

EVIDENCE OF PLASTICITY IN THE REPRODUCTION OF A TREMATODE PARASITE: THE EFFECT OF HOST REMOVAL

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ABSTRACT: The parasitic trematode *Proctoeces lintoni* requires 3 hosts (intertidal mussels, keyhole limpets, and clingfish) to complete its life cycle. The densities and size structure of host communities are modified by selective human harvesting. This study examined clutch and egg size of *P. lintoni* in 3 adjacent sites in rocky intertidal areas of central Chile presenting differences in the levels of human disturbance (i.e., from a fully protected marine reserve to free open-access areas). We found significant differences in parasite fecundity among sites. An increase in number of eggs was observed inside protected marine areas compared with open-access areas, suggesting a plastic response of the parasite reproductive strategies to the host community modification. These results show that host removal by humans in coastal ecosystems can strongly influence parasite life history traits.

Human harvesting is considered to be one of the major causes of biodiversity deterioration (Vitousek et al., 1997; Sale et al., 2005). Intense and uncontrolled harvesting removes individuals on the basis of traits that include size, behavior, and location. Selective harvesting could, therefore, negatively affect growth, maturation timing, density, and species biomass, leading to dramatic and irreversible effects such as local, or even global, extinction (Vermeij, 1993; Coleman and Williams, 2002). Moreover, through the harvesting of a few target species, humans can cause numerous indirect cascading effects on the structure and dynamics of entire communities (Hockey, 1994; McClanahan, 1997; Diaz, 2001). Castilla (1999) illustrated such a scenario in the rocky intertidal food web of central Chile, where human predation on a keystone species, a carnivorous muricid gastropod (*Concholepas concholepas*), caused community-wide trophic cascade effects.

Despite the increasing number of studies focusing on marine food web structure and human effects, relatively few have incorporated parasites (Marcogliese and Cone, 1997; Marcogliese, 2002; Thompson et al., 2005). Recently, Loot et al. (2005) considered parasite responses to food web alterations in intertidal rocky ecosystems of central Chile and demonstrated indirect human effects on the parasitic trematode *Proctoeces lintoni*. This parasite requires 3 distinct hosts to complete its life cycle. The first intermediate host is the mussel *Perumytilus purpuratus*, in which the parasite produces cercariae. Cercariae leave the mussels to infect the gonads of the second intermediate host, the keyhole limpet *Fissurella* spp., where they develop into the metacercariae stage (George-Nascimento and Quiroga, 1983). The infected limpet is then ingested by the definitive host, the clingfish *Sicyases sanguineus*, wherein the parasite reaches sexual maturity and begins egg production (George-Nascimento et al., 1998; Oliva and Zegers, 1988). These hosts are all directly or indirectly influenced by human harvesting in positive or negative ways. For instance, the keyhole limpet and clingfish are strongly harvested by local fishermen (Oliva and Castilla, 1986; Durán et al., 1987), who represent size-selective predators by removing larger individuals

first (Moreno et al., 1984; Castilla and Durán, 1985). Conversely, cover of mussels significantly decreases in nonharvested sites (see Loot et al. [2005] for a schematic illustration of the rocky intertidal food web). Therefore, host densities and size structure are modified, resulting in significant changes in parasite population dynamics (Loot et al., 2005).

Growing evidence demonstrates reproductive plasticity in all organisms, including mammals (e.g., Reilly et al., 2006), invertebrates (e.g., McGovern, 2003), fish (e.g., Aubin-Horth and Dodson, 2004), and plants (Barot et al., 2005). This sort of plasticity offers organisms the opportunity to produce phenotypes that are thought to confer high fitness in response to changes in environmental conditions during their lifetimes (Stearns, 1992). This could be particularly important for parasitic organisms that are restricted to the displacement of their hosts. In our view, a change in host community structure, as previously demonstrated in intertidal rocky habitats of central Chile (Loot et al., 2005), might also have the potential to induce changes in parasite reproductive strategies. Parasites are generally seen as highly prolific egg producers because of the massive losses suffered by infective stages during transmission (Arneberg et al., 1998). Poulin (1998) suggested that parasites with complex life cycles could be under greater pressure to evolve higher fecundity than sister clades with simpler life cycles because each egg has a very small probability of reaching the next host. Indeed, pressure from the host or the environment might constrain the evolution of egg production.

Our aim with this study was to quantify variability of egg production (clutch size and egg size) in the parasite *P. lintoni* in response to changes in host density and size structure induced by human harvesting. To do this, we compared parasite egg production of limpet parasites among 3 rocky intertidal sites varying in human harvesting intensity, ranging from a protected marine reserve to free open-access areas where harvesting of hosts is intense and largely unregulated (Castilla and Durán, 1985; Castilla and Bustamente, 1989; Durán and Castilla, 1989).

MATERIALS AND METHODS

Study sites

Samples were collected in 15 localities along a 1.5-km coastline at Las Cruces (33°31'S, 71°38'W) in central Chile. These localities are presented in Loot et al. (2005) and belong to 3 different adjacent sites, i.e., a protected marine area, (Estación Costera de Investigaciones Marinas [ECIM]), which has been closed to fishermen and tourists since

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TABLE I. (a) Abundance of host communities: mean percent cover (\pm SE) of mussels *Perumytilus purpuratus* (%), mean densities (\pm SE) of limpets *Fissurella crassa* (individuals per 0.25 m²) and mean densities (\pm SE) of clingfish *Sicyases sanguineus* (individuals per 100 m of shore per 30 min) at the 3 study sites. (b) Prevalence (%) of the parasite *Proctoeces lintoni* in the hosts (mussels, limpets, and clingfish) at the 3 study sites (see Loot et al. [2005] for more details).

Study site	Mussels (% cover)	Limpets (ind. [0.25 m] ⁻²)	Clingfish (ind. [100 m] ⁻¹ [30 min] ⁻¹)
a) Host abundance			
LCN	24.04 \pm 3.45	0.32 \pm 0.11	0.65 \pm 0.18
ECIM	1.02 \pm 0.30	0.52 \pm 0.11	6.30 \pm 1.23
LCS	27.64 \pm 4.51	0.81 \pm 0.25	1.35 \pm 0.64
b) Parasite prevalence (%)			
LCN	2.2	25.0	54.5
ECIM	3.9	63.3	62.5
LCS	1.3	34.3	82.1

December 1982; Castilla and Durán, 1985; Durán et al., 1987) and 2 largely unregulated harvesting areas (Las Cruces South [LCS] and Las Cruces North [LCN]). These sites were directly exposed to wave and presented similar geological characteristics, thus limiting abiotic dissimilarities (Oliva and Castilla, 1986; Cornelius et al., 2001). To improve statistical power, the localities belonging to the same site were pooled. Significantly more people were recorded at LCN ($\bar{x} \pm$ SE, 13.1 \pm 1.28 people per 100 m of coast per 30 min) than at LCS (3.52 \pm 0.61 people [100 m coast]⁻¹ [30 min]⁻¹) (see Loot et al., 2005). Site replication was not possible for logistical reasons (particularly for the protected marine area, which is unique in Chile). Differences in abundance and size structure of host community (mussels, keyhole limpets, and clingfish) and parasite prevalence among the 3 study sites are detailed in Table I (see also Loot et al., 2005).

Biological material

The metacercariae in keyhole limpets provided an ideal system for such an investigation. Indeed, metacercariae of *P. lintoni* have been shown to become ovigerous (i.e., progenetic metacercariae) in invertebrate host *Fissurella* spp. (Balboa et al., 2001). Thus, parasite egg production is easily quantified by examining individual progenetic worms in limpet gonads, which contrasts with most previous studies in which fecal egg counts are divided by the number of worms in a host to estimate mean egg production. The ability to reach precocious maturity in limpets could be a response to the scarcity of the final host (Oliva and Huaquin, 2000) or could facilitate the transmission of parasites in limpets large enough to escape predation by clingfish (Loot et al., 2005). The prevalence of progenetic parasites observed in *F. crassa* from ECIM (93.1%), LCS (91.8%), and LCN (89.3%) was not significantly different among the 3 sites ($\chi^2 = 0.197$, 2 df, $P = 0.9902$).

Moreover, this parasite is associated with economically exploited hosts for which there is good information on the effects of humans on populations dynamics (Castilla and Durán, 1985; Durán et al., 1987; Loot et al., 2005).

Parasite analysis in keyhole limpets

Limpet samples were collected by hand during low tide in January 2002. Sample size was low because we did not want to alter local populations inside the intertidal zone. We analyzed 34 specimens of *Fissurella crassa* (all harboring progenetic parasites) from the rocky intertidal zone of ECIM (9 specimens), LCS (17 specimens), and LCN (8 specimens). The mean size of limpets was not significantly different between sites (ANOVA, $F_{2,31} = 2.9417$, $P = 0.068$; ECIM 60.47 \pm 15.93 mm, LCS 53.39 \pm 6.17 mm, LCN 48.01 \pm 13.88 mm). In the laboratory, the gonad of each limpet was isolated and sifted under high-pressure water in a 0.5-mm mesh sieve. We examined the material retained under a stereomicroscope and counted all specimens of *P. lintoni*

(no other trematode species was found). Parasites were then fixed in acetic acid–formalin–alcohol (AFA) and preserved in solution with 70% alcohol and glycerine (Pritchard and Kruse, 1982). Progenetic *P. lintoni* were counted (ECIM, $n = 54$; LCS, $n = 49$; LCN, $n = 21$) and measured to the nearest millimeter. After dissecting the uterus, all eggs were extracted and diluted in distilled water. A microscope and digital image analysis (ProPlus 1.3 for Windows 95) were used to determine egg number and mean eggs size (μ m) for each progenetic parasite.

Statistical analysis

Because the different parasite clutch and egg size relationships have already been documented in the literature (see Discussion), we decided to analyze these 2 variables separately. We used 2 linear mixed-effects models to test for site effects (i.e., human disturbance and different host community structure on egg size and number). A mixed linear model is a generalization of standard linear models, with the generalization being that the sampling effort allows unbalanced design (Pinheiro and Bates, 2000). In our models, limpets were used as the random factors, with parasites nested within limpets. Site was considered a fixed factor. We included limpet size, parasite body size, and the total number of parasites (immature and mature metacercariae) within each limpet as covariates because parasite fecundity might be correlated with these variables (Poulin, 1998). The interactions between site and limpet size, site and parasite size, and site and total number of parasites were also evaluated. A model selection approach on the basis of Akaike Information Criteria (AIC; MacNally, 2000; Johnson and Omland, 2004) was used to assess the predictive power of the independent variables. In total, 26 models were assessed for each reproductive parameter (i.e., egg sizes and number of eggs), and models were compared and selected with likelihood ratio tests (Lr tests).

Additionally, the relative explanatory power of each variable was assessed using hierarchical partitioning (Chevan and Sutherland, 1991; MacNally, 2000). In hierarchical partitioning, all possible models in a multiple regression setting are jointly considered to identify the most likely causal factor. This process involves computation of the increase of the fit of all models with a particular factor compared with an equivalent model without that factor (see Chevan and Sutherland, 1991; MacNally, 2000; Heikkinen et al., 2005, for more details). Hierarchical partitioning provided a relative explanatory power for each variable, which is segregated into independent and joint effects (i.e., caused jointly with other variables). Large, positive joint effects (relative to their independent effects) indicated highly colinear variables, whereas negative values indicated that a variable acted as a suppressor variable (Chevan and Sutherland, 1991). Statistical significances of the independent contributions of variables were tested by a randomization routine that yielded Z scores for the generated distribution and a measure of statistical significance based on an upper 0.95 confidence limit (Heikkinen et al., 2005).

To meet the assumption of normality, egg number was square root-transformed. Statistical analyses were performed with R 2.2.1 (lme function for the mixed models and hier.part function for the hierarchical partitioning; R Development Core Team 2005, <http://www.r-project.org/>).

RESULTS

We observed different reproductive strategies among study sites, with higher egg number and smaller egg size within the nonharvested area of ECIM compared with the 2 others sites (LCS and LCN) (Fig. 1). A single mixed model was selected to predict the variation observed in egg size (Table II).

This model included the 4 main effects and the 3 interactions (i.e., the more complete model). Limpet size had a significant effect on parasite egg size (Table II). However, site did not contribute significantly to the variation observed in egg size. Concerning egg number, the mixed model selected (Table II) included only the site effect. Multiple comparisons revealed that egg number was significantly higher within ECIM compared with the 2 other sites (contrast tests, ECIM vs. LCS, $P < 0.05$; ECIM vs. LCN, $P < 0.05$) and that there was no difference

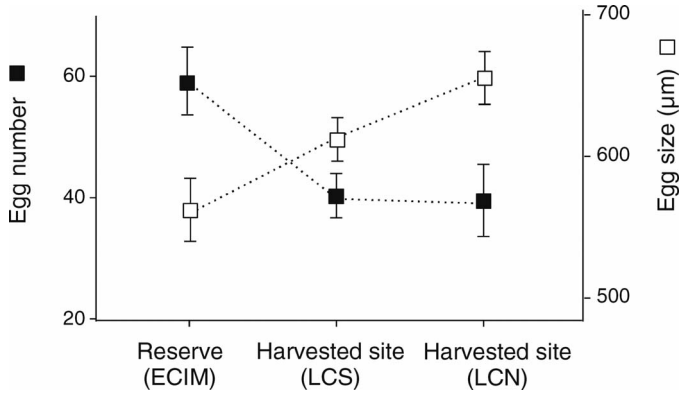


FIGURE 1. Mean number (\pm SE) of eggs and mean egg size (\pm SE) of the parasite *Proctoeces lintoni* observed in the marine reserve (ECIM) and in the 2 open-access areas (LCS and LCN).

between the 2 harvested sites (contrast tests, LCS vs. LCN, $P > 0.05$).

Hierarchical partitioning showed that the explanatory power was shared relatively evenly among the 4 main effects when considering egg size (Fig. 2A). Indeed, the 3 factors (i.e., site, limpet size, and parasite number) had significant independent effects, and overall joint effects between variables were relatively high. In contrast, when considering egg number, the independent effect of site explained 60% of the variation, whereas other variables had nonsignificant independent effects (Fig. 2B). Moreover, joint effects had a low contribution in explaining egg number variation.

DISCUSSION

The establishment of a small marine reserve in a rocky intertidal zone of central Chile led to important changes in the

TABLE II. Mixed-model analyses of the fecundity (egg size and egg number) of the parasite *Proctoeces lintoni* in response to the size of the host, the size of the parasite, the total number of parasites in a given limpet, and human exclusion (i.e., site). Site was considered fixed, and limpet (with parasites nested within limpets) was considered a random factor, whereas size of the host, size of the parasite, and total number of parasites were covariables. Significant P -values ($P < 0.05$) are in bold.

Source of variation	Selected model AIC	Response	
		Egg size	Egg no.
		1,415.44	517.29
Limpet size	$F_{1,27}$ P	11.556 0.002	—
Parasite size	$F_{1,84}$ P	0.155 0.695	—
Total no. of parasites	$F_{1,84}$ P	1.596 0.211	—
Site	$F_{2,27}$ P	1.066 0.358	4.752 0.016
Limpet size \times site	$F_{2,27}$ P	2.754 0.081	—
Parasite size \times site	$F_{2,84}$ P	1.424 0.246	—
Total no. of parasites \times site	$F_{2,84}$ P	0.242 0.785	—

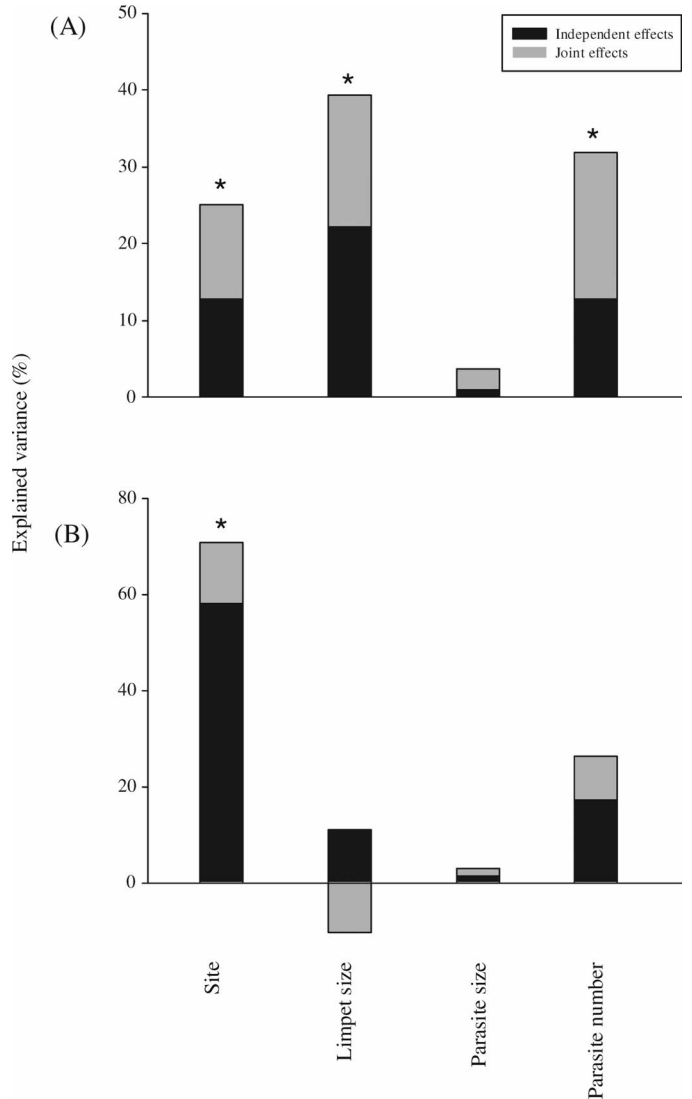


FIGURE 2. The independent and joint contributions (given as the percentage of the total explained variance) of the predictor variables explaining egg size (A) and number of eggs (B) for the parasite *Proctoeces lintoni*. Significant independent effects are indicated with an asterisk (*).

prevalence and intensity of infection by *P. lintoni* (Loot et al., 2005). We compared clutch size and egg size of the progenetic *P. lintoni* metacercariae among physically similar environments showing differences in host community composition, and we showed that the parasite reproductive strategies varied at a small spatial scale. Specifically, we demonstrated that *P. lintoni* shifted from the production of many small eggs in the marine reserve to the production of few large ones in harvested areas. Although our analysis did not control for all confounding factors, our results suggest that harvesting of coastal marine communities could be a significant factor that shapes such a response.

Individual parasite reproductive output is partitioned between offspring quality and quantity. Our results show a clear difference between factors that influence egg size and number. For instance, we found that egg size is determined by limpet size,

parasite site, number of conspecifics, and site, whereas egg number is only determined by the site effect.

Several studies have shown that parasite reproductive strategy is affected by the general quality of the host, on the basis of its age, size, diet, or immune status (Ito et al., 1986; Poulin, 1996; Tsai et al., 2001; Rossin et al., 2005). In our study, we have demonstrated that parasites within limpets of large body size will produce bigger eggs rather than maximizing egg number. Because our sampling effort was not specifically designed to test for relationships between host size and parasite reproductive output, these latter results need to be considered with caution.

On the other hand, the positive relationship between parasite body size and fecundity has been largely documented in a range of free-living taxa (Stearns, 1992; Roff, 2002; Einum and Fleming, 2004). For parasites, Rossin et al. (2005) showed that both egg number and egg volume of the endoparasitic nematode *Graphidioides subterraneus* were positively correlated with female body size. However, Lefebvre and Poulin (2005) demonstrated a nonsignificant relationship between parasite size and the number of eggs for the progenetic trematode *Coitocaecum parvum*. In parallel with the latter study, we did not find evidence for a positive relationship between parasite size and individual reproductive output. This can be explained by the parasite's reproductive size within the limpet host, which is at the minimal size at which it can lay eggs (see Lefebvre and Poulin, 2005).

Changes in egg numbers and egg size could also be explained by the number of conspecifics sharing a host, which should influence the parasite's per capita average fecundity (Anderson, 1993). For instance, experimental studies suggest that high intensity of infection has a negative effect on per capita egg production in many helminths (Jones et al., 1989). In our study, statistical analyses revealed that conspecific effects were relatively weak in explaining egg size and nonsignificant in explaining egg number.

The most striking finding of our study is that site represents a significant determinant to predict and explain parasite egg number. The differences between harvested and nonharvested areas could be related to the alteration of host communities by human harvesting. Alternatively, we could hypothesize that these patterns resulted from differences in abiotic factors. However, because the 2 human-harvested areas (LCS and LCN) were the most spatially distant (see Fig. 1 in Loot et al., 2005), they should exhibit larger differences in abiotic factors and thus in parasite egg number. On the contrary, these 2 harvested sites showed similar parasite fecundity, thus strengthening our first hypothesis.

In the marine reserve (ECIM) ground cover of the first intermediate host (*P. purpuratus*) was low compared with harvested areas (Loot et al., 2005). Thus, in ECIM, massive larval mortality could occur during the transmission of *P. lintoni* to *P. purpuratus*. It is generally assumed that the evolution of parasite reproductive strategies has been driven by the likelihood of survival and host infection during the transmission phases of the life cycle (Jennings and Calow, 1975; Calow, 1983). Therefore, we suggest that the local modification of clutch size in the marine reserve could be a response to the low percentage of cover of mussels and could promote the encounter between eggs/larvae and mussels. In marine systems, tidal

flows can cause substantial transport of small-bodied animals, and thus, important gene flow of parasite and invertebrate is generally assumed (e.g., Véliz et al., 2004). Thus, the response we observed was more likely purely plastic. Some evidence of phenotypic plasticity in other parasite systems supports this line of argument. For instance, Poulin (2003) demonstrated that the parasitic trematode *C. parvum* can accelerate its development in its amphipod intermediate host in the absence of chemical cues emanating from its definitive host. He argued that *C. parvum* detects the physiological changes in its crustacean host associated with predator-induced responses. This led him to conclude that the trematode can use information about its opportunities of transmission to adjust its life history schedule. In this study, we hypothesize that *P. lintoni* responds to maximize encounter rate with mussel hosts, but it is unlikely that parasites are able to detect changes in population density of mussels by emanating cues from the mussels. However, limpets recruit into mussel beds (Castilla, 1999) and live in their proximity to seek refuge from predators. Differences in mussel abundance might, therefore, cause changes in limpet physiology or behavior that are detectable to reproductive parasites.

Our study illustrates a case in which changing environmental conditions (the removal of invertebrate hosts) can induce adjustments of parasite life history traits. Even if our study has considered relatively few study sites and our knowledge is still too limited to account for the specific mechanism behind the observed patterns, it seems essential to consider parasite life history strategies when predicting long-term population changes of human-exploited species.

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