. The gastrointestinal tract of each clingfish was dissected and sifted with water under high pressure. We examined the material retained in a 0.5-mm-mesh sieve under a stereomicroscope and counted all *P. lintoni*.

We collected 202 *F. crassa* from the intertidal zone of ECIM (30 specimens), EQ (36 specimens), LCS (64 specimens), and LCN (72 specimens) that encompassed the size range observed in the field. In the laboratory, the gonad of each limpet was isolated, weighed, and sifted with water under high pressure. We examined the material retained in a 0.5-mm-mesh sieve under a stereomicroscope and counted and weighed all specimens of *P. lintoni*. To evaluate the effect of the parasite on the fecundity of *F. crassa*, the percentage of parasitic biomass related to gonadic weight was determined for each individual. The parasitic biomass represents a conservative estimate of the damaged gonadic tissue (Oliva 1993).

We collected 2509 mussels from the intertidal zone of ECIM (308 specimens), EQ (909 specimens), LCS (599 specimens), and LCN (693 specimens). In the laboratory, each individual was dissected to determine the presence of *P. lintoni* cercariae. We calculated the prevalence (percentage of infected host individuals) and parasitic load as the mean number of parasites per host (Margolis et al. 1982; Bush et al. 1997). The abundance of parasites was corrected for differences in limpets and clingfish body size. Sample sizes of mussels, limpets, and clingfish at ECIM and EQ were small because we did not want to alter local populations inside these protected areas.

Statistical Analysis

We performed statistical analyses with SPSS release 6 (Norusis 1993), and analysis of variance (ANOVA) to compare host and parasite abundances among the four study sites. Because tourism activities and regulated extraction of commercial species are allowed at the management area of EQ, and because ECIM is a fully implemented no-take reserve, we could not consider these two protected areas as replicates. Therefore, we considered "site" as a fixed factor with four levels, each differing in the intensity of human harvesting, and used a Tukey multiple comparison test (Zar 1999) to establish the pattern of differences among sites. Data were log-transformed to meet ANOVA assumptions of homoscedasticity. Some log-transformed data, however, were heteroscedastic according to a Levene test for variance homogeneity. Because nonparametric tests do not solve this problem and ANOVA is relatively robust to small deviations of this assumption (Underwood 1997), we proceeded with ANOVA, but interpreted probabilities close to 0.05 with caution. We compared the parasite prevalence among the four study sites with a contingency table and the chi-square test (Zar 1999). For multiple-comparison tests, significance levels were Bonferroni adjusted.

Results

Human Activity

Large differences in the number of people were observed among the sites. As expected, no people were observed inside ECIM throughout the study period. The number of people differed significantly among the other three sites ($F = 71.461$; df = 2,107; $p < 0.001$). Significantly more people were recorded at LCN (mean ± SE, 13.1 ± 1.28 people/100 m coast/30 minutes) than at LCS (3.52 ± 0.61 people), and more were recorded at LCS than at EQ (0.6 ± 0.14 people; Tukey test, $p < 0.001$). At LCS divers and fishers are free to fish, but access, particularly for tourists, is limited by the presence of a fence (Manríquez & Castilla 2001). This limited access to LCS could explain the low level of human activity observed in this area in comparison with LCN.

Abundance of Host Community

There were significant differences in densities of clingfish *S. sanguineus* among the four sites (Fig. 2a; $F = 15.958$; df = 3,71; $p < 0.001$), with significantly higher densities in the marine reserve of ECIM and the management area of EQ than at open-access sites (Tukey test, $p < 0.001$). No significant differences were seen between ECIM (6.3 ± 1.23 individuals) and EQ (4.53 ± 1.17 individuals, Tukey test, $p = 0.515$) or between LCS (1.35 ± 0.64 individuals) and LCN (0.65 ± 0.18 individuals, Tukey test, $p = 0.973$). For all limpet sizes, mean densities of *F. crassa* were not different among the four study sites (Fig. 2b; $F = 1.210$; df = 3,188; $p = 0.307$).

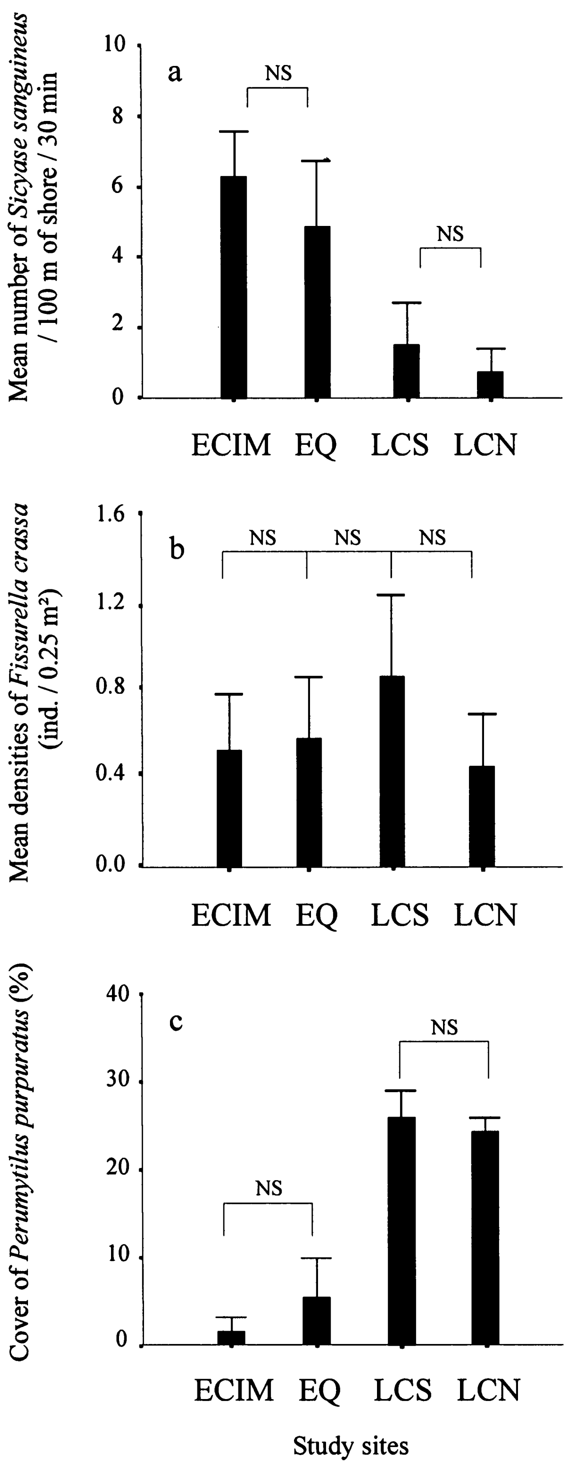

*Figure 2. (a) Mean number (± SE) of clingfish (*Sicyases sanguineus*) at the four study sites; only clingfish longer than 15 cm were considered. (b) Mean number (± SE) of keyhole limpets (*Fissurella crassa*). (c) Mean percentage of cover (± SE) of the mussel *Perumytilus purpuratus*. Brackets above the bars indicate means that are not significantly different from each other.*

The percentage of cover of *P. purpuratus* was markedly different among the sites (Fig. 2c; $F = 21.823$; df = 3, 188; $p < 0.001$). The highest covers were in the open-access areas of LCN (24.04% ± 3.45, for middle and low zones together) and LCS (27.64% ± 4.51) and were not significantly different from each other (Tukey test, $p = 0.276$). At the management area of EQ (5.58% ± 1.18) and at ECIM (1.02% ± 0.30), mean percentage covers of *P. purpuratus* were low and not significantly different (Tukey test, $p = 0.906$).

Size Structure of Host Community

The size distribution of *S. sanguineus* also differed among sites (Fig. 3a). Clingfish were larger at ECIM than at any other site. Clingfish larger than 30 cm in total length accounted for 11.5% of all individuals recorded at ECIM; there were no clingfish larger than 30 cm at the other three sites.

The mean size of *F. crassa* differed markedly among sites as well (Fig. 3b; $F = 65.986$; df = 3, 433; $p < 0.001$), with significantly larger limpets at ECIM (61.32 ± 1.86 mm) than at the MEA of EQ (43.73 ± 1.71 mm; Tukey test, $p < 0.001$) and larger at these two sites than at open-access areas. The mean limpet sizes at LCS (20.9 ± 2.17 mm) and at LCN (20.71 ± 2.57 mm) were not significantly different (Tukey test, $p = 0.483$).

Parasite Analysis

The prevalence of *P. lintoni* observed in *S. sanguineus* from ECIM (62.5%), EQ (81.2%), LCS (82.1%), and LCN (54.5%) was not significantly different among the four sites ($\chi^2 = 4.56$, df = 3, $p > 0.05$). The mean parasite abundance observed in clingfish from ECIM (2.01 ± 1.10 individuals), EQ (2.61 ± 0.53 individuals), LCS (1.94 ± 0.35 individuals), and LCN (1.51 ± 0.37 individuals) did not significantly differ among the four sites ($F = 1.170$; df = 3, 67; $p = 0.328$).

The prevalence of *P. lintoni* in *F. crassa* varied significantly among the sites ($\chi^2 = 35.61$, df = 3, $p < 0.001$). The prevalence of limpets observed at ECIM (63.33%) and EQ (80.55%) was significantly higher than that observed at LCS (34.37%) and LCN (25%; chi-square test, $p < 0.001$). There were no significant differences between the protected areas ECIM and EQ ($\chi^2 = 2.441$, df = 1, $p > 0.05$) and between the harvested areas LCS and LCN ($\chi^2 = 2.478$, df = 1, $p > 0.05$). The mean parasite abundance also differed among sites ($F = 19.074$; df = 3, 198; $p < 0.001$). The highest values were recorded at ECIM (8.66 ± 2.31 individuals) and EQ (9.88 ± 2.50 individuals) and were not significantly different from each other (Tukey test, $p = 0.428$). Mean abundances at LCS (2.54 ± 0.62 individuals) and at LCN (1.43 ± 0.41 individuals) were low and not significantly different from each other (Tukey test, $p = 0.421$).

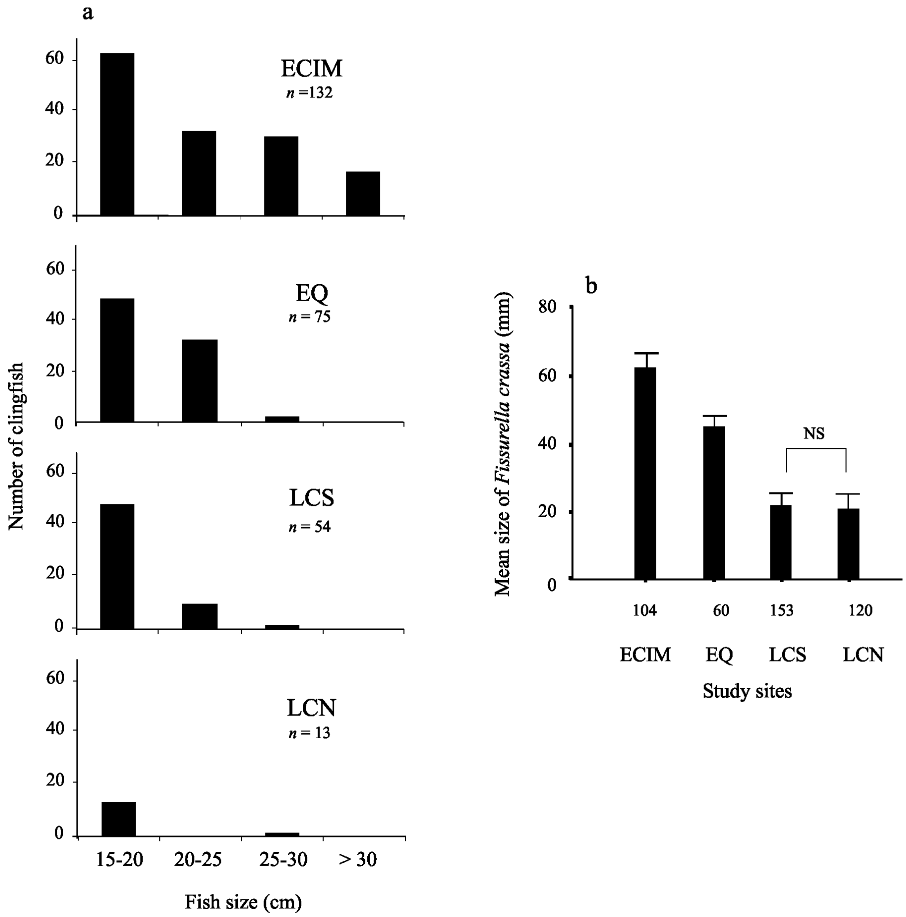

*Figure 3. (a) Size distribution of clingfish (*Sicyases sanguineus*) observed at the four study sites: only clingfish longer than 15 cm were considered (*n = *number of clingfish observed). (b) Mean size (± SE) of* Fissurella crassa*. Sample size (*n*) is indicated below each bar. Brackets above the bars indicate means that are not significantly different.*

Even small limpets (20–50 cm) had greater parasitism inside the MPAs than in open-access areas (Fig. 4). Despite differences in prevalence and parasitic loads among sites, the average parasitic biomass in the gonads of *F. crassa*—an indication of gonad damage—was not significantly different among ECIM (3.35 ± 1.14), EQ (3.27 ± 0.87), LCS (2.14 ± 0.62), and LCN (2.06 ± 0.76) ($F = 0.373$; df = 3,84; $p = 0.773$).

The prevalence of *P. lintoni* in mussels varied significantly among study sites ($\chi^2 = 12.162$, df = 3, $p < 0.001$). The prevalence of mussels observed at ECIM (3.89%) and EQ (4.07%) was significantly higher than that observed at LCS (1.33%) and LCN (2.16%) (χ^2 test, $p < 0.001$). No significant differences were found between the protected areas ECIM and EQ ($\chi^2 = 0.018$, df = 1, $p > 0.05$) or between the harvested areas LCS and LCN ($\chi^2 = 1.264$, df = 1, $p > 0.05$).

Discussion

As in many other MPAs of the world, the establishment of a small marine reserve in central Chile led to rapid changes in the abundance and sizes of commercially exploited species (Wantiez et al. 1997; Castilla 1999; Halpern & Warner 2002; Willis et al. 2003). In Chile these initial changes had cascading effects throughout the food web, producing a large and long-lasting transformation of the entire community that contrasts sharply with open-access areas (Castilla 1999). The regulation of harvesting within the newly imposed MEAs of El Quisco also had positive effects on the abundance and sizes of commercial species (Castilla 1994; Castilla et al. 1998).

Our results showed that the human harvest of coastal marine communities can also alter the dynamics of embedded parasite populations, leading to increased levels of parasitism inside protected areas. The life cycle of the digenea *P. lintoni* encompasses host species in three different trophic levels—mussels, keyhole limpets, and clingfish—which are all directly or indirectly altered by human harvest in positive or negative ways.

First, the exclusion of local fishers and recreational tourists in ECIM and the regulation of harvesting in EQ led to a significant increase in the size of keyhole limpets (*F. crassa*) compared with the populations at the two harvested sites (LCS and LCN; Fig. 5a & 5b). Among the 13 species of the genus *Fissurella* along the Chilean coastline, *F. crassa* presents the greatest catch per unit effort (37 individuals/hour) collected by onshore (mostly intertidal) fishers (Oliva & Castilla 1986). In addition, humans are size-selective predators, removing larger individuals

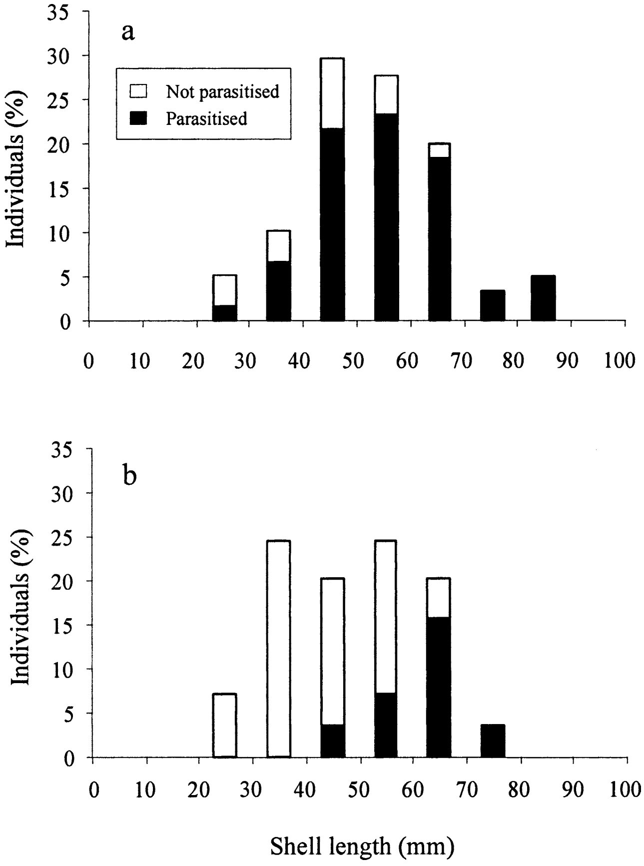

Figure 4. Percentage of parasitized and unparasitized Fissurella crassa *of different sizes (a) inside the marine reserve (Estación Costera de Investigaciones Marinas [ECIM]) and the management and exploitation area (Caleta El Quisco [EQ]) and (b) in the open-access areas (Las Cruces South [LCS] and Las Cruces North [LCN]).*

first (Moreno et al. 1984; Castilla & Durán 1985). The average density of *F. crassa* within the ECIM reserve was 4.3 individuals/m^2 and only 2.4/m^2 in harvested areas (Oliva & Castilla 1986). Our field data indicate that, after 16 years of human exclusion, the density of *F. crassa* inside ECIM had decreased to 2.1 individuals/m^2, and that density did not differ significantly from that seen at the two harvested sites, LCS and LCN. This long-term decrease in limpet density could be related to an overall low level of limpet recruitment inside the reserve (Castilla 1999). Indeed, keyhole limpets recruit heavily in beds of the intertidal mussel *P. purpuratus* (Oliva & Castilla 1986), which were decimated by the predatory gastropod *C. concholepas* after human exclusion and have not recovered since (Castilla & Durán 1985; Durán & Castilla 1989; Navarrete & Castilla 2003; Fig. 5a & 5b).

Our results also show that protecting the coastline against human exploitation produced a significant increase in density and size of clingfish, *S. sanguineus*, in protected areas in comparison with harvested areas (LCS and LCN; Fig 5a & 5b). It was expected that humans would have strong effects on populations of this fish. Durán et al. (1987) found that, on the rocky shores at Las Cruces alone, the annual catch of *S. sanguineus* amounts to about 333 ± 174 kg and 651 ± 341 individuals. Yet it had not been demonstrated previously that small marine reserves, such as ECIM, could protect this mobile fish species and allow it to attain larger sizes and densities.

Following changes in the population structure of hosts, there was a marked change in *P. lintoni* infection rates among the four study sites with different levels of human intervention. The proportion of *F. crassa* parasitized and parasite abundance varied markedly among the sites. Limpets were more infected in the protected areas (ECIM and EQ) than in the open-access areas (LCS and LCN).

Because prevalence and intensity of infection tend to increase with body size for *F. crassa* (Oliva & Diaz 1988), greater parasitism could simply reflect the existence of older and larger limpets inside marine reserves (see Sasal et al. 1996). The most striking finding of our study, however, is that even small limpet individuals have greater parasitism in marine reserves and MEAs than in open-access areas. In other words, higher parasitism is not simply a consequence of parasite accumulation with host age, but a significant change in parasite dynamics. Small limpets may be infected when infection rates exceed a critical threshold, thus explaining the results observed at EQ and ECIM. This change in parasite dynamics may explain the higher prevalence of infection in mussels in the MPAs, despite the fact that mussels were significantly less abundant in these areas.

The infection rate possibly depends on the density of the final host. Indeed, it is a general assumption in models of parasite infection dynamics that increased densities of final hosts increase the transmission probability among host species (May & Anderson 1979; Begon et al. 1996; Bustnes et al. 2000). For instance, Dufour et al. (1995) showed that higher abundance of the fish *Diplodus annularis*, the potential final host of the acanthocephalan parasite *Ancanthocephaloides propinquus,* promotes the parasite life cycle. Thus, the life cycle of *P. lintoni* could be facilitated in the protected areas as a result of the higher densities of the potential definitive host, *S. sanguineus*. We observed no significant differences in clingfish infection between protected and unprotected areas, however, which suggests that the higher limpet infection observed in ECIM and EQ does not represent an important local source of propagules of *P. lintoni* to clingfish. It is therefore likely that at ECIM and EQ many specimens of *P. lintoni* in *Fissurella* never complete their life cycle in the clingfish.

Moreover, Cancino and Castilla (1988) showed that this fish species cannot eat limpets larger than about 5 cm long (see also Duarte et al. 1996; authors, personal

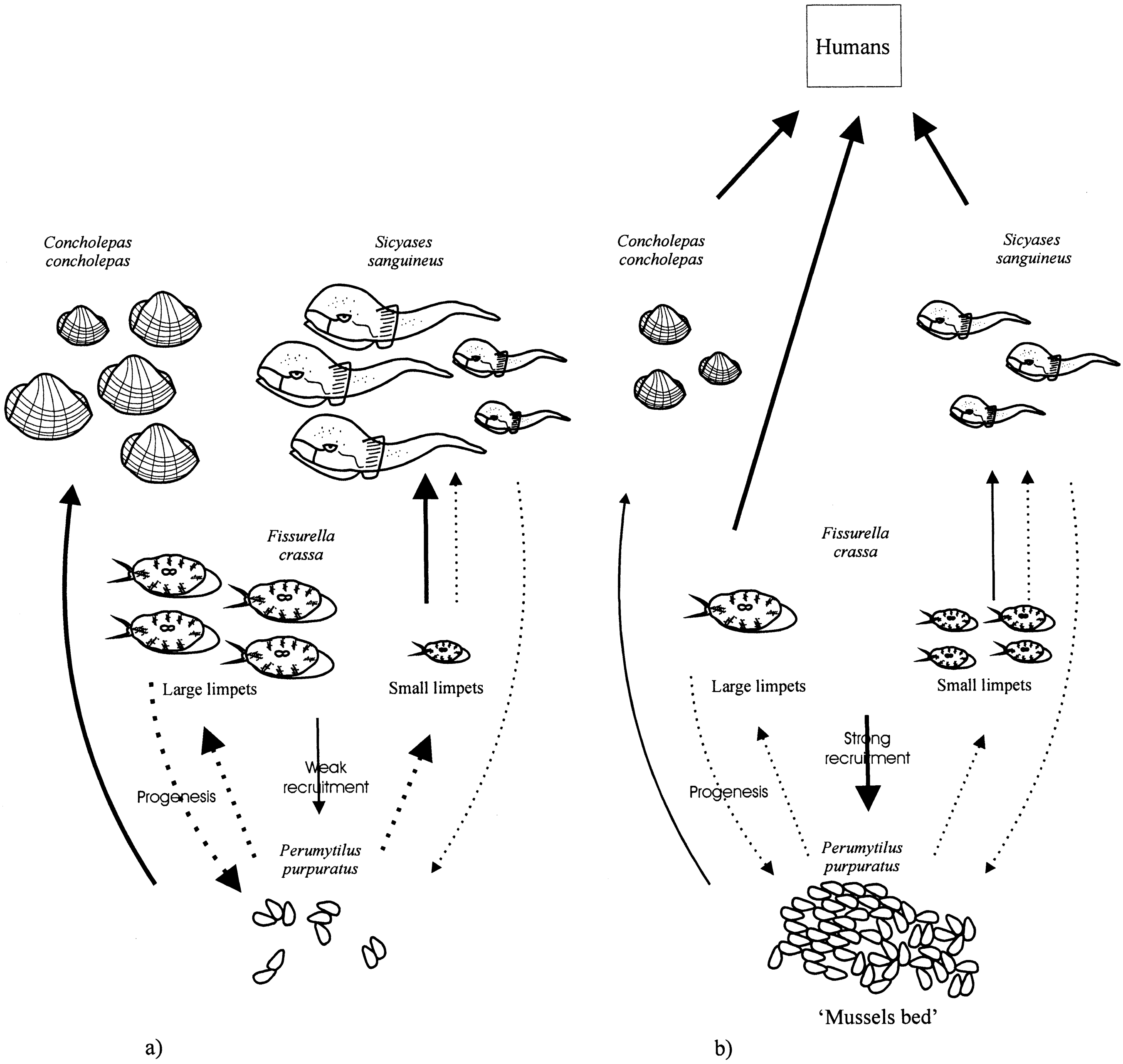

*Figure 5. Schematic illustration of the rocky intertidal food web in central Chile: (a) without humans (Estación Costera de Investigaciones Marinas [ECIM] and Caleta El Quisco [EQ]) and (b) with humans (Las Cruces South [LCS] and Las Cruces North [LCN]). Arrows with solid lines represent predation and recruitment, and arrows with dotted lines represent parasite transmission paths. The width of the arrows reflects strong (wide) or weak (narrow) interactions. The size of individuals represented (*F. crassa *and* S. sanguineus*) is proportional to the approximate real size of each species. The number of individuals represented (*P. purpuratus, F. crassa, *and* S. sanguineus*) is proportional to the approximate density of each species.*

observations). Larger limpets, which carry a larger parasite load, would thus represent a dead end for the parasite life cycle; therefore, the higher abundance of *S. sanguineus* may not be the only cause of increased overall parasitism in marine reserves.

Differences in parasite infection rates produced by human harvesting could also be explained by the shortening of the parasite life cycle through progenesis, which leads to sexual maturity in intermediate hosts (Poulin & Cribb 2002). Advanced development of *P. lintoni* occurs in large limpets and may shorten the residence time necessary for maturation in the final host (Balboa et al. 2001). Oliva and Huaquin (2000) observed that metacercaria larvae of *P. lintoni* develop precociously into the adult stage within the second intermediate host, *F. crassa,* and more than 90% of larvae had viable eggs in their uteri. This ability to reach precocious maturity in limpets could eliminate the need for *S. sanguineus* as a definitive host (Oliva & Huaquin 2000), which would facilitate the transmission of parasites in limpets larger than 5 cm that escape predation by clingfish. In the marine reserve and the MEA of El Quisco, where a large proportion of limpets are larger than 5 cm, the process of progenesis could explain the higher prevalence and abundance of parasites in the *F. crassa* population, including small limpets (Fig. 5).

Changes in *P. lintoni* infection rates could also be explained by changes in the abundance of other suitable hosts among the four study sites. For instance, *Proctoeces maculatus* has been found in 59 species of teleosts, 14 species of gastropods, 3 species of bivalves, and 1 polychaete (Bray 1983). Oliva et al. (1999) reported sporocysts and encysted metacercaria of *Proctoeces* sp. in the muricid gastropod *C. concholepas* of northern Chile. Further studies are required to reveal other favorable hosts in rocky intertidal habitats and to permit a better understanding of the dynamics of the parasitic trematode *P. lintoni*. Regardless of the specific mechanisms, our findings demonstrate that human exploitation of marine species has indirect effects on the population dynamics of the parasite *P. lintoni*.

Interestingly, the impact of metacercariae on the reproductive potential of limpets was not significantly different between the open-access areas and the protected areas where parasite burden was higher. Pathogenic effects on clingfish were probably minimal because of the short residence time of the parasite in the clingfish gastrointestinal tract. Moreover, adult parasites rarely have negative effects on their hosts (Faliex & Morand 1994). In the same way, the prevalence in mussels was very low (no more than 4.1%), which means that the negative impact on the mussel population will also be limited. Thus, the high level of parasitism in protected areas, especially in limpet intermediate hosts, did not appear to have serious detrimental effects on the host community. These results support the general idea that parasitic systems could be a good indicator of ecosystem health or stability (Combes 1996).

Our results illustrate a case in which the host-parasite system can respond to even moderate levels of protection from human exploitation. Each species of parasite may have different responses in relation to the level of protection. For instance, we found no evidence of a higher negative impact of *P. lintoni* on the fecundity of *F. crassa* in protected areas; however, it is possible that other parasite species have negative impacts on host communities. Consequently, we emphasize the need to consider the embedded parasite community when predicting long-term population changes of exploited species after marine reserves have been established. Even if our knowledge is still too limited to draw general conclusions, it seems essential to consider, and perhaps even to preserve, parasites when preserving biodiversity (Combes 1996).

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Literature Cited

Addessi, L. 1994. Human disturbance and long-term changes on a rocky intertidal community. Ecological Applications **4:**786–797.

Balboa, L., M. George-Nascimento, and F. P. Ojeda. 2001. Differential precocious sexual development of *Proctoeces lintoni* (Digenea: Fellodistomidae) in three sympatric species of keyhole limpets *Fissurella* spp. may affect transmission to the final host. The Journal of Parasitology **87:**1164–1167.

Begon, M. B., J. L. Harper, and C. R. Townsend. 1996. Ecology: individuals, populations and communities. 3rd edition. Blackwell Science, Oxford, United Kingdom.

Bray, R. A. 1983. On the fellodistomid genus *Proctoeces* Odhner, 1911 (Digenea), with brief comments on two other fellodistomid genera. Journal of Natural History **17:**321–339.

Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. Geographic variation of southeastern Pacific intertidal communities. Marine Ecology Progress Series **224:**21–34.

Bush, A. O., K. D. Lafferty, M. L. Lotz, and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. The Journal of Parasitology 575–583.

Bustnes, J. O., K. V. Galaktionov, and S. W. B. Irwin. 2000. Potential threats to littoral biodiversity: is increased parasitism a consequence of human activity? Oikos **90:**189–190.

Cancino, J. M., and J. C. Castilla. 1988. Emersion behaviour and foraging ecology of the common Chilean clingfish *Sicyases sanguineus* (Pisces: Gobiesocidae). Journal of Natural History **22:**249–261.

Castilla, J. C. 1994. The Chilean small-scale benthic shellfisheries and the institutionalization of new management practices. Ecology International Bulletin **21:**47–64.

Castilla, J. C. 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. Trends in Ecology & Evolution **14:**280–283.

Castilla, J. C., and R. H. Bustamente. 1989. Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on *Durvillaea antarctica* (Phaeophyta, Durvilleales). Marine Ecology Progress Series **50:**203–214.

Castilla, J. C., and L. R. Durán. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). Oikos **45:**391–399.

Castilla, J. C., P. Manríquez, J. Alvarado, A. Rosson, C. Pino, C. Espoz, R. Soto, D. Oliva, and O. Defeo. 1998. Artisanal 'Caletas' as units of production and co-managers of benthic invertebrates in Chile. Pages 407–414 in G. S. Jamieson and A. Campbell, editors. Proceedings of the north Pacific symposium on invertebrate stock assessment and management. Special publication. Fisheries and Aquatic Sciences, National Research Council, Ottawa, Ontario.

Combes, C. 1996. Parasites, biodiversity and ecosystem stability. Biodiversity and Conservation **5:**953–962.

Cornelius, C., S. A. Navarrete, and P. A. Marquet. 2001. Effects of human activity on the structure of coastal marine bird assemblages in central Chile. Conservation Biology **15:**1396–1404.

Duarte, W. E., G. Asencio, and C. A. Moreno. 1996. Long-term changes in population density of *Fissurella picta* and *Fissurella limbata* (Gastropoda) in the marine reserve of Mehuin, Chile. Revista Chilena de Historia Natural **69:**45–56.

Dufour, V., J. Y. Jouvenel, and R. Galzin. 1995. Study of a Mediterranean reef assemblage. Comparison of population distributions between depths in protected and unprotected areas over one decade. Aquatic Living Resources **8:**17–25.

Durán, L. R., and J. C. Castilla. 1989. Variation and persistence of the middle rocky intertidal community of Central Chile, with and without human harvesting. Marine Biology **103:**555–562.

Durán, L. R., J. C. Castilla, and D. Oliva. 1987. Intensity of human predation on rocky shores at Las Cruces in Central Chile. Environmental Conservation **14:**143–149.

Edgar, G. J., and N. S. Barrett. 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. Journal of Experimental Marine Biology and Ecology **242:**107–144.

Faliex, E., and S. Morand. 1994. Population dynamics of the metaccercarial stage of the bucephalid trematode, *Labratrema minimus* (Stossich, 1887) from Salses-Leucate lagoon (France) during the cercarial shedding period. Journal of Helminthology **68:**35–40.

George-Nascimento, M. L., and G. Quiroga. 1983. Descripción de una nueva especie de trematodo *Proctoeces humbolti* n. sp. (Digenea: Fellodistomatidae), parásito de las lapas *Fissurella* spp. Bruguiere 1789 (Mollusca: Archaeogastropoda). Parasitología al Dia (Chile) **7:**100–103 (in Spanish).

George-Nascimento, M., L. Balboa, M. Aldana, and V. Olmos. 1998. Las lapas *Fissurella* spp. (Mollusca: Archaeogastropoda) y el pejesapo *Sicyases sanguineus* (Pisces: Gobiesocidae) son huéspedes secuenciales de *Proctoeces lintoni* (Digenea: Fellodistomidae) en Chile. Revista Chilena de Historia Natural **71:**169–176 (in Spanish).

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters **5:**361–366.

Hockey, P. A.R. 1994. Man as a component of the littoral predator spectrum: a conceptual overview, in Rocky Shores: exploitation in Chile and South Africa. Pages 17–31 in W. R. Siegfried, editor. Springer-Verlag, Berlin.

Kingsford, M. J., A. J. Underwood, and S. J. Kennelly. 1991. Humans as predators on rocky reefs in New South Wales, Australia. Marine Ecology Progress Series **72:**1–14.

Manríquez, P. H., and J. C. Castilla. 2001. Significance of marine protected areas in central Chile as seeding grounds for gastropod *Concholepas concholepas*. Marine Ecology Progress Series **215:**201–211.

Margolis, L., G. W. Esch, J. C. Holmes, A. M. Kuris, and G. A. Schad. 1982. The use of ecological terms in parasitology (Report of an *ad hoc* committee of the American Society of Parasitologists). The Journal of Parasitology **68:**131–133.

May, R.M., and R.M. Anderson. 1979. Population biology of infectious diseases: part II. Nature **280:**455–460.

Morand, S., and E. A. Gonzalez. 1997. Is parasitism a missing ingredient in model ecosystems? Ecological Modelling **95:**61–74.

Moreno, C.A., K. M. Lunecke, and M. I. López. 1986. The response of an intertidal *Concholepas concholepas* (Gastropoda) population to protection from man in southern Chile and the effects on benthic sessile assemblages. Oikos **46:**359–364.

Moreno, C. A., J. P. Sutherland, and J. F. Jara. 1984. Man as a predator in the intertidal zone of southern Chile. Oikos **42:**155–160.

Navarrete, S. A., and J. C. Castilla. 2003. Experimental determination of predation intensity in an intertidal predator guild: dominant versus subordinate prey. Oikos **100:**251–262.

Norusis, M. J. 1993. SPSS for Windows. Base system user's guide release 6.0. SPSS, Chicago.

Oliva, M. E. 1993. Effect of an adult trematode, *Proctoeces lintoni* (Fellodistomidae), on the gonadosomatic index of *Fissurella limbata* (Archaeogastropoda). Acta Parasitologica **38:** 155–156.

Oliva, D., and J. C. Castilla. 1986. The effect of human exclusion on the population structure of keyhole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile. Marine Ecology **7:**201–217.

Oliva, M. E, and M. A. Diaz. 1988. Aspectos cuantitativos de la infeccion por *Proctoeces humbolti* (Trematoda: Fellodistomatidae) en la población de *Fissurella maxima* Sowerby (Mollusca: Gastropoda) de Los Vilos, Chile. Revista de Biologia Marina (Chile) **22:**157–168 (in Spanish).

Oliva, M.E., and L. Huaquin. 2000. Progenesis in *Proctoeces lintoni* (Fellodistomidae) parasite of *Fissurella crassa* (Mollusca: Archaeogastropoda) in latitudinal gradient in the Pacific coast of South America. The Journal of Parasitology **86:**768–772.

Oliva, M. E., and A. A. Vega. 1994. Effect of *Proctoeces lintoni* (Digenea) on the Fecundity of *Fissurella crassa* (Archaeogastropoda). Memorias do Instituto Oswaldo Cruz, Rio de Janeiro **89:**225 (in Portuguese).

Oliva, M. E., A. N. Olivarez, C. D. Diaz, and M. V. Pasten. 1999. Parasitic castration in *Concholepas concholepas* (Gastropoda: Muricidae) due to larval digenean in northern Chile. Diseases of Aquatic Organisms **36:**61–65.

Osorio, C., H. Díaz, and M. Ríos. 1986. Prevalencia de *Proctoeces humbolti* George-Nascimento & Quiroga 1983 (Digenea, Fellodistomidae) en la población de *Fissurella maxima* Sowerby 1835 (Mollusca, Gastropoda) de Los Vilos, Chile. Revista de Biologia Marina, Valparaíso **22:**157–168 (in Spanish).

Paine, R. T., and A. R. Palmer. 1978. *Sicyases sanguineus*: a unique trophic generalist from the Chilean intertidal zone. Copeia **1:** 75–81.

Payne, H. E., and J. C. Castilla. 1994. Socio-biological assessment of common property resource management: small-scale fishery unions in Central Chile. Out of the Shell **4:**10–14.

Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. Nature **350:**669–674.

Pinnegar, J. K., et al. 2000. Trophic cascades in benthic marine ecosystems : lessons for fisheries and protected-area management. Environmental Conservation **27:**179–200.

Poulin, R., and T. H. Cribb. 2002. Trematode life cycles: short is sweet? Trends in Parasitology **18:**176–183.

Sasal, P., E. Faliex, and S. Morand. 1996. Parasitism of *Gobius bucchichii* Steindachner, 1870 (Teleostei, Gobiidae) in protected and unprotected marine environments. Journal of Wildlife Diseases **32:**607–613.

Shears, N. T., and R. C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Marine Ecology Progress Series **246:**1–16.

Sullivan, J. T., T. C. Cheng, and H. K. Howland. 1985. Studies on parasitic castration: castration of *Ilyanassa obsoleta* (Mollusca: gastropoda) by several marine trematodes. Transactions American Microscopical Society **104:**154–171.

Underwood, A. J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, United Kingdom.

Wantiez, L., P. Thollot, and M. Kulbicki. 1997. Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. Coral Reefs **16:**215–224.

Willis, T. J., R. B. Millar, and R. C. Babcock. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. Journal of Applied Ecology **40:**214–227.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey.