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Castrating effects of trematode larvae on the reproductive success of a highly parasitized population of *Crepipatella dilatata* (Caenogastropoda) in Argentina

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Abstract *Crepipatella dilatata* (Calyptraeidae) is a common intertidal or shallow subtidal protandric hermaphroditic gastropod. Intertidal snails from Puerto Madryn, Chubut, Argentina (42°46′37″S, 64°54′51″ W), showed a high prevalence, up to 46 %, of a castrating larval microphallid trematode. Reproductive success was studied during a 2-year period from September 2007 to August 2009, and the results were compared to those from an unparasitized subtidal sample. Brooding females and males were never found infected. The proportion of brooding females was higher in months with a higher prevalence of infection. The number of brooding females in the intertidal sample was higher than in the subtidal sample. Generalized linear models were utilized to determine the effects of parasitism on the reproductive success of the host population. Anticipated reproduction in smaller females in the intertidal sample, increased reproductive success in months with higher prevalence, and unparasitized males are interpreted as fitness responses to ensure host population survival when the prevalence of trematode infection is high.

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Introduction

Intertidal and upper littoral zones of seashores support an abundant fauna of invertebrates and fish, and the large number of birds that feed on them promotes complex trematode life cycles (Sokolova 1995). Parasitism in mollusks can greatly affect several life history characteristics, including reproductive success, and can even alter the community structure (Fredensborg and Poulin 2006; Wood et al. 2007). The trematodes of the family Microphallidae are common in marine intertidal environments (Galaktionov and Skirnisson 2000; Fredensborg et al. 2005). Their life cycles involve snails hosting sporocysts (asexual larval stage) that release cercariae (free-living dispersive larvae) and crustaceans hosting encysted metacercariae. Birds are the definitive hosts and become infected by consuming crustaceans with infective metacercariae, which develop into the adult form. Occasionally, the life cycle is abbreviated because the snail hosts have encysted metacercariae within the sporocysts, which suppress the free cercarial stage (Yamaguti 1975).

Trematoda larvae cause partial or complete host castration in their first intermediate hosts (Lauckner 1980). In host populations with a high prevalence of infection, parasitic castration may negatively affect their reproductive potential unless there are mechanisms that compensate for reproductive losses. For example, a population with the complete castration of aged hosts can remain viable because the younger individuals have a high resistance to parasites and can reproduce successfully (Granovitch et al. 2000; Galaktionov and Dobrovolskij 2003). Females of *Littorina saxatilis* (Gastropoda: Littorinidae) from populations heavily infected with trematodes showed higher fecundity compared to females from populations with a low prevalence of infection (Sokolova 1995; Granovitch et al. 2009).

At the beginning of a study on the reproductive biology of an intertidal population of the slipper snail, *Crepipatella dilatata* (Calyptraeidae), at Puerto Madryn (located in the southwestern Atlantic Ocean), an unusually high prevalence (up to 46 %) of a larval trematode belonging to the genus *Maritrema* (Digenea: Microphallidae) was observed. Sporocysts with cercariae of *Maritrema* sp. were found infecting the gonad and digestive gland of their intermediate host, *C. dilatata* (Gilardoni et al. 2011). The metacercarial stage was also found to infect crustaceans, and the adult was found to parasitize the kelp gull, *Larus dominicanus* (Diaz et al. 2011, 2012).

Crepipatella dilatata occurs from 21°S on the Pacific coast of the Magellan Strait up to Nuevo Gulf (42°30′S) in the Atlantic Ocean (Penchaszadeh et al. 2001). This gastropod inhabits consolidated or rocky substrates from lower intertidal and subtidal levels to a depth of approximately 20 m. It is a sedentary species often associated with mussel beds. The adults are filter feeders and are protandric consecutive hermaphrodites with a complete sex change and direct development. The eggs are laid in capsules protected by a maternal shell and are released as juveniles (Gallardo 1976; Penchaszadeh et al. 2001).

In this study, we documented the incidence of sporocysts of the microphallid trematode *Maritrema* sp. in a population of *Crepipatella dilatata* and compared snails from the intertidal and subtidal habitats to determine the potential impact of this trematode on the reproductive success of the host population.

Materials and methods

Study area

From September 2007 to August 2009, approximately 75 snail specimens were collected each month from the intertidal area of Punta Cuevas (42°46′37″S, 64°54′51″W), Puerto Madryn, Chubut Province, Argentina ($n = 1,642$). Sampling was conducted during low tides using a square of 144 cm^2 in size to randomly include all size classes. Females carrying egg capsules, which are found under their shells, were transported separately to the laboratory.

To compare the effect of parasitism on the reproductive success of the highly parasitized sample at Punta Cuevas with a population with few parasites, two other intertidal samples were studied at Punta Este (42°47′21″S, 64°57′03″W) and Cerro Avanzado (42°49′37″S, 64°53′03″W) ($n = 103$ and 102, respectively). Parasite prevalence in these two intertidal samples was very similar to that of Punta Cuevas (Chi-square test, $X_3^2 = 3.65$; $P = 0.16$). At Puerto Madryn, subtidal snails unavailable to the birds that act as definitive parasite hosts were sampled in March, May, June, and August 2008

(Almirante Storni pier, 42°44′12″S, 65°01′36″ W, at a depth of approximately 4 m). *Crepipatella dilatata* ($n = 656$) living on the shells of the mytilid bivalve, *Aulacomya atra*, were collected by scuba diving. In this case, and for comparative purposes, we considered the unparasitized condition as an extreme situation of low infection intensity. Although the intertidal snails may be exposed to greater extremes in temperature, their habitat in low intertidal experiences no more than 30 min of exposure to air at low tide. Additionally, the cryptic behavior of *C. dilatata* helps it avoid the effects of extreme environmental factors.

Data collection

Shell length (SL), which is the maximum distance between the apex and the opposite anterior margin of the shell, was measured with a caliper. The visceral mass was removed, and the presence of sporocysts was assessed under a stereomicroscope. Each specimen was separated from the shell and sexed under a stereomicroscope by looking for either a penis or a mature female gonad. When the sex could not be assessed in this manner, the individual was processed for routine histology and the sections were examined under a light microscope. Sex changes were characterized by the presence of a partially atrophied penis and the remnant male germinal cells within the acini containing the developing oocytes. Histological sections were also examined in cases where both sporocysts and female gonad remnants were observed under the stereomicroscope. In fully castrated gastropods, the sex could not be established because the gonad was completely replaced by sporocysts.

Data analysis

To evaluate the relationship between the shell length and sex stages (immature I, male M, sex change S, female F, and parasitized P), we performed a Kruskal–Wallis test (Siegel and Castellan 1998) and a test for a pairwise comparison of the subgroups (Conover 1999). The effect of parasitism on the reproductive success of *C. dilatata* was evaluated by the presence or absence of parasites, the presence or absence of females carrying egg capsules, and the number of egg capsules per female. Different models were used to test these response variables with regard to the following explanatory variables: sea surface temperature, photoperiod, gastropod shell length, prevalence of infection, and site (in the comparative analyses of two situations: parasitized samples and snails free of parasites). Data on sea surface temperature (SST) and photoperiod were collected monthly from the internet (Toms and Omi, NASA; Lammi 1996–2008). The prevalence of infection was calculated following the method described by

Bush et al. ([1997]). In Fig. 3, the monthly SST data, photoperiod, and prevalence were pooled and presented on a seasonal basis to make temporal patterns more evident.

Data analyses were based on generalized linear models (GLMs) (McCullagh and Nelder [1989]). To study the effect of parasitism on the *C. dilatata* population, the following relationships were tested:

- the presence or absence (binary response) of parasites as a function of SST, photoperiod, and SL; and
- the presence or absence (binary response) of egg capsules (considering females as a group) as a function of SST, photoperiod, SL, and the prevalence of infection.

The reproductive parameters of the intertidal sample of *C. dilatata* were compared to the subtidal unparasitized sample to evaluate the effect of parasitism on the reproductive fitness of the two groups of snails. A Kruskal–Wallis test (Siegel and Castellan [1998]) was performed to evaluate differences in the size frequency distributions of the intertidal and subtidal samples. The presence or absence (binary response) of females carrying egg capsules (considering females as a group) was analyzed as a function of the site (intertidal or subtidal) and SL. The relationship of the number of egg capsules to the site (intertidal and subtidal) and SL was tested.

The Akaike's information criterion (AIC) was used to determine the best model for the analyzed data set. Model selection was performed with an IT approach using Akaike's information criterion (AIC) and model averaging (Burnham and Anderson [2002]; Grueber et al. [2011]). The AIC values (Akaike [1973]) and the AIC for small samples (AICc) (Hurvich and Tsai [1989]) were calculated for each model. Because the count data (number of egg capsules) were over-dispersed, we calculated an AIC modified by the principle of quasi-likelihood, or QAIC, and a version of QAIC for small sample sizes, QAICc (Burnham and Anderson [2002]). From the AICc differences (Δi), where $\Delta i = AICc_i - AICc_{min}$, Akaike weights ($w_i$) (Akaike [1978]) were obtained for all candidate models. For each data set, the models were ranked by their w_i values. The model with the highest w_i was considered the one with the best supporting data (Burnham and Anderson [2002]). Model averaging was calculated using candidate models, which together account for the 95 % confidence level. The top model set was averaged using the zero method (Symonds and Moussalli [2011]), where the best AIC model was not strongly weighted.

All statistical analyses were performed in R (R Development Core Team [2011]). The standardized function to input variables is available within the *arm* package (Gelman et al. [2009]). Model selection and averaging were calculated with the *MuMIn* package (Barton [2009]).

Results

Crepipatella dilatata is a protandric hermaphrodite. The males at Punta Cuevas reached maturity at a minimum SL of ~4.5 mm. Sex change began at approximately this size, after evacuation of the male gametes. Sex change was gradual, with the males, females, and transitional stages of sex change (intersexes) having SLs of 4.5–15.0.

The snails with SLs greater than 15.0 mm were all females.

The intertidal sample of *Crepipatella dilatata* at Punta Cuevas was affected by sporocysts of *Maritrema* sp. This was the only trematode found in the gonad, and it caused castration. Males and females carrying egg capsules were never found parasitized. The smallest parasitized snails had an SL of 7.0 mm. The parasites affected snail specimens with SLs ranging from 7.0 to 29.5 mm. Approximately 14 % (78 of 574) of the parasitized females had gonads with developing sporocysts and remnant oocytes, sometimes in an advanced stage of vitellogenesis; however, histological evidence revealed that these cells were undergoing lysis.

A marked overlap in SL ranges corresponding to the different sexual stages (I, M, S, F, or P) was observed (Fig. [1]; the number of individuals in each group is reported in Online Resource 1). However, the SL was significantly different among the sexual stages (Kruskal–Wallis test, H4 = 889.34, $P < 0.0001$). Pairwise comparisons after the Kruskal–Wallis analysis all showed differences ($P < 0.05$), with the exception of the SL of the immature and male stages ($P = 0.53$). Parasitized snails and unparasitized females had similar ranges of SLs; however, the infected snails had a longer SL ($P < 0.05$).

The presence of parasites was studied as a function of SST, photoperiod, and host SL. The full model considered the main effects, double interactions, and one triple interaction among the explanatory variables. Nineteen candidate models were compared (Online Resource 2a). The model with the highest weight was the full model ($w = 0.19$), and an averaged model involved the main effects and all the interactions (Table [1]). The main effects had a greater relative importance than the interactions, and the most important variable was SL (100 %). The frequency of parasites increased with increasing SL (Fig. [2]). For each one-unit change (1 mm) in SL, the probability of finding a parasitized snail increased 19.68 ± 1.27 times. The sea surface temperature and photoperiod were less important (88 and 69 %, respectively). These variables had low odds, and the photoperiod had odds near one; therefore, the percentage of change was not significant and the probability of snails being parasitized decreased 1.21 ± 1.18 times for each one-unit change (1 °C) in surface seawater temperature.
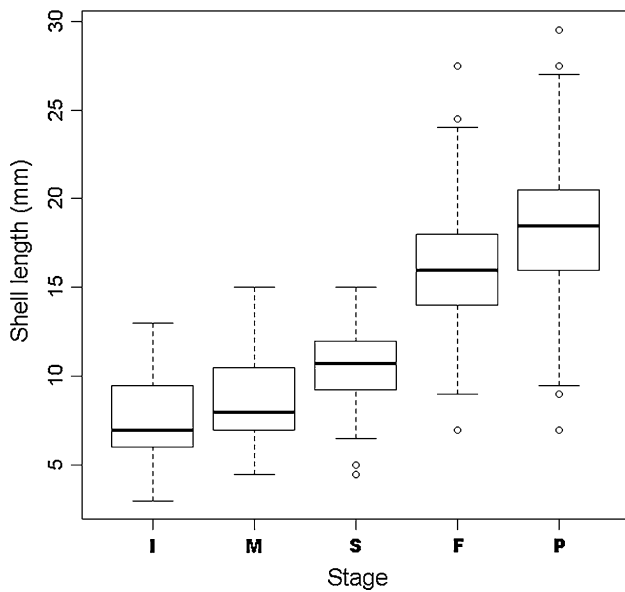
Fig. 1 Relationship between snail SL and each sex stage (*I* immature, *M* male, *S* sex change, *F* female, *P* parasitized) in the intertidal sample of *Crepipatella dilatata*
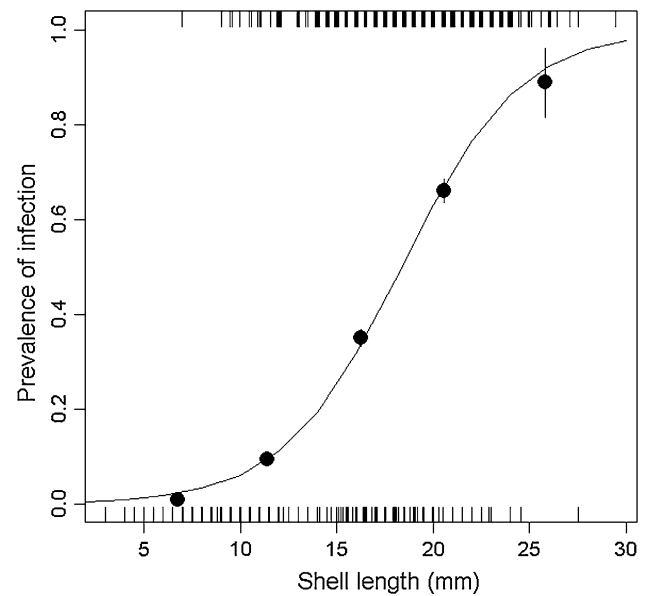
Fig. 2 Logistic regression of the presence or absence of parasites as a function of SL in an intertidal sample of *Crepipatella dilatata*. The *tick marks* along the *bottom* and *top lines* show the locations of the data points along the x-axis. The *black dots* indicate the mean and SE of the predicted proportions

The monthly prevalence of infection in the intertidal *C. dilatata* population varied from 17.4 to 46.3 % (mean = 33.2 %). For the female stages only, the prevalence of infection was 28.6–68.1 %, with a mean of 44.5 %. The percentage of females carrying egg capsules was 8.32–20 %. Both the prevalence and percentage of females carrying egg capsules followed similar seasonal patterns with an increase in winter (Fig. 3). The presence of females carrying egg capsules as a function of SST, photoperiod, SL, and monthly prevalence of infection in females resulted in a full model that considered the main effects and double, triple, and quadruple interactions between the explanatory variables. A total of 167 candidate models were compared (Online Resource 2b). The model with the highest weight (*w* = 0.10) involved all the main effects and 3 double interactions. The averaged model involved the main effects, 6 double interactions, and 4 triple interactions (Table 2). All the main effects had a

relatively high importance (95–100 %). The presence of females carrying egg capsules was positively related to the SL. The model indicated that the probability of finding females carrying egg capsules increased 2.57 ± 1.21 times for each one-unit (1 mm) change in the female SL. The environmental variables were negatively correlated with the presence of females carrying egg capsules. The probability of finding females carrying egg capsules decreased 2.46 ± 1.27 times for each one-unit change (1 °C) in SST, and 1.17 ± 1.25 times for each one-unit change (1 h) in photoperiod. The probability of finding females carrying egg capsules slowly increased (1.20 ± 1.22 times) with increasing prevalence.

In the subtidal sample of *C. dilatata*, no snail was found to be infected. The mean SL of the subtidal snails was significantly different from that of the intertidal snails

Table 1 Summary results after model averaging: the effect of each parameter on the presence or absence of parasites in an intertidal sample of *Crepipatella dilatata*

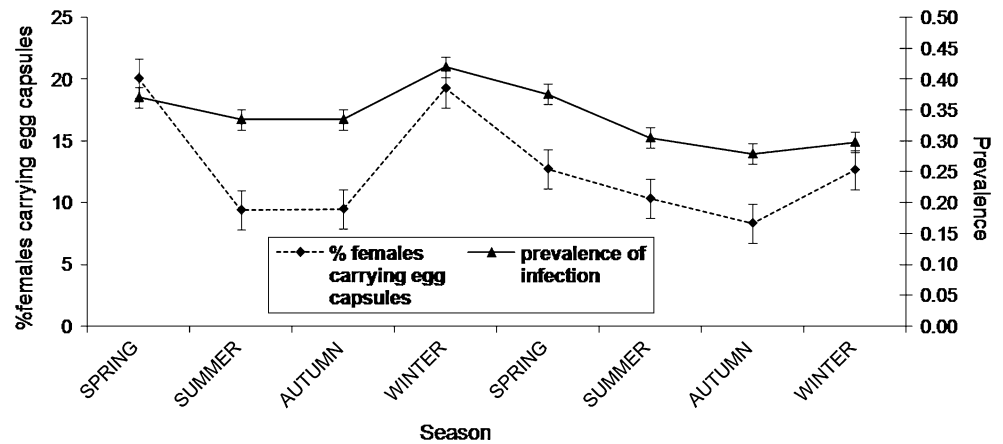| Parameter	Coefficient	Unconditional SE	Confidence interval		Relative importance
			Lower	Upper	
Intercept	−0.994	0.0775	−1.15	−0.843	–
Photoperiod	0.0953	0.151	−0.20	0.39	0.69
SL	2.98	0.24	2.51	3.45	1
SST	−0.187	0.166	−0.513	0.139	0.88
Photoperiod*SL	−0.34	0.432	−1.190	0.506	0.55
Photoperiod*SST	0.0506	0.239	−0.418	0.519	0.28
SL *SST	−0.204	0.386	−0.961	0.552	0.54
Photoperiod*SL*SST	−0.478	1.05	−2.540	1.59	0.2

(Kruskal–Wallis test, H1 = 89.46, $P < 0.001$; for this test, only the time period during which both populations were sampled was considered). In the subtidal sample, the smaller snails (5–10 mm SL) were proportionally more abundant, and the females were larger, reaching an SL of up to 33 mm (Online Resource 3).

The GLM analyses were performed for the following relationships: (1) the presence or absence of females carrying egg capsules as a function of site (intertidal or subtidal) and SL and (2) the number of egg capsules as a function of site and SL. The full model considered the main effect and a double interaction between the explanatory variables. Five candidate models for each analysis were compared (Online Resource 2c, d). In the GLM of the presence or absence of females carrying egg capsules, the model with the highest weight ($w = 0.86$) involved all the main effects and the double interaction. The averaged

model involved the main effects and a double interaction (Table 3). The presence of females carrying egg capsules was significantly affected by site, host SL, and their interaction. For each one-unit change (1 mm) in SL, the probability of finding females carrying egg capsules increased 1.73 ± 1.37 times in the intertidal sample and 8.08 ± 2.58 times in the subtidal sample. The probability of finding females carrying egg capsules in the subtidal sample was 3.38 ± 1.48 times lower than the intertidal sample (Online Resource 4). In the intertidal sample, the females carrying egg capsules were smaller than in the subtidal sample (Fig. 4).

In the GLM analysis of the number of egg capsules per female, the model with the highest weight ($w = 0.58$) involved the SL only, and the averaged model involved the two main effects (Table 4), and the number of egg capsules was influenced only by the SL (Fig. 5). For each one-unit

Fig. 3 Prevalence of infection and percentage of females carrying egg capsules as a function of season (monthly data pooled)

Table 2 Summary results after model averaging: the effect of each parameter on the presence or absence of females carrying egg capsules in an intertidal sample of *Crepipatella dilatata*

Parameter	Coefficient	Unconditional SE	Confidence interval		Relative importance
			Lower	Upper	
Intercept	−0.962	0.124	−1.21	−0.718	
Photoperiod	−0.156	0.223	−0.59	0.282	0.96
SL	0.945	0.193	0.567	1.32	1
Prev.	0.184	0.198	−0.2	0.572	0.95
SST	−0.901	0.237	−1.36	−0.436	1
Photoperiod*SL	0.0335	0.296	−0.55	0.613	0.34
Photoperiod*prev.	−0.947	0.604	−2.13	0.237	0.84
Photoperiod*SST	−1.17	0.679	−2.5	0.161	0.88
SL*prev.	0.0919	0.268	−0.43	0.617	0.37
SL*SST	−0.495	0.483	−1.44	0.452	0.69
Prev.*SST	0.229	0.401	−0.56	1.01	0.46
Photoperiod*SL*prev.	−0.0459	0.292	−0.62	0.527	0.05
Photoperiod*SL*SST	−0.00719	0.27	−0.54	0.522	0.06
Photoperiod*prev.*SST	0.0454	0.441	−0.82	0.91	0.1
SL*prev.*SST	−0.0955	0.403	−0.89	0.695	0.08

Table 3 Summary results after model averaging: the effect of each parameter on the presence or absence of females carrying egg capsules of *Crepipatella dilatata* belonging to the intertidal and subtidal samples

[a] The intertidal location was the reference category

Parameter	Coefficient	Unconditional SE	Confidence interval		Relative importance
			Lower	Upper	
Intercept	−1.82	0.185	−2.18	−1.46	
Location (subtidal)[a]	−1.22	0.390	−1.99	−0.745	1
SL	0.55	0.318	0.073	1.17	1
Location*SL	1.54	0.630	0.305	2.78	0.89
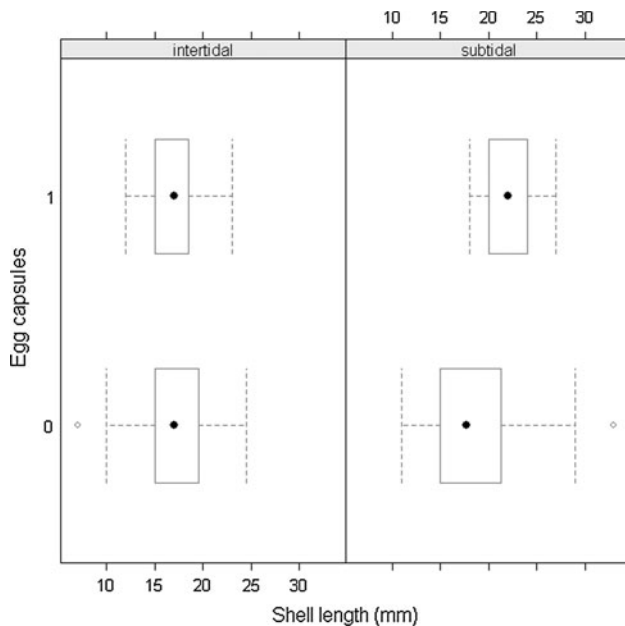
Fig. 4 Comparison of the presence or absence of egg capsules (*0* absence; *1* presence) as a function of SL in each sample (intertidal and subtidal) of *Crepipatella dilatata* (only data for March, May, June, and August 2008 for both groups were used)

change (1 mm) in SL, the number of egg capsules per female increased 1.47 ± 1.10 times. There were no differences (odds near 1) between the number of egg capsules per female in the intertidal and subtidal samples.

Discussion

The intertidal *Crepipatella dilatata* population in this study was highly infected by the trematode larvae of *Maritrema* sp. This infection was previously reported by Gilardoni et al. (2011). Notably, other Calyptraeidae species, including *Crepidula fornicata* from Massachusetts and Rhode Island (Pechenik et al. 2001) and the Wadden Sea (Thieltges et al. 2006) and *Crepidula plana* and *Crepidula convexa* from New England (Pechenik et al. 2012), were reported as refractory to infection by trematodes. The level of intertidal stress is not likely to be very intense because the cryptic behavior (no more than 30 min of exposure to

air) of *C. dilatata* helps it avoid the effect of extreme environmental factors. The subtidal *C. dilatata* were not affected by larval digeneans, most likely because the miracidia released by seabirds are dispersed in the water column and have no contact with snails at a depth of 4 m. In the intertidal sample studied, no snail with an SL less than 7 mm was found parasitized. Approximately 14 % of the parasitized females had a few remaining oocytes undergoing lysis, suggesting that the parasitized *C. dilatata* may be considered fully castrated. The range of SLs corresponding to females (7.0–27.5 mm) and parasitized snails (7.0–29.5 mm) largely overlapped, although the parasitized snails were larger.

The prevalence values increased along with the host SL. Previous studies suggested that increments in prevalence are most likely related to a longer exposure to infective forms (Sousa 1983; Lafferty 1993; Taskinen and Valtonen 1995; Oliva et al. 1999; Fredensborg et al. 2005; Fredensborg and Poulin 2006). In the case of *C. dilatata*, adult snails are filter feeders, and larger specimens have higher filtering rates, thereby facilitating contact with miracidia in the incoming water current.

The prevalence of infection in *C. dilatata* was high year round and varied from a minimum of 17.4 % to a maximum of 46.3 %. Because the presence of parasites determines the castration of infected snails, the high prevalence of trematodes represents a severe reduction in the number of reproductively active snails in the population.

Female *C. dilatata* carrying egg capsules were observed year round. In the intertidal population, the proportion of females brooding egg capsules was 7.7–51.6 %, and the proportion of brooding females was higher in months with a lower SST, as reported by Gallardo (1977) for *C. dilatata* from Puerto Montt, Chile. The prevalence of infection followed the same pattern as the percentage of females carrying egg capsules (Fig. 3).

As was observed in the intertidal sample, the proportion of females carrying egg capsules in the subtidal sample was positively correlated with SL. However, in the intertidal sample, brooding females were smaller and more numerous. Maturation at a smaller size and the higher fecundity of uninfected hosts in heavily infected populations of gastropods was previously reported by Lafferty (1993),

Table 4 Summary results after model averaging: the effect of each parameter on the number of egg capsules in females of *Crepipatella dilatata* belonging to the intertidal and subtidal samples

[a] The intertidal location was the reference category

Parameter	Coefficient	Unconditional SE	Confidence interval		Relative importance
			Lower	Upper	
Intercept	2.03	0.0437	1.95	2.12	
Location (subtidal)[a]	−0.0549	0.0996	−0.25	0.14	0.4
SL	0.383	0.094	0.198	0.567	1
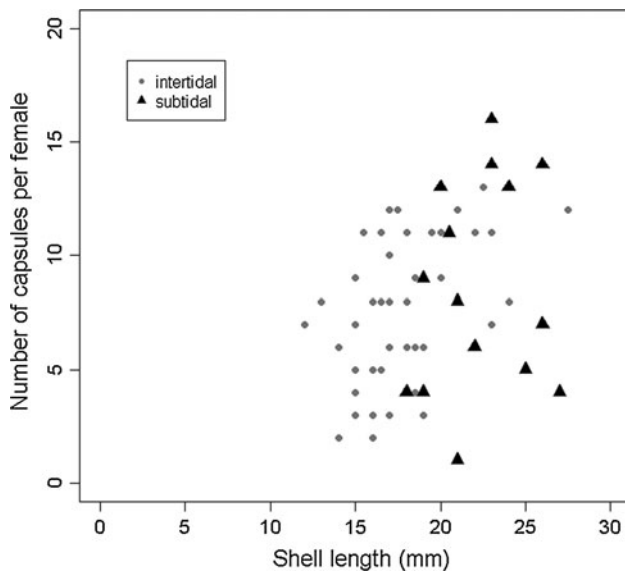
Fig. 5 Comparison of the number of egg capsules as a function of SL in each sample (intertidal and subtidal) of *Crepipatella dilatata* (only data for March, May, June, and August 2008 for both groups were used)

Sokolova (1995), Krist (2001), Fredensborg and Poulin (2006) and Granovitch et al. (2009). The mechanism by which parasitization affects the growth of females is currently unknown; however, one possible explanation is that host fecundity has evolved under different selection pressures that are associated with different trematode prevalence levels (Granovitch et al. 2009). Moreover, in calyptraeids, other processes, such as the social control of sex change (Coe 1936; Warner et al. 1996; Collin et al. 2005), might be involved. The sex-related reproductive value of any individual strongly depends on the size and number of other group members, and a conditional response in sexual expression would be highly adaptive (Warner 1988; Collin 1995). It might be argued that the large number of castrated females in the *C. dilatata* population results in a deficiency of brooding females, which accelerates the sex change in smaller specimens.

We suggest there is a compensatory reproductive mechanism in intertidal snails to overcome the loss of reproductive individuals caused by the high prevalence of the castrating parasite. The negative pressure of parasitism on reproduction increases with size because the prevalence

values are higher in larger size classes. The fact that smaller brooding females and males were never found infected may be interpreted as a selectively preserved mechanism leading to successful reproduction and the survival of the population through time. Precocious reproduction may represent a trait selectively preserved throughout the evolution of life histories of the members of the host–parasite system. Granovitch et al. (2009) reported in *Littorina saxatilis* a mechanism where the fecundity of females in older age classes increases in parallel with the increasing trematode prevalence over approximately two decades. Previous studies reported that females from heavily infected *L. saxatilis* populations have a higher fecundity than those from populations with a low prevalence of infection (Sokolova 1995; Granovitch et al. 2009).

Although the size range of the subtidal snails was similar to that of the intertidal snails, the former had a greater proportion of smaller individuals, corresponding to the immature, male, and sex change stages (Online Resource 4). A similar pattern was observed by Sokolova (1995) in uninfected and moderately infected populations of *L. saxatilis* in the White Sea. This shape of the size (=age) frequency distributions has been theoretically predicted for populations with balanced mortality and birth rates (Pianka 1978). In contrast, heavily infected populations of *L. saxatilis* had a different age structure, characterized by a deficiency of juveniles (Sokolova 1995). Our results also suggest a reduced recruitment of juveniles in the intertidal sample, possibly as a consequence of the reproductive potential of the host population due to the high prevalence of *Maritrema* sp. infection.

It seems that in the highly parasitized intertidal sample of *C. dilatata*, more than one of the previously mentioned mechanisms compensates for the loss of reproductive individuals caused by parasitic castration. It could be argued that the anticipated reproduction in smaller females, the males not affected by parasites, and the increased proportions of brooding females in periods of a higher prevalence of infection are probable fitness responses to support population persistence under severe infection pressures.

Local variation in the prevalence of trematodes may be correlated with the density of intermediate hosts, with the abundance of final hosts, and with a number of environmental factors, such as temperature, photoperiod, and tides

(e.g., Kuris and Lafferty 1994; Skirnisson et al. 2004; Curtis 2007). In nature, temperature influences the development and activity of the intra-molluskan trematode stages (Ginetsinkaya 1988). Previous studies have demonstrated that elevated temperatures may impact the proliferation of parasites, by increasing the production of cercariae or promoting the maturation of larvae at higher temperatures (e.g., Marcogliese 2004; Fredensborg et al. 2005; Poulin and Mouritsen 2006). In this study, for the prevalence of infection, there was a negative association with SST and photoperiod. This phenomenon may be related to the abundance of birds, which are the final hosts for the parasite, on the intertidal shores of Puerto Madryn during the winter. During warmer seasons, tourism exerts intense human pressure on the intertidal sandy and rocky shores. This habitat alteration possibly generates a negative impact on bird communities by modifying their habits and therefore affecting the transmission of the parasites to their final hosts. The impact of tourism on several aspects of shorebird biology, particularly on habitat availability and breeding success, has previously been reported (Yasué and Dearden 2008).

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