

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 substrata, 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, Castric-Fey 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* Carl-

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gren, 1936 (Chadwick 1987). It is possible also to examine competitive interactions between larvae and adults in this system, because members of another species, *Balanophyllia elegans* Verrill, 1864, release large, benthic larvae (Gerrodette 1981, Fadlallah & Pearse 1982).

Through field surveys, and field and laboratory experiments, I demonstrate that: (1) some Californian anthozoans exhibit subtidal vertical zonation, (2) they interact in a linear dominance hierarchy, (3) the abundance, distribution, and/or population structure of subordinate and intermediate species is influenced by the competitive dominant, (4) larval-adult interactions mediate some of these processes.

Field work was conducted at the Hopkins Marine Life Refuge (HMLR), Monterey County, California, USA (36° 37.4' N, 121° 54' W). The site consists of granite outcroppings interspersed with sand channels that slope down to a sand plain at 12 to 15 m water depth. A dense forest of giant kelp *Macrocystis pyrifera* (Linnaeus, 1771) grows on these rocks during most of the year. Sessile invertebrates are especially dense on rocks in the deeper parts of the kelp forest where few understory algae grow (Pearse & Lowry 1974).

At least 13 species of anthozoans occur in the kelp forest at HMLR (Pearse & Lowry 1974). Three ahermatypic scleractinian corals and 1 corallimorpharian occupy exposed rock surfaces at 5 to 15 m depth in the outer parts of the kelp bed. The corallimorpharian *Corynactis californica* forms large aggregations of polyps each 10 to 25 mm in diameter (Morris et al. 1980, Chadwick 1987). The coral *Astrangia lajollaensis* Durham 1947 forms encrusting colonies of 5 mm diameter polyps; each colony may live for 40 yr or more (Fadlallah 1982). *Balanophyllia elegans* is a solitary coral with 10 mm diameter polyps (Morris et al. 1980), that each have a lifespan of 5 to 10 yr (Fadlallah 1983). *Paracyathus stearnsii* Verrill, 1869 produces solitary coral polyps with oral disks up to 20 mm in diameter (Pearse & Lowry 1974).

MATERIALS AND METHODS

Patterns of spatial distribution. I quantified patterns of vertical distribution and abundance of the above anthozoans on 3 large rocks that extended 2.5 to 4.5 m in height above a sand plain at 11 to 12 m water depth. The abundance of anthozoans was determined from photographs taken by height above the sandy bottom (the anthozoans appeared to be distributed with reference to height rather than depth, Pequegnat 1964). Six 12 × 18 cm framed photographs were taken of randomly-selected areas at an interval of 0.5 m up the vertical sides and along the horizontal top of each rock.

The quadrat size was chosen as large enough to enclose many polyps (up to 160), yet small enough for identification of each polyp.

To assess abundances, photographic transparencies were projected onto a screen and the number of polyps of each anthozoan species determined per 12 × 18 cm area (= $\pi/0.0216 \text{ m}^2$) and then converted to the number per 0.01 m². Percent cover was estimated via a uniform array of 100 points superimposed on the projected image.

Patterns of interaction. To investigate the possibility of competitive interactions within and between the species, I observed the outcomes of contacts between randomly selected polyps at 8 to 15 m depth. Polyps were considered to interact if close enough for their extended tentacles or mesenterial filaments to touch, within ca 5 mm inter-skeletal or inter-column distance. For each interaction, the outcome was noted as: damage to one individual, damage to both, or damage to neither. Injuries were visible as an area of dead or damaged tissue, or exposed calcareous skeleton along the region of contact.

Laboratory experiments were conducted to determine the time course of interactions, and to compare the outcomes of experimental and natural contacts. I collected the corals at HMLR, transported them to the Joseph M. Long Marine Laboratory of the University of California at Santa Cruz (USA), and cemented them underwater onto glass microscope slides (7.5 × 5 cm) with Sea Goin' Poxxy Putty (Permalite Plastics Corporation, Newport Beach, CA 92663, USA). Adjacent to each coral I attached a polyp of another coral species, at <5 mm inter-skeletal distance, but not in direct skeletal contact. Individuals of *Corynactis californica* also were collected from HMLR, and a piece of barnacle shell bearing a single corallimorpharian polyp was cemented adjacent to each coral. I set up at least 20 pairs of polyps in each of the 6 possible combinations of the 4 species. To monitor effects of within-species contact, 20 individuals of each species were cemented into contact with conspecifics, and these slides interspersed with those bearing heterospecific pairs. Only full-sized, undamaged adults were used (sizes given above). The anthozoans were maintained in plastic trays supplied with running seawater at ambient sea temperature (11 to 17 °C), and fed adult brine shrimp *Artemia salina* each week to saturation; the shrimp were readily consumed by all polyps. Percent tissue damage to each polyp was determined monthly for 6 mo.

Field removal experiment. Based on results from the above experiments, I investigated long-term effects of competition with *Corynactis californica* on *Balanophyllia elegans*. The reverse experiment was not performed, because previous work (Chadwick 1987) indicated that *C. californica* unilaterally damages *B. ele-*

gans. 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 × 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 × 4 cm) were subjected to each treatment.

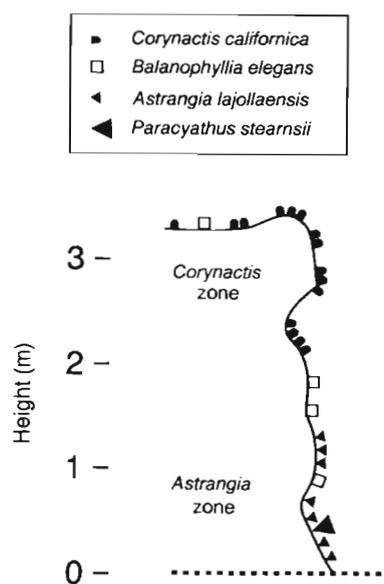


Fig. 1. Habitat profile of 4 anthozoan species on subtidal rocks at Hopkins Marine Life Refuge, Monterey County, California, USA. Sandy substratum along rock base is at 11 to 15 m water depth. Symbols represent individual polyps; not drawn to scale

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 × 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 $24.4 \pm 7.3\%$ ($\bar{x} \pm SE$) cover at 1.5 m height to $56.1 \pm 7.5\%$ 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 = $29.9 \pm 7.2\%$, $\bar{x} \pm SE$), while *Corynactis californica* occurred at highest densities near the rock tops ($53.5 \pm 6.6\%$ cover at 2.5 m height). *Balanophyllia elegans* occurred at low density throughout ($7.5 \pm 1.9\%$ cover at 1.5 m height), and *Paracyathus stearnsii* appeared only along the rock bases at very low densities ($0.8 \pm 0.4\%$ 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

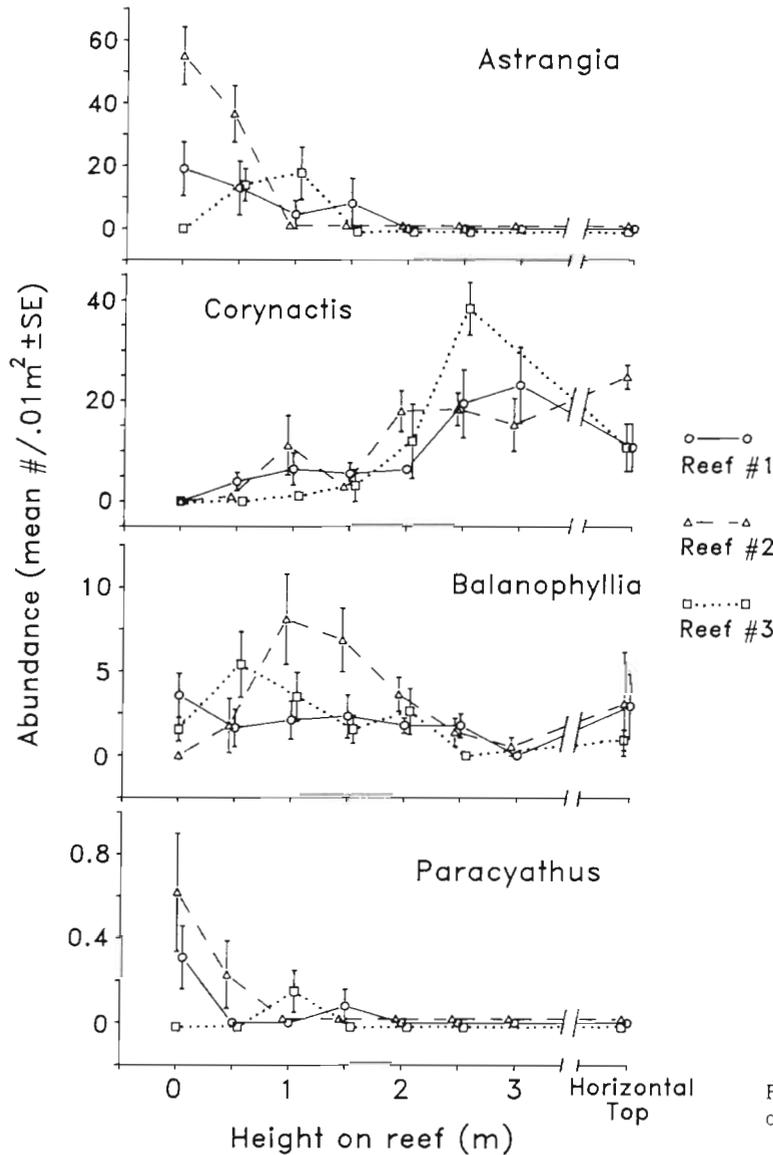


Fig. 2. Patterns of vertical abundance of anthozoans on 3 subtidal reefs at Hopkins Marine Life Refuge, Monterey County, California, USA

Table 1. Two-way ANOVA of anthozoan abundance on subtidal rocks at Hopkins Marine Life Refuge, Monterey County, California, USA

Species	Source of variation	DF	Mean square	F	p
<i>Corynactis californica</i>	Rock	2	43.09	0.58	ns
	Height	5	1609.89	21.97	***
	Rock × height	10	222.10	3.03	**
	Error	90	73.28		
<i>Astrangia lajollaensis</i>	Rock	2	997.25	6.07	**
	Height	5	2144.31	13.05	***
	Rock × height	10	1077.57	6.56	***
	Error	90	164.36		
<i>Balanophyllia elegans</i>	Rock	2	21.41	2.09	ns
	Height	5	28.64	2.80	.
	Rock × height	10	28.94	2.83	**
	Error	90	10.23		
<i>Paracyathus stearnsii</i>	Rock	2	0.13	2.60	ns
	Height	5	0.25	5.12	***
	Rock × height	10	0.12	2.53	.
	Error	90	0.05		

. p < 0.05, ** p < 0.01, *** p < 0.001, ns = not significant

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 ($n =$

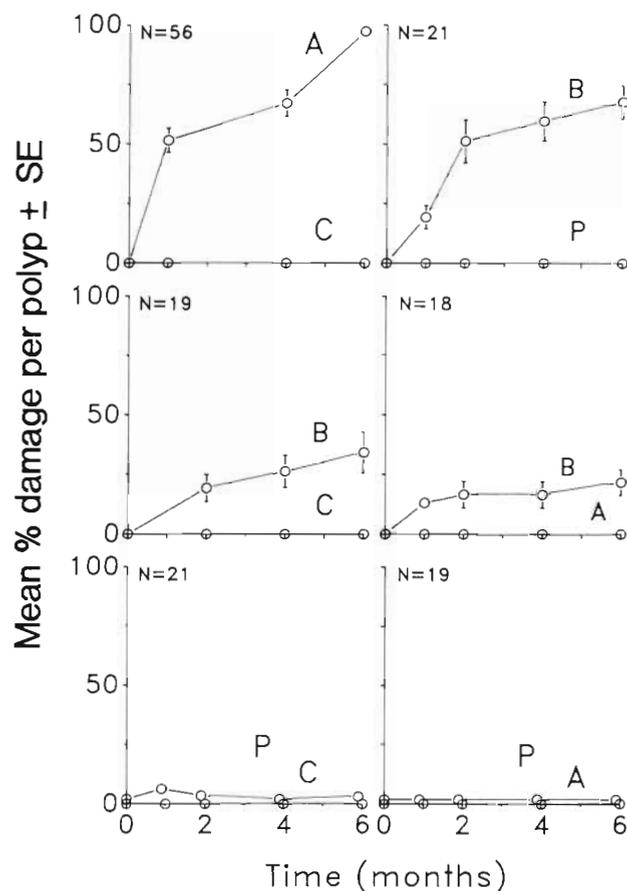


Fig. 3. Variation among species pairs in effects of interspecific contact in the laboratory. A = *Astrangia lajollaensis*, C = *Corynactis californica*, B = *Balanophyllia elegans*, P = *Paracyathus stearnsii*

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. → = anthozoan listed in the horizontal column injured the anthozoan listed in the vertical column; 0 = no injury, in parentheses: number of cases observed

	<i>Paracyathus stearnsii</i>	<i>Corynactis californica</i>	<i>Astrangia lajollaensis</i>	<i>Balanophyllia elegans</i>
<i>Paracyathus stearnsii</i>	0 (20)	0 (7)	0 (49)	→ (3) 0 (1)
<i>Corynactis californica</i>		0 (28)	→ (25)	→ (54) 0 (4)
<i>Astrangia lajollaensis</i>			0 (19)	→ (36) 0 (19)
<i>Balanophyllia elegans</i>				0 (20)

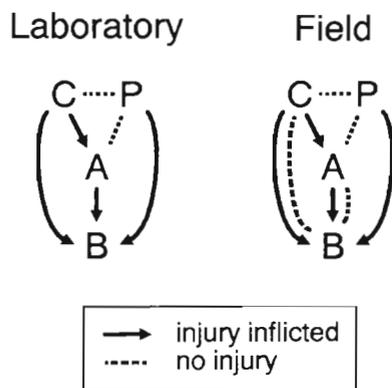


Fig. 4. Dominance hierarchies among selected subtidal anthozoans in California, derived from laboratory experiments and field observations. See Fig. 3 for abbreviations

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

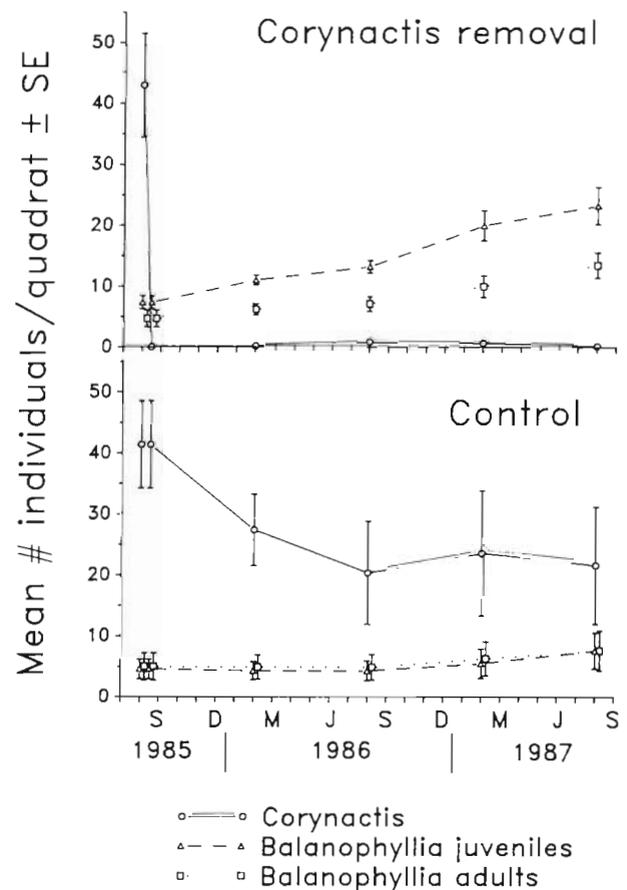


Fig. 5. Effect of removal of polyps of a competitive dominant, *Corynactis californica*, on the abundance of a subordinate, *Balanophyllia elegans*, during a 2 yr field experiment

(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.

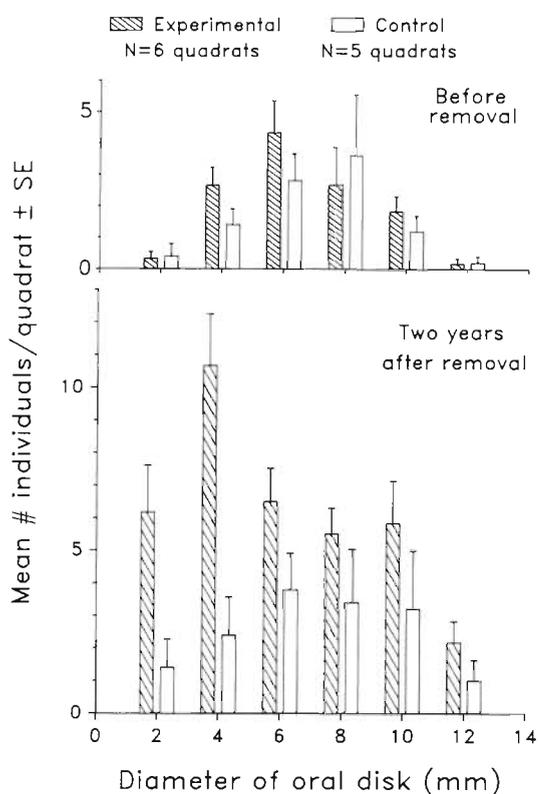


Fig. 6. Population size structure of a competitive subordinate, *Balanophyllia elegans*, before and 2 yr after removal of a dominant, *Corynactis californica*, in experimental field quadrats

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 \pm 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*

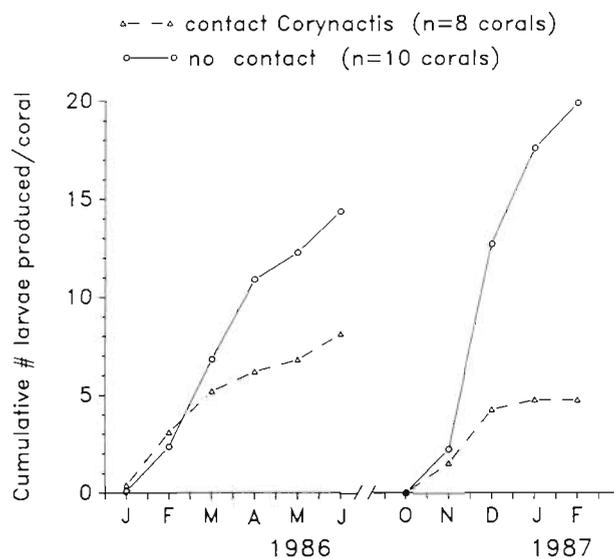


Fig. 7. Effect of *Corynactis californica* polyp contacts on larval production by *Balanophyllia elegans* during portions of 2 reproductive seasons in the laboratory

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 % ($\bar{x} \pm$ 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 via asexual reproduction. 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, $H = 2.41$, $p = 0.30$).

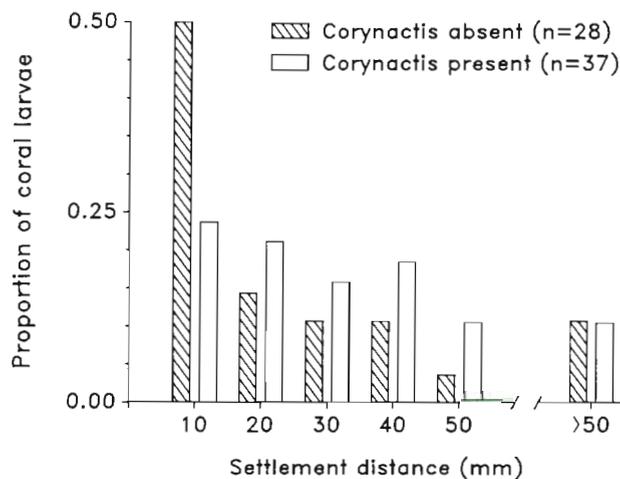


Fig. 8. Effect of presence of *Corynactis californica* polyps on settlement sites of *Balanophyllia elegans* larvae in the laboratory. Settlement distance = distance from each metamorphosed larva (juvenile coral) to nearest shell, with *C. californica* polyps present or absent

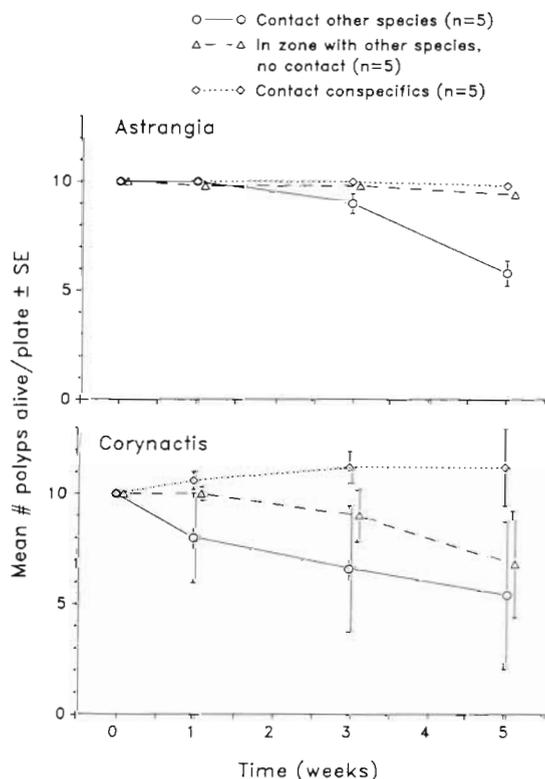


Fig. 9. Survival and asexual increase of cross-transplanted polyps in the field. Upper: competitive intermediate *Astrangia lajollaensis*; lower: competitive dominant *Corynactis californica*

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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