Spatial distribution and the effects of competition on some temperate Scleractinia and Corallimorpharia

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ABSTRACT: The impact of interference competition on coral community structure is poorly understood. On subtidal rocks in the northeastern Pacific, members of 3 scleractinian coral species (Astrangia lajollaensis, Balanophyllia elegans, Paracyathus stearnsii) and 1 corallimorpharian (Corynactis californica) were examined to determine whether competition exerts substantial influence over their abundance and distributional patterns. These anthozoans occupy >50% cover on hard substrate, and exhibit characteristic patterns of spatial distribution, with vertical zonation and segregation among some species. They interact in an interspecific dominance hierarchy that lacks reversals, and is linear and consistent under laboratory and field conditions. Experiments demonstrated that a competitive dominant, C. californica, influences the abundance and population structure of a subordinate, B. elegans, by (1) reducing sexual reproductive output, (2) increasing larval mortality, (3) altering recruitment patterns. Field cross-transplants revealed that the dominant also affects vertical zonation of a competitive intermediate, A. lajollaensis, by killing polyps that occur near the tops of subtidal rocks. It is concluded that between-species competition, mediated in part by larval-adult interaction, strongly influences the structure of this temperate anthozoan assemblage.

INTRODUCTION

Scleractinian corals and other anthozoans exhibit diverse aggressive behaviors, which have been proposed to mediate interference competition on tropical reefs (references in Sebens 1976, Chadwick 1988a, review by Lang & Chornesky 1991). However, controversy exists over the impact of competitive behavior on coral community structure. In some areas, disturbances such as wave action and predation may limit coral abundance to levels below those at which competition is important (Connell 1978, Bradbury & Young 1982, Dollar 1982). In the tropics, coral competitive interactions mediated by aggression appear to exert community effects mainly on reef slopes where physical disturbance is low and coral density high (Grigg & Maragos 1974, Maragos 1974, Benayahu & Loya 1981, Sheppard 1982).

Because field observations alone cannot elucidate the processes that underlie distributional patterns, long-term manipulation of natural populations is necessary to reveal competitive and other interactions. However, field experiments on competition among tropical anthozoans have extended only 11 mo (Romano 1990), and long-term manipulations have not been conducted on temperate anthozoans.

In temperate marine habitats, anthozoans such as actinian sea anemones, corallimorpharians, and ahermatypic scleractinian corals may dominate benthic communities on hard substrata (Pequegnat 1964, Turner et al. 1969, Castri-C-F ey et al. 1978, Schmieder 1985, Lissner & Dorsey 1986), and the extent to which their competitive interactions influence community structure is of interest. An assemblage of 4 interacting anthozoans on subtidal rocks on the California coast is particularly amenable to experimental analysis, in contrast with tropical reef assemblages which contain up to 54 species of interacting corals (Sheppard 1979). Directed interspecific aggression, resulting in substantial damage to opponents, has been documented in 1 of the Californian species, Corynactis californica Car-
B. elongated, unilaterally damages C. californica cated that vertical sides and along the horizontal top of each rock. Formed, because previous work (Chadwick 1987) indicated small-scale, randomly-selected areas at an interval of 0.5 m up the reverse experiment was not performed, because previous work (Chadwick 1987) indicated that C. californica uni laterally damages B. elen-
I selected 3 adjacent rocks, each 8 to 10 m in height above sandy substratum at 15 m depth, with flat horizontal tops and steep sides. On the vertical sides, I used steel pegs to mark eleven 12 x 18 cm quadrats that contained both polyps of B. elegans and of C. californica. I randomly selected 6 of the 11 quadrats for experimental manipulation and left 5 unmanipulated as controls, interspersed among the 3 rocks. In the 6 experimental plots I removed all polyps of C. californica by scraping them off the rock with a putty knife; all other organisms were left intact. Every 6 mo for 2 yr, I photographed the quadrats and removed stray coral-limorpharians in the experimental plots. Photographic transparencies were projected onto a screen, and the number of polyps, and oral disk diameter of each coral, were calculated. All B. elegans corals > 6 mm oral diameter were classified as adults (Chadwick 1988b).

**Laboratory experiments on larval-adult interaction.**

To examine interactions between the benthic larvae of Balanophyllia elegans and adult polyps of Corynactis californica, members of each species were maintained in aerated trays of natural seawater at ambient sea temperature (11 to 17 °C). Each week the water was changed and the polyps fed adult brine shrimp Artemia salina to saturation.

The first experiment assessed the effect of prolonged contact with Corynactis californica polyps on the number of brooded larvae released by Balanophyllia elegans. I used 10 experimental corals that had contacted C. californica polyps and 10 control corals that had been isolated from contact for 6 mo, as part of experiments on behavioral interactions (see above). These contact conditions were continued during experiments on larval-adult interaction. Because it was necessary to segregate experimental and control groups, to prevent mixing of their larvae, the trays were exchanged each week to minimize effects due to differences in the trays alone. The number of larvae released by corals in each group was determined weekly over portions of 2 reproductive seasons (Fadlallah & Pearse 1982).

The second experiment examined the effect of Corynactis californica polyps on the survival of Balanophyllia elegans larvae, and on larval settlement sites, using larvae obtained in the first experiment. Fifteen larvae were placed into each of 2 plastic trays. One contained 4 haphazardly-spaced barnacle shells that covered < 25% of the tray bottom, and each bore 10 to 20 polyps of C. californica. The other tray contained shells lacking C. californica. After 1 wk I counted the number of larvae and settled corals, and measured the distance from each settled coral to the nearest shell in the tray. At the end of each of 4 week-long trials, all larvae and corals were removed, the water changed, and at least 15 new larvae added to each treatment.

**Field transplant experiment.** A short-term transplant experiment was conducted on a subtidal rock that contained large aggregations of the 2 most abundant species, Corynactis californica and Astrangia lajollaensis, to determine whether interspecific competition influences their vertical distributional patterns. Polyps were transplanted (1) within their zone of origin, (2) into the zone containing the other species and contacting that species, or (3) into the zone containing the other species but not in interspecific contact (zones in Fig. 1). Ten polyps of either A. lajollaensis or C. californica on each of 5 plexiglass plates (4 x 4 cm) were subjected to each treatment.

Members of 3 clones of each species were collected from isolated rocks at 8 to 12 m depth in HMLR (after Fadlallah 1982), and were randomly assigned to the treatments. In the laboratory, the polyps were cemented along the edge of each plate in 2 rows of 5 polyps each (details above), maintained in plastic trays of aerated natural seawater at 15 °C, and returned to the field in less than 1 mo. A 5 x 5 cm area on the rock was cleared for attachment of each plate, by removing all sessile organisms with a hammer and chisel. For the treatments involving contact with other anthozoans, the plates were cemented < 5 mm from resident polyps. I monitored the number and condition of all transplanted polyps weekly for 5 wk.
RESULTS

Patterns of spatial distribution

Members of the 4 anthozoan species covered much of the substratum on subtidal rocks, from 24.4 ± 7.3 % (% ± SE) cover at 1.5 m height to 56.1 ± 7.3 % cover at 2.5 m height, and some exhibited vertical zonation (Figs. 1 & 2). Astrangia lajollaensis was most abundant near the rock bases (% cover at 0.5 m height = 29.9 ± 7.2 %, % ± SE), while Corynactis californica occurred at highest densities near the rock tops (53.5 ± 6.6 % cover at 2.5 m height). Balanophyllia elegans occurred at low density throughout (7.5 ± 1.9 % cover at 1.5 m height), and Paracyathus stearnsii appeared only along the rock bases at very low densities (0.8 ± 0.4 % cover at 0.1 m height) (Fig. 2; note scale differences among vertical axes). A 2-way ANOVA of the effects of rock and height on abundance showed significant variation with height for all 4 species, and no variation among rocks except for in A. lajollaensis (Table 1). Significant interaction effects of rock and height (Table 1) reflect that vertical zonation patterns varied slightly among rocks (Fig. 2). Zonation occurred only on large rocks with nearly vertical sides, and appeared to break down on smaller rocks, or those with more irregular shape.

Patterns of interaction

Laboratory experiments revealed wide variation in damage among species pairs (Fig. 3). A non-parametric ANOVA of % damage to polyps after 6 mo of contact
showed significant heterogeneity among the 12 possible 1-way interactions (Kruskal-Wallis test, $H = 292.23, p < 0.01$). In 4 out of 6 possible species combinations, significantly greater damage was inflicted on 1 member of the pair than on the other (Mann-Whitney $U$ tests, $U = 315$ to 3136, $p < 0.01$ in all cases), indicating interspecific dominance.

Both *Corynactis californica* and *Paracyathus stearnsii* exhibited little injury during interactions (Fig. 3), and no significant difference among species contacted (Kruskal-Wallis tests, $H = 0$ and 3.87, $p = 1.0$ and 0.14, respectively). Polyps of *Astrangia lajollaensis* were severely damaged by *C. californica*, but not by the other corals, while *Balanophyllia elegans* polyps were injured, to varying degree, by members of all other species (significant variation among species contacted, $H = 88.12$ and 20.03, respectively, $p < 0.01$ in both cases).

Although *Paracyathus stearnsii* did not inflict apparent injury on *Corynactis californica*, within 1 mo, 86.4% ($n = 22$) of *C. californica* polyps avoided contact by bending away. Within 2 mo, *C. californica* polyps had moved out of contact with *P. stearnsii* polyps, and most (68.2%, $n = 22$) remained at least 5 mm distant during the 11 mo of observation.

Of the 20 polyps in each species that contacted conspecifics, all remained expanded and undamaged except for 1 *Balanophyllia elegans* polyp that died after 1 mo.

Few instances of aggressive behavior were detected during monthly observations. In $< 1$% of pairs ($n = 154$), polyps extruded short, 1 mm length mesenterial filaments, which did not adhere to or damage opponents. More frequent (hourly) observations have shown that *Corynactis californica* attacks opponents via massive extrusion of mesenterial filaments (Chadwick 1987).

The dominance hierarchies derived from laboratory experiments (Fig. 3) and field observations (Table 2) were essentially the same (Fig. 4). One difference was that, in the laboratory, all ($n = 18$) contacts with *Astrangia lajollaensis* resulted in unilateral damage to *Balanophyllia elegans* (Fig. 3), whereas in the field, 34.5% ($n = 55$) of such contacts were benign (Table 2). Most *B. elegans* polyps in the field were taller than adjacent *A. lajollaensis* polyps, so their tentacle crowns segregated vertically, and both polyps remained expanded and undamaged. In contrast, during laboratory contacts, the polyps were positioned with their tentacle crowns at the same height above the substratum.

In the field, as in the laboratory (see above), conspecific polyps did not appear to injure each other (Table 2).
Table 2. Outcomes of natural interactions among selected anthozoans on subtidal rocks, 10 to 15 m depth, at Hopkins Marine Life Refuge, Monterey County, California, USA. $\rightarrow$ anthozoan listed in the horizontal column injured the anthozoan listed in the vertical column; $0 = $ no injury, in parentheses: number of cases observed

<table>
<thead>
<tr>
<th></th>
<th>Paracyathus stearnsii</th>
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<th>Astrangia lajollaensis</th>
<th>Balanophyllia elegans</th>
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<td>Balanophyllia elegans</td>
<td>0 (20)</td>
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Fig. 4. Dominance hierarchies among selected subtidal anthozoans in California, derived from laboratory experiments and field observations. See Fig. 3 for abbreviations

Field removal experiment

At the start of the field experiment, the abundance of *Corynactis californica* polyps, and juvenile and adult *Balanophyllia elegans* polyps, did not vary significantly between experimental and control quadrats (Mann-Whitney U tests, $U = 16, 23$ and $14$, $p = 0.85, 0.16$ and $0.85$, respectively). Two years after removal of *C. californica*, juvenile *B. elegans* were significantly more abundant in experimental than in control quadrats ($U = 30$, $p < 0.01$), while the number of adult *B. elegans* did not vary significantly ($U = 24$, $p = 0.10$) (Fig. 5). The abundance of *C. californica* in control quadrats decreased over 2 yr, but remained significantly higher than that in experimental plots ($U = 4$, $p < 0.05$). Photographs revealed that the same *C. californica* individuals were present throughout the study, so the observed drop in abundance was not due to annual population turnover.

The size-structure of the *Balanophyllia elegans* population also shifted after removal of *Corynactis californica* (Fig. 6). At the start of the experiment, the size distributions of *B. elegans* in control and experimental quadrats did not vary significantly in location (Mann-Whitney U test, $U = 1550$, $p = 0.32$) or in shape (Kolmogorov-Smirnov test, $D = 0.104$, $p = 0.67$). After 2 yr, the median size of *B. elegans* in the experimental quadrats was significantly smaller than in control plots (Mann-Whitney U test, $U = 6768$, $p = 0.01$), and the shape of the size-frequency distribution differed significantly between treatments (Kolmogorov-Smirnov test, $D = 0.28$, $p < 0.01$). Photographs revealed that this was due to massive juvenile recruitment in areas where the dominant, *C. californica*, had been removed, rather than to variation in individual growth rates.
Laboratory experiments on larval-adult interaction

Polyps of Balanophyllia elegans that had contacted Corynactis californica polyps for 6 mo in the laboratory produced fewer larvae per individual during spring 1986 than did control corals, and this gap widened during the following reproductive season (Fig. 7). Because the corals in each treatment were cultured as a group, their reproductive output could not be monitored individually, and a statistical test could not be applied.

After they emerged from parent corals, the benthic larvae of Balanophyllia elegans suffered significantly higher mortality in trays with Corynactis californica (mean mortality ± SE = 56.53 ± 12.97 %, n = 4 trials of 15 larvae each) than in those without (6.08 ± 2.41 %, n = 4 trials of 15 larvae each) (G-test of independence on original frequency data, G = 52.09, p < 0.01). In addition, larvae that metamorphosed into juvenile corals settled at significantly greater distances from shells bearing C. californica polyps than they did from empty shells (Mann-Whitney U test, U = 688, p < 0.05) (Fig. 8). During behavioral observations, 4 B. elegans larvae, that were placed in contact with C. californica polyps, adhered to the polyp tentacles and were consumed within 20 min.

Field transplant experiment

At the start of the experiment, all Corynactis californica and Astrangia lajollaensis polyps were undamaged and firmly attached to the plates. Within 1 wk, A. lajollaensis polyps transplanted up into contact with C. californica polyps exhibited tissue damage. After 5 wk, only 58.0 ± 5.8 % (X ± SE) of A. lajollaensis polyps remained alive on these plates, compared with > 95 % survival of polyps in the other 2 treatments (Fig. 9) (significant variation in survival among treatments, Kruskal-Wallis test, H = 10.76, p < 0.01). Polyps on the plate edges, where they faced interspecific contact, were killed, while inner polyps remained alive.

The Corynactis californica polyps transplanted into contact with conspecifics, multiplied asexually. However, those transplanted down into the Astrangia lajollaensis zone decreased in number (Fig. 9; zones in Fig. 1). Within 1 wk, many C. californica polyps in the A. lajollaensis zone became covered with sediment, inflated their lower columns, and partly detached their pedal disks from the substratum; after 5 wk, many had disappeared from the plates (Fig. 9). C. californica polyps in the outer row facing interspecific contact did not suffer greater mortality than did inner polyps protected from contact. Survival of C. californica polyps varied widely within each treatment (Fig. 9), and at 5 wk did not differ significantly among treatments (Kruskal-Wallis test, H = 2.41, p = 0.30).
DISCUSSION

This study demonstrates that certain scleractinian corals and corallimorpharians exhibit vertical zonation on temperate subtidal rocks, a phenomenon well known for corals on tropical reef slopes (Sheppard 1979, 1982, Benayahu & Loya 1981). The zonation pattern is consistent among sites in Central and Southern California, at different depths and vertical scales (Pequegnat 1964, Chadwick 1988b; Figs. 1 & 2). This evidence supports the idea that anthozoan abundance depends on proximity to the top and base of each rock, probably due to vertical gradients in physical (sand scour, water flow) and biological (competition, predation) factors.

One such factor limiting Balanophyllia elegans abundance (Fig. 2) appears to be spatial competition with Corynactis californica (Fig. 5). The laboratory experiments revealed that the competitive mechanism works via larval-adult interactions, and effects on fecundity. Since juveniles of B. elegans recruit locally (Gerrodette 1981), any factor that reduces larval production (Fig. 7) directly affects local population size. In addition, after the larvae emerge from parent corals and crawl about on the substratum (Gerrodette 1981), contact with C. californica may greatly reduce larval survival (see ‘Results’). Finally, the settlement patterns of larvae may be altered, due to predation on larvae that come too close to C. californica, or detection and avoidance of C. californica by the larvae. Either process would lead to the observed halo of low coral recruitment around laboratory aggregations of C. californica (Fig. 8), and also explain the increased field recruitment of corals in the absence of C. californica (Figs. 5 & 6). Avoidance of dominant competitors also is exhibited by larvae of other sessile invertebrates (Grosberg 1981).

The transplant experiment demonstrates that polyps of the competitively intermediate species, Astrangia lajollaensis, are killed upon contact with those of the dominant Corynactis californica, whereas if isolated from contact, A. lajollaensis polyps can survive for at least 5 wk in the C. californica zone (Fig. 9). Together with laboratory experiments (Fig. 3) and field observations (Table 2) that indicate unilateral injury of A. lajollaensis by C. californica, these data support the hypothesis that A. lajollaensis abundance is reduced near subtidal reef tops due to competitive interference by C. californica.

The 2 species differ also in ability to exploit unoccupied space. Corynactis californica clones can asexually produce new polyps in <5 wk (Fig. 9), and are known to exhibit high rates of clonal replication (Chadwick & Adams in press). In contrast, Astrangia lajollaensis has been estimated by Fadlallah (1982) to asexually produce only 0.12 new buds polyp−1 yr−1. This difference in replication rate, plus the behavioral dominance of C. californica over A. lajollaensis, may allow C. californica clones to monopolize space, and success-
fully exclude newly settled colonies of *A. lajollaensis* from upper rock areas.

Because the transplant experiment involved introducing contact between adult polyps, it does not reveal patterns of larval recruitment, which may cause the observed zonation of adult polyps. The factors limiting the vertical distributions of these species might be better elucidated by clearing areas at different heights on the rocks and observing recruitment patterns, as done in part for *Balanophyllia elegans* (Figs. 5 & 6). However, this approach is impractical due to rare sexual recruitment in both *Corynactis californica* (Carlisle et al. 1964, Turner et al. 1969) and *Astrangia lajollaensis* (Fadlallah 1982).

On rocky intertidal substrata, physical factors appear to set the upper limits of many species, while biological interactions control their lower limits (Underwood & Denley 1984). On large subtidal rocks, the inverse pattern may hold; lower limits may be determined by extreme physical conditions near the sand-rock interface, such as low water flow (Pequegnat 1964), sedimentation, and/or sand scour (N. Chadwick pers. obs.), while upper limits may be influenced by competition, as demonstrated here, or other biological interactions. The vertical zonation patterns of anthozoans on shallow temperate rocks appear to be controlled in part by physical gradients, and in part by competition and other interactions among the species.

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