

Parasitic castration: host species preferences, size-selectivity and spatial heterogeneity

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Summary. This study investigates host-parasite population dynamics in a marine intertidal community of three barnacle host species (*Balanus glandula*, *Chthamalus fissus* and *C. dalli*). Our paper addresses the following questions: (1) Does prevalence (percentage parasitism) differ among the three host species? (2) What are the spatial and temporal population dynamics within the community? and (3) Does the parasite exhibit size-selective behaviour in any of the three host species? Significant differences in prevalence were found among the three host species; the parasitic castrator (*Hemioniscus balani*) most heavily infected the least abundant host. Parasitism occurred throughout the year and also showed significant spatial variation. *H. balani* showed size-selective parasitism in *C. fissus*, but not in *C. dalli*. Consequently, the population effects of parasitic castration in *C. fissus* depend both upon the host population size structure and the intensity of the parasite's size-selectivity.

Key words: Parasitic castration – Marine – Size-selectivity

Community ecology of host-parasite ensembles has been relatively unexplored. Little is known of host species preferences, or spatial-temporal population dynamics in multi-host species communities. Moreover, although host size-selectivity has been found in many single host systems (Curtis and Hurd 1983; Sousa 1983; Minchella et al. 1985; Vogel and Bundy 1987), host size-selectivity in multi-host communities has not been investigated. Comparison of size-specific prevalence (percent parasitism) patterns among sympatric host populations may allow discrimination between two competing explanations for the generally found positive correlation between prevalence and host size: either parasites passively accumulate with host age or parasites actively select older hosts.

This study investigates host-parasite population dynamics in a marine intertidal community of three host species. *Hemioniscus balani* is an epicarid isopod that parasitically castrates adults of three species of barnacles (*Chthamalus fissus*, *C. dalli* and *Balanus glandula*) (Crisp 1968; Hines 1976; S. Blower unpublished work) that occur together in the high intertidal region at Hopkins Marine Station (Monterey Co.), California (HMS). Infection by only one *H. balani* causes complete castration of the host and parasitism by more than one *H. balani* is rare.

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The life cycles of both the parasite and the host include two distinct stages: an oceanic free-living larva and a sessile adult. However, the host species are simultaneous hermaphrodites; whilst the parasite is a protandrous hermaphrodite. *H. balani* passes through three developmental stages before finally attaching to its definitive host and metamorphosing into a female. The female attaches to the surface of the barnacle's ovaries and sucks out the ovarian fluid; thus preventing egg development without impairing sperm production. Consequently, parasitic castration by *H. balani* effectively transforms hermaphroditic hosts into males. Therefore, because barnacles are sessile organisms requiring internal cross-fertilization, parasitic castration can have important consequences for host population dynamics (Blower and Roughgarden 1987). Our paper addresses the following questions: (1) Does prevalence differ among the three host species? (2) What are the spatial and temporal host-parasite population dynamics within the community? (3) Does the parasite exhibit size-selective behaviour in any of the three host species?

Materials and methods

We carried out a spatial and temporal survey of parasitism in the three host species at HMS. The spatial survey was carried out in the summer of 1984. Three randomly positioned quadrat (34.56 cm²) samples were selected at each of seven sites, at the same tidal height, within the barnacle intertidal zone. Each quadrat was marked and the area within the quadrat photographed. The resulting slide was projected onto a screen and used to construct a map of the spatial location of each barnacle; each of which was identified to genus and numbered. The map was taken to the intertidal habitat where the numbered barnacles were removed and placed in individual wells in a tissue culture tray. In the laboratory the hosts were examined for parasites and the *Chthamalus* hosts were dissected for species identification.

The survey results were then used to select a high and a low parasitism site for the temporal survey. Every four weeks from 20th November 1984 to 19th January 1986 samples ($n=16$) were taken. The survey was terminated when the local population of the least abundant species, *C. fissus*, became severely depleted. At each site randomly selected barnacles were removed; fifty *B. glandula* and a minimum of twenty five of each *Chthamalus* species. Additional *Chthamalus* were collected to ensure that the correct sample

size of *C. fissus* was collected as *Chthamalus* barnacles could not be identified to species in the field. In the laboratory the hosts were dissected, identified to species, and examined for parasitism and reproductive condition.

Data for the spatial and temporal survey were pooled to assess species prevalence patterns. Data from the spatial survey were analysed for spatial heterogeneity in parasitism by logit analysis after fitting a log-linear model to the data. Then site prevalence patterns were explored to see if they could be explained on the basis of host spatial pattern and host density. Host spatial pattern was assessed by using a density independent measure, Morisita's index of dispersion, I_{δ} (Morisita 1959). The index was calculated by subdividing the sampled quadrats into smaller blocks and counting the number of hosts within each block. The index was calculated as shown in Eq. (1).

$$I_{\delta} = \frac{n \sum_i X_i(X_i - 1)}{N(N - 1)} \quad (1)$$

where X_i is the number of hosts in the i th block ($i = 1, \dots, n$), n is the total number of blocks and N is the total number of hosts. The index is equal to one for a random distribution, greater than one for an aggregated distribution and less than one for a regular distribution. The significance of departure of the index from randomness was tested by calculating F_0 as shown in Eq. (2).

$$F_0 = \frac{I_{\delta}(N - 1) + n - N}{n - 1} \quad (2)$$

which was tested against an F-distribution with $df_1 = n - 1$ and $df_2 = \infty$.

Data from the temporal survey were used to assess the temporal dynamics of infection, the brood cycles of the three host species and size-selective parasitism. The average number of broods produced by each host species were calculated by summing the reproductive fraction of the population in each sample over a year, dividing by the brood development time and averaging over the two sites.

Results

Significant differences in prevalence were found among the three host species (2×3 contingency test, $X^2 = 226.39$, $P \ll 0.001$) and between the two *Chthamalus* species (2×2 contingency test with Yates correction, $X^2 = 10.60$, $P < 0.01$). *B. glandula*, the most abundant species, was rarely infected (0.10%; $n = 3043$), *C. dalli* infection was higher (5.72%; $n = 2010$) and *C. fissus*, the least abundant species, was the most highly infected (8.96%; $n = 1004$).

Since parasitic infection in *B. glandula* was so low, only the two *Chthamalus* species were used in the analysis of spatial heterogeneity. A log-linear model was fitted to the data in the three-way contingency table (species \times site \times parasitism). Calculation of a Pearson goodness of fit statistic for the chosen model revealed no significant difference between the observed and expected frequency data ($X^2 = 10.50$, $df = 7$, $P > 0.16$). This analysis revealed significant spatial heterogeneity in parasitism ($P < 0.01$). Calculated coefficients from the log-linear model were used in a logit analysis to calculate the log-odds ratio (risk) of parasitism. The overall risk was only 3.43%, but the risk ranged from 1.22% to 8.29% depending upon the site. The level of para-

Table 1. Morisita's index of aggregation (I_{δ}) for the three host species

Site	<i>Balanus glandula</i>		<i>Chthamalus fissus</i>		<i>Chthamalus dalli</i>			
	I_{δ}	pattern	I_{δ}	pattern	I_{δ}	pattern		
A	1.07	**	A	1.18	R	1.09	*	A
B	1.05	*	A	—	—	1.11	—	R
C	1.21	***	A	3.27	***	A	1.04	R
D	1.11	*	A	1.14	R	1.12	*	A
E	1.18	**	A	—	—	1.13	—	R
F	1.57	R	1.58	R	1.17	R	R	
G	1.01	R	1.16	R	1.00	R	R	

Key: R = random spatial pattern; A = aggregated spatial pattern

Significance of aggregation: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

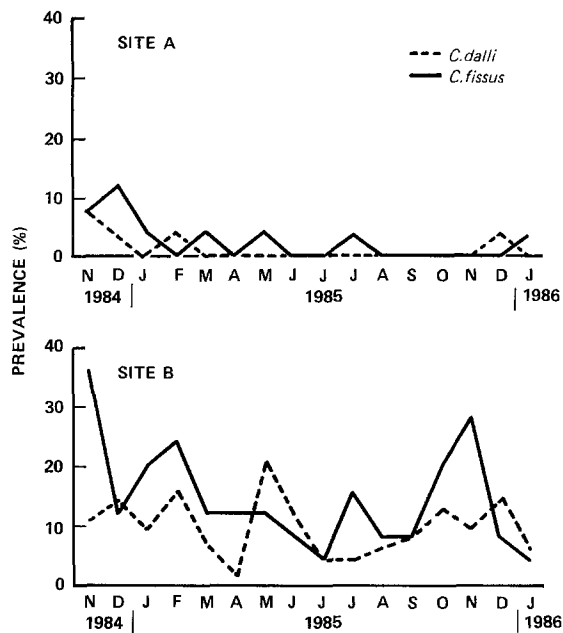


Fig. 1A, B. Temporal patterns of prevalence at a low parasitism (A) and a high parasitism (B) site

sitism in the two *Chthamalus* species at the seven sites was significantly correlated (Spearman rank correlation coefficient = 0.85, $P < 0.05$). The two *Chthamalus* species did not show differences in their spatial pattern (Table 1), but *B. glandula* showed a greater tendency to aggregation than either *Chthamalus* species. However, no significant relationships could be discerned for either of the two *Chthamalus* species between parasitism and host aggregation or parasitism and host density. Although, parasitism was highest at the two sites (A and D) where *C. dalli* populations were spatially aggregated.

Prevalence patterns for the two temporal survey sites are shown in Fig. 1. Parasitism occurred throughout the year in both *Chthamalus* species, but no infected *B. glandula* were found throughout the temporal survey. Figure 1 shows that spatial heterogeneity in parasitism and species prevalence differences were maintained throughout the year. The brood cycles of the three host species are shown in Fig. 2. *B. glandula* had the shortest brooding season (December–

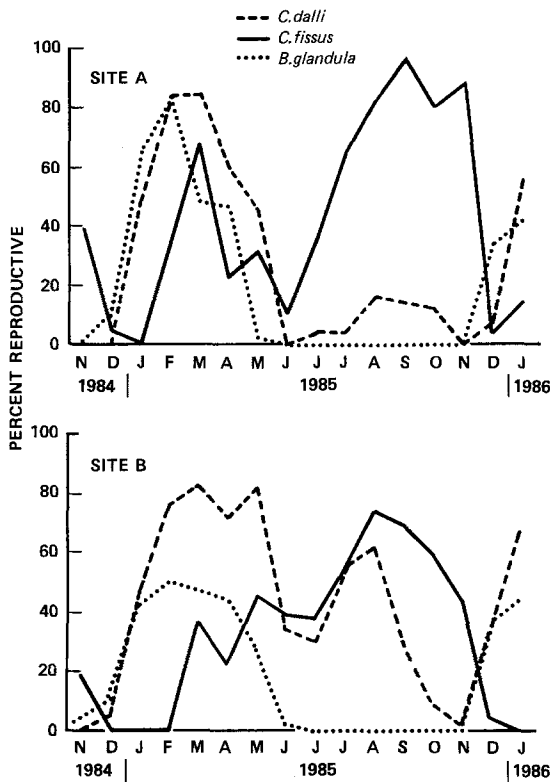


Fig. 2. Brooding cycles of the three host species of barnacles at HMS

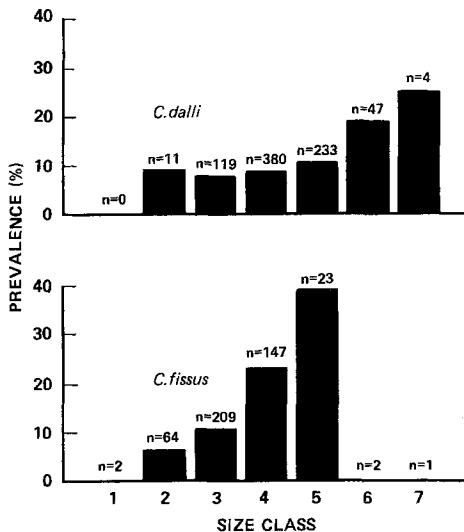


Fig. 3. Size-selective prevalence patterns for *H. balani* in its two principal host species

June); whereas both *Chthamalus* species brooded throughout the year. Brooding parasites were also found throughout the year. There was considerable spatial variation in the percentage brooding for all three host species between the two sites. However, no significant temporal relationship could be discerned between percentage brooding and parasitism for either of the two *Chthamalus* species. The number of broods produced by the three host species differed considerably (*B. glandula* 2.40, *C. dalli* 4.78, *C. fissus* 10.33), and was significantly correlated with the prevalence of infection (Spearman rank correlation = 1, $P \ll 0.001$).

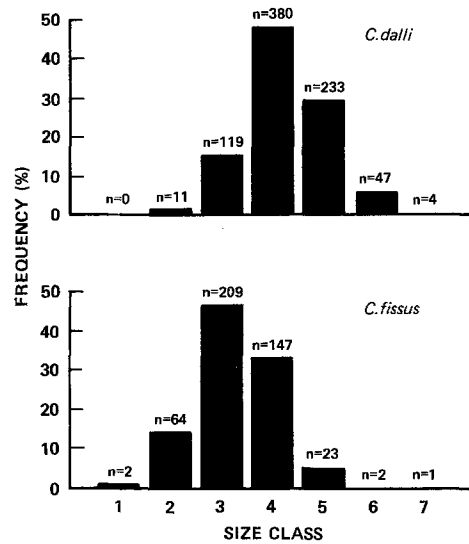


Fig. 4. Size structure of the two principal host species

Host size-selectivity was examined using data from the high parasitism site in the temporal survey. Size-specific prevalence patterns for the two *Chthamalus* species are shown in Fig. 3. *H. balani* was size-selective in *C. fissus* (2×4 contingency test, $X^2 = 22.34$, $P < 0.001$), whereas in *C. dalli* it was not (2×4 contingency test, $X^2 = 6.63$, $P > 0.08$); although the size structure of the two populations were fairly similar (Fig. 4). A multiplicative power law can be fitted to the *C. fissus* data ($y = ax^b$ where $y = \%$ parasitism, $x =$ host size class, $a = 1.40$, $b = 2.01$, $r^2 = 0.96$).

Discussion

H. balani showed host species selectivity, selecting *C. fissus*, the least abundant host to infect the most. The reason for this preference is unknown; however, *H. balani* is effectively diverting barnacle reproduction into parasite reproduction and examination of the three hosts brooding patterns reveals significant differences among them. *C. fissus*, the most highly infected species, produces the highest number of broods per year and has the longest brooding season. Therefore, the net reproductive rate of *H. balani* will presumably be greatest in *C. fissus*, assuming that barnacle larva to parasite larva conversion efficiency is of the same order of magnitude for the three host species.

Parasitic castration was spatially heterogeneous, as has been found in several other systems (Anderson and May 1979; Curtis and Hurd 1983). Parasitism was unrelated to host spatial pattern or to host density; this finding is in contrast to our results from a recent field experiment in which parasitism in *C. dalli* increased both with increasing host aggregation and host density (Blower and Roughgarden unpublished work). However, the field manipulation involved a factorial design in which the treatments consisted of specific combinations of *C. dalli* spatial pattern and density. Consequently, the effects of the two factors were independently evaluated and the interaction between different levels of the two factors assessed. In the survey, spatial pattern and density effects are confounded and hence the true relationships are obscured. Furthermore, although the host density range of the experiment and survey were com-

parable, in the experiment we investigated a wider range of host spatial pattern than in the survey.

Certain sites may be more likely to receive parasite larvae due to their position in relation to current patterns or distance from the offshore kelp bed; kelp forest communities have been shown to be recruitment filters for intertidal communities at HMS (Gaines and Roughgarden 1987). Therefore, as prevalence patterns of the two *Chthamalus* species were highly correlated, it is probable that the spatial heterogeneity that we found in parasitism was the result of this differential exposure of certain sites to parasites. Short term temporal prevalence patterns varied, but spatial heterogeneity and species infection differences were maintained throughout the year. Parasitism occurs throughout the year, because both the parasite and the principal host species life-cycles are synchronized and continuously brood.

H. balani showed size-selectivity in this preferred host, *C. fissus*, but not in *C. dalli*; the form of the selectivity relationship is similar to that for other size-selective parasites (Curtis and Hurd 1983; Sousa 1983; Minchella et al. 1985; Vogel and Bundy 1987). A comparison of the size-selective prevalence patterns in the two *Chthamalus* species (Fig. 3) suggests that parasites are not passively accumulating in the older and larger hosts, but are actively selecting *C. fissus* hosts. Larger barnacles produce larger broods (Hines 1976) and, consequently, larger female parasites. Epicarid isopod brood size increases with female size (Bourdon 1968; Beck 1980), hence size-selective behaviour increases the net reproductive rate of the parasite. Size-selective behaviour also greatly effects the impact that parasitic castration has on the reproductive output of the host population. Although the overall incidence of parasitism is low in *C. fissus* (8.96%); older and potentially more productive individuals have a much greater risk of parasitism (39.13% in size class 5). Therefore, unless both size-selectivity and the host population size structure are considered, the effects of parasitic castration on host reproduction can be greatly underestimated.

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