

# THE ROLES OF COMPENSATORY MORTALITY, PHYSICAL DISTURBANCE, AND SUBSTRATE RETENTION IN THE DEVELOPMENT AND ORGANIZATION OF A SAND-INFLUENCED, ROCKY-INTERTIDAL COMMUNITY

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**Abstract.** Manipulative experiments (using fenced exclosures, fence controls, and unmanipulated controls), as well as successional and community structure studies were performed near Dutch Harbor, San Nicolas Island, California to examine the importance of the anemone *Anthopleura elegantissima*, the sand tube worm *Phragmatopoma californica*, and macroalgae, in the structure and development of a sand-influenced community.

Following the removal of *Anthopleura elegantissima*, the cover of opportunistic algae such as *Cladophora columbiana*, *Chaetomorpha linum*, and Ralfsiaceae increased during the 1st 6 mo, whereas *Corallina vancouveriensis* and *Hydrolithon decipiens* suffered bleaching and decreased in abundance as a result of aerial exposure. The density of grazing molluscs (*Tegula funebris*, littorines, limpets, and chitons) also increased during the 1st 6 mo, then declined markedly, coincident with the recruitment and growth of the sand tube building polychaete, *Phragmatopoma californica*.

In the upper-intertidal area (above +1.1 m relative to mean lower low water), *Phragmatopoma californica* showed little recruitment (<1% cover after 25 mo) after removal of *Anthopleura elegantissima*. Investigations of secondary succession following total biota removal revealed that *A. elegantissima* achieved preremoval cover after 2 yr. In the mid-zone (+0.7 to +1.0 m), experimental anemone removal resulted in recruitment and domination by *P. californica* (>70% cover after 20 mo). *Anthopleura elegantissima* again regained preremoval abundance (26% cover) in the successional studies after 2 yr. At low levels (below +0.5 m), where sand burial did not occur, *P. californica* persisted even when contiguous with *A. elegantissima* aggregations. Successional data indicated that *P. californica* achieved preremoval levels in <12 mo, whereas *A. elegantissima* was unsuccessful at recruiting into these regions.

It is suggested that the stress of exposure to air (desiccating and thermal effects) and heavy sand inundation, as well as differential abilities to sequester and dominate available free space, are responsible for the developmental and structural patterns in this community. At desiccated and thermally stressed upper-intertidal levels, *Anthopleura elegantissima* facilitates colonization and subsequent survival of coralline algae and small *Phragmatopoma californica* aggregations while simultaneously inhibiting the recruitment of opportunistic macroalgae. *Phragmatopoma californica* can rapidly colonize and retain newly available free space in low- to mid-intertidal regions with reduced aerial exposure stress. At mid-levels, the upper-intertidal patterns prevail, but when released from *A. elegantissima* inhibition by disturbance, *P. californica* colonies show extensive development. However, in mid-intertidal regions, compensatory mortality of *P. californica* caused by sand deposition prevents these large aggregations from persisting and *A. elegantissima* becomes dominant. In the low-intertidal zones, with little sand-related stress, *P. californica* inhibits both *A. elegantissima* and macroalgae, while it may enhance recruitment and survival of its own juvenile stages in a self-facilitating strategy of larval selectivity. Therefore, the importance of *A. elegantissima* depends on compensatory mortality of the superior competitor *P. californica*, caused by periodic stresses (e.g., exposure to air and sand inundation) and physical disturbance.

**Key words:** algae; *Anthopleura elegantissima*; California; colonization patterns; community structure; desiccation; disturbance; *Phragmatopoma californica*; rocky intertidal; sand inundation; stress; succession.

## INTRODUCTION

A long-standing concern of ecologists has been the elucidation of diversity, distribution, and abundance patterns during community development. Modern emphasis has moved from descriptions based on observation and intuition to an experimental, hypothesis-testing approach. The latter has provided greater predictive insight into the role of such factors as the

physical environment (e.g., substrate stability, Sousa 1979; log damage, Dayton 1971; storms, Connell 1978; sewage, Murray and Littler 1978; light, Hay 1981), predation (e.g., Dayton 1971, Lubchenco 1978), and competition (e.g., Connell 1961, Muller 1966, Dayton 1975).

The classical viewpoint (Cowles 1899, Clements 1916) of community development through time has undergone major contemporary modifications (Drury and Nisbet 1973, Horn 1974, Connell and Slatyer 1977), with alternative concepts (i.e., inhibition, tol-

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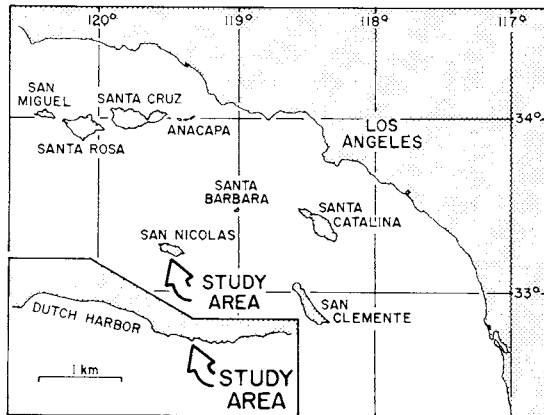


FIG. 1. Southern California coastline showing San Nicolas Island and location of study site near Dutch Harbor.

erance) included with the former directional replacement ("relay," Egler 1954 or "facilitative," Connell and Slatyer 1977) of species.

The purpose of this research is to examine the physical and biological interactions controlling the successional distributions and abundances of organisms in a rocky intertidal system disturbed by periodic sand inundation, influenced by a gradient of exposure to air, and containing the anemone *Anthopleura elegantissima* as the primary substrate occupier. We will propose and present evidence for an important interplay of species interactions, that vary as a function of stress and disturbance and that determine community development and organization. By stress, we mean physiological constraints which preclude or limit the production of individuals; by disturbance, we refer to biotic or abiotic factors causing the removal of organisms.

*Anthopleura elegantissima* (see Hand 1955 for description) is a common Pacific coast anemone that occurs singly or more often (Francis 1973a, Sebens 1980) in dense aggregations (clones) of genetically identical individuals produced by binary longitudinal fission. These clonal assemblages are frequently characteristic (though they occur elsewhere) of shorelines, from embayments to exposed coasts, influenced by suspended and deposited sand (Ford 1964, Ricketts et al. 1968, Littler 1980), or by thermal (Jennison 1978), sewage (Littler and Murray 1975), or chronic oil pollution (Littler 1980). The upper range of *A. elegantissima* on emergent substrata may exceed +1.5 m relative to mean lower low water (Hand 1955, Littler 1979). Clonal *A. elegantissima* are adapted morphologically, as individuals and aggregations (Francis 1973a, 1976, Koehl 1977, Shick et al. 1979), reproductively (Hand 1955, Francis 1973a, Sebens 1980), behaviorally (Hart and Crowe 1977), and physiologically (Shick et al. 1979) to the stresses caused by sand deposition and desiccation. In addition, an *Anthopleura elegantissima* aggregation may drastically alter the surrounding

physical environment at low tide by contracting into a moisture-retaining carpet of small cushions covered with fragments of rock, shells, sand, and other debris that are held by the adhesive papillae (verrucae) of the body wall (Hart and Crowe 1977).

In light of the above-mentioned adaptations and growth form, we predict that *Anthopleura elegantissima* in clonal mats is maintained as the dominant space occupier through stresses caused by exposure to air and sand burial. These moisture-retaining mats may facilitate the recruitment and survival of species living in the understory between individual anemones while opportunistic species are prevented from utilizing space by either interference or exploitation of resources. We have used community structure studies, as well as selective (*A. elegantissima*) and total biota removal experiments to test these predictions. Furthermore, we show that the pathways of development in this structurally simple community depend on an interplay of the tolerances of component species to environmental stress and physical disturbance, as well as the species' competitive abilities and life history strategies.

#### STUDY SITE

This investigation was conducted on San Nicolas Island, Ventura County, California (Fig. 1). The southwestern shoreline, composed of sandy beaches and intermittent sandstone points, is typical of many coastal areas throughout the Southern California Bight.

The site selected for study (Fig. 1) is a nearly horizontal ( $\approx 1^\circ$  incline) point, interrupted near the seaward margin by deeply cut surge channels that run parallel to the shoreline. The point is exposed to direct wave action from all but the most northerly swells and is influenced by periodic sand deposition and removal (Fig. 2) produced by the differential action of winter and summer waves. Contrary to seasonal cycles of sand inundation reported elsewhere for the Pacific coast of North America (Hedgpeth 1957, Markham 1973, Shepard 1973), the winter months show maximal sand deposition while in the summer this location is generally free from sand burial. Even during periods of heavy sand inundation, the seaward and raised portions of the point, including the surge channels, remain unburied.

#### METHODS

Experimental manipulations were performed in early December 1977 and permanent 0.15-m<sup>2</sup> quadrats were monitored until January 1980 (partial monitoring, only of *Phragmatopoma californica* and *Anthopleura elegantissima*, was continued after September 1979). Three treatments were used in this analysis (each with six replicates) as follows: (1) enclosures from which *A. elegantissima* was removed and denied access by a stainless steel mesh fence, (2) fence controls with

openings through the mesh fence to allow access to *A. elegantissima* and other mobile organisms while testing for the effect of the fence itself, and (3) controls free from the influence of experimental manipulations. There were no initial differences in the abundance of *A. elegantissima* among treatment groups ( $P > .05$ , ANOVA), which had a mean density of 1842 individuals/m<sup>2</sup> throughout the study area (exclosures,  $1794 \pm 170$  individuals/m<sup>2</sup> [ $\bar{x} \pm SE$ ],  $56 \pm 6\%$  cover; fence controls,  $1752 \pm 94$  individuals/m<sup>2</sup>,  $52 \pm 2\%$ ; controls,  $2023 \pm 245$  individuals/m<sup>2</sup>,  $68 \pm 3\%$ ). Exclosure and fence control quadrats (50 × 30 cm) were centered within 85 × 65 cm stainless steel wire mesh fences (10 cm tall, 1.6-mm [16-gauge], 1.3-mm mesh) providing a buffer zone of at least 15 cm between the quadrat and the fence. Fences were attached with galvanized lag bolts, expanding lead anchors, and quick-set marine epoxy secured in holes drilled into the bedrock. After initial *A. elegantissima* removal from exclosures, intruders (which never amounted to >2% cover) were removed following each sampling period up to and including June 1978. Experimental and control quadrats were all horizontally oriented and situated at tidal levels between +0.7 and +1.3 m (0 datum mean lower low water [MLLW]).

The principal method of quantifying abundances was a non-disturbing photogrammetric technique yielding parallax-free samples that were used to assess cover of macroalgae and macroinvertebrates and densities of macroinvertebrates. Each permanently marked quadrat was photographed with color and infrared slide film (transparencies) using cameras equipped with electronic flash units. In the laboratory, transparencies were projected onto a dot pattern (1.0 dot/cm<sup>2</sup>) and the number of "hits" per taxon was scored. Two such "scorings" were performed for each transparency (after movement between scorings) with a minimum of 150 dots per scoring. Cover abundances for each species were expressed as the ratio of the number of hits to the total number of dots for both scoring trials. See Sousa (1979) and Littler (1980) for a discussion of the advantages and disadvantages of this technique (replicate scorings rarely varied more than  $\pm 5\%$ ). Species noted in the field, but not abundant enough to be scored, were given a trace (i.e., 0.1%) value. Densities of invertebrates (as well as cover of all taxa) were recorded in the field and checked in photo-samples when possible.

The infrared transparencies were used in conjunction with the color slides during scoring trials to expedite differentiation of macroalgal species, to permit assessment of blue-green algal cover, and to enable bleached, dead, and unhealthy algal thalli to be recognized. Variations in fluorescence in the infrared according to chlorophyll content and health make this possible.

The community studied was primarily two-dimensional, but when layering did occur, multiple photo-

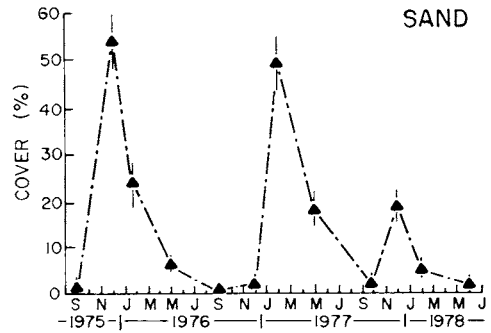


FIG. 2. Seasonal percent cover pattern of sand throughout the entire intertidal range (mean lower low water to +5.0 m,  $N = 45$ ) near Dutch Harbor, San Nicolas Island. Bars represent standard errors of means.

graphs and extensive field notes were taken after moving upper layers aside to ensure full assessment of lower layers. Only for one species, *Hydrolithon decipiens*, did it prove difficult to obtain abundance data in nonremoval quadrats because of this alga's occurrence beneath individual anemones. However, the presence of bleached *H. decipiens* was ascertainable.

A number of taxa were recorded as multispecies complexes because of current taxonomic or identification problems; these will be presented as such here (e.g., *Chthamalus fissus/dalli*).

Further data were obtained on the patterns of community development following complete removal of the biota in nearby 50 × 30 cm quadrats (disturbed) and on the overall seasonal distribution and abundance patterns of macroalgae and macroinvertebrates (undisturbed quadrats). These data were collected between September 1975 and June 1978. Similar photogrammetric methods were used in the disturbed and undisturbed treatments and are explained in detail by Murray and Littler (1979), and Littler (1980), respectively. In the community development studies, seasonal effects were integrated by initiating successional plots during all four quarters of the year. Mean biotic recovery data were then obtained by averaging results for intervals (e.g., 12 mo from initiation) regardless of the time of initiation.

Two experiments were conducted to examine the effect of sand burial on survival of *Phragmatopoma californica*. In the first, aggregations of *P. californica* were collected intact and placed in 570-L, recirculating, refrigerated seawater systems filled with artificial seawater and maintained at 16°C. *Phragmatopoma californica* individuals were counted in each of eight aggregations and placed into 47 cm long × 23 cm wide × 21 cm deep polycarbonate trays within the 570-L tank. Five of these aggregations were buried in sand for 5 d; air stones and water jets provided aeration and maintained circulation. Three unburied aggregations served as controls. Live individuals were recounted 24 h after removal from the sand.

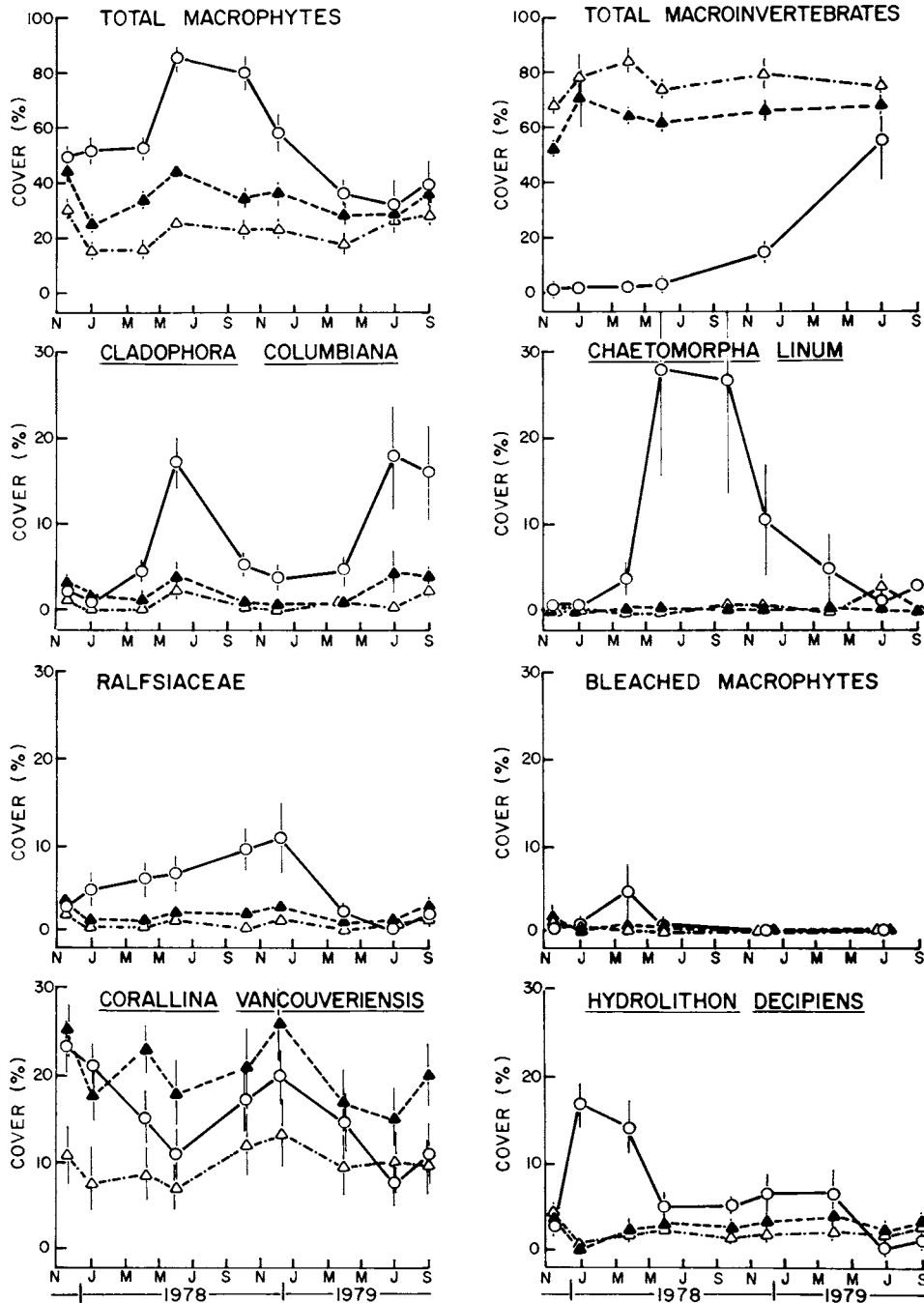


FIG. 3. Percent cover of macrophytes and macroinvertebrates following removal of *Anthopleura elegantissima*. Open circles = fenced enclosures, open triangles = unmanipulated controls, and closed triangles = fence controls. Bars represent standard errors of means ( $N = 6$  per treatment).

In the field, four permanently marked quadrats (0.15 m<sup>2</sup>) with >50% cover of *Phragmatopoma californica* were monitored before (April 1980) and after (June 1980) a 56–58 d period of sand burial. Four unburied quadrats from a nearby location (<100 m distance)

served as controls. The percentage and location of living *P. californica* and damaged tube remains were obtained with the photographic technique described previously.

Parametric and nonparametric comparative statis-

tical analyses were utilized. Arcsine transformations of percentage data were implemented in parametric analyses.

## RESULTS

### Initial community structure: cover and density

Nineteen macroalgae were found in enclosure, fence control, and control areas at the initial assessment and total macroalgal cover was  $44.6 \pm 5.5\%$  ( $\bar{x} \pm SE$ ),  $49.5 \pm 2.7\%$ , and  $35.3 \pm 3.1\%$ , respectively. The following nine taxa accounted for  $>90.0\%$  of the primary space covered by macroalgae in all treatments: *Corallina vancouveriensis* ( $39.7 \pm 4.0\%$ ), *Hydrolithon decipiens* ( $13.3 \pm 1.6\%$ ), blue-green algae ( $12.1 \pm 2.4\%$ ), Ralfsiaceae ( $6.6 \pm 0.9\%$ ), *Gelidium coulteri/pusillum* ( $5.5 \pm 1.1\%$ ), *Gigartina canaliculata* ( $4.3 \pm 1.8\%$ ), *Cladophora columbiana* ( $3.9 \pm 1.8\%$ ), *Polysiphonia acuminata* ( $3.2 \pm 1.0\%$ ), and *Ceramium spp./Centroceras clavulatum* ( $3.1 \pm 0.9\%$ ). There were no significant differences ( $P > .05$ , ANOVA) between enclosure, fence control, and control areas at the time of initial sampling except for *Corallina vancouveriensis*, which showed significantly lower ( $P < .05$ , ANOVA) cover in controls than in enclosures and fence controls.

Total macroinvertebrate cover was initially  $57.6 \pm 5.5\%$ ,  $54.6 \pm 2.9\%$ , and  $69.9 \pm 2.9\%$  for enclosures, fence controls, and controls, respectively. The most abundant throughout was *Anthopleura elegantissima* (mean of all treatments  $58.7\%$ ), with the six next most abundant invertebrates all showing mean cover values of  $<1.0\%$ . None of the sessile macroinvertebrates exhibited significant cover differences ( $P > .05$ , ANOVA) between treatment types at sampling initiation.

The most numerous macroinvertebrates were *A. elegantissima* ( $1842 \pm 327$  individuals/m<sup>2</sup>,  $\bar{x} \pm SE$ ) and *Tegula funebris* ( $209 \pm 70$ /m<sup>2</sup>) along with lesser numbers of *Epitonium tinctum* ( $34 \pm 15$ /m<sup>2</sup>), *Pagurus hirsutiussculus venturensis* ( $31 \pm 16$ /m<sup>2</sup>), and *Collisella scabra* ( $18 \pm 10$ /m<sup>2</sup>). None of the macroinvertebrates exhibited significant differences in density between treatments at sampling initiation ( $P > .05$ , Mann-Whitney *U* test). In addition to the 20 macrophyte taxa and 24 macroinvertebrates encountered in December 1977, 12 additional macrophytes and 13 macroinvertebrates appeared sporadically thereafter.

Because the quadrats were distributed over a tidal range of 0.5 m (+0.7 to +1.3 m), there were two distinct tidal height groupings: a lower group from +0.7 to +1.0 m and an upper group from +1.1 to +1.3 m. Each treatment type included four quadrats in the lower zone and two in the upper zone. Analysis of variance revealed no differences in cover or density of macroinvertebrates between tidal levels ( $P > .05$ ). Of the macroalgae, two taxa, *Ceramium spp./Centroceras clavulatum* and *Polysiphonia hendryi* (both primarily epiphytic on *Corallina vancouveriensis*), ex-

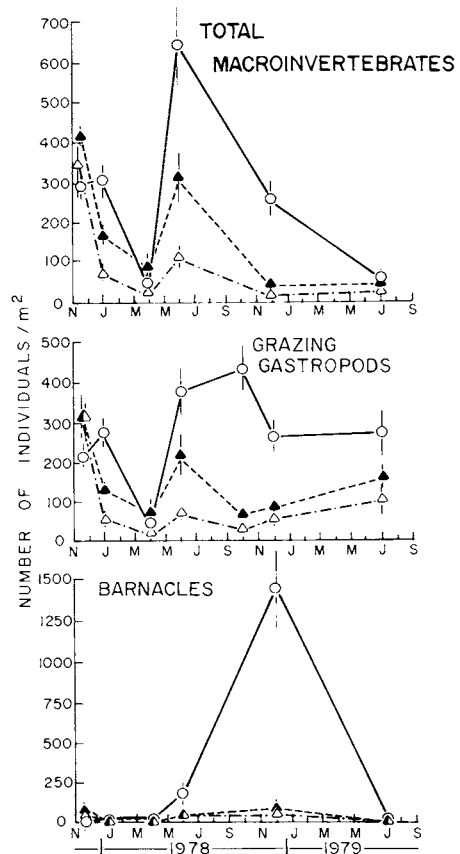


FIG. 4. Density (number per square metre) of macroinvertebrates following removal of *Anthopleura elegantissima*. Open circles = fenced enclosures, open triangles = unmanipulated controls, and closed triangles = fence controls. Bars represent standard errors of means ( $N = 6$  per treatment). Total macroinvertebrate density (top) excludes anemones and sessile polychaetes.

hibited reduced cover in the higher of the two zones, indicating probable desiccation limitation for these finely branched filamentous forms.

### Seasonality

The two control treatments (Figs. 3 and 4) provide information on seasonal changes in this community. Reduced abundances in winter 1977–1978 are apparent for macroalgal cover (Fig. 3), and for total invertebrate density (Fig. 4, see caption). Wilcoxon signed-rank analysis (hereafter Wilcoxon test) indicated a significant ( $P < .05$ ) reduction in total macroalgal cover for both control treatments following 6 wk of sand burial in the winter of 1977–1978. The substrate relinquished by macroalgae was assumed by macroinvertebrates (Fig. 3), primarily *Anthopleura elegantissima*.

Macroalgal cover increased into the summer of 1978 in both control treatments and exhibited relative stability thereafter (Fig. 3), a phenomenon common to all taxa except *Corallina vancouveriensis* (Fig. 3). The

macroinvertebrates exhibited a similar increase into the 1978 summer (Fig. 4), followed by a fall-winter decline.

#### *Effect of Anthopleura elegantissima removal*

Important changes, unrelated to seasonal variation, occurred after the removal of the dominant space-occupying macroinvertebrate, *Anthopleura elegantissima*. Following the experimental provision of primary space, a significant increase in total macroalgal cover was observed during the period from early December 1977 to June 1978 (Fig. 3;  $P < .05$ , Wilcoxon test). This phenomenon was due principally to significant gains in opportunistic species such as *Cladophora columbiana*, *Chaetomorpha linum*, and Ralfsiaceae (Fig. 3,  $P < .05$ , Wilcoxon test). No such large increase occurred in the two control treatments.

Apart from the gains by macroalgae during the period from December 1977 to June 1978 (both a seasonal and exclusion-related phenomenon, Fig. 3), increased mortality of long-lived macroalgae (indicated by bleaching) also occurred in the exclosures. Significant increases ( $P < .05$ , Wilcoxon test) in the total cover of bleached algal thalli (primarily *Corallina vancouveriensis* and *Hydrolithon decipiens*) were noted in April 1978 (Fig. 3) in exclosure quadrats only. This algal bleaching culminated in mortality in both *C. vancouveriensis* and *H. decipiens* (Fig. 3), which exhibited significant decreases in cover during the period from January to June 1978, after the experimental exclusion of *Anthopleura elegantissima* ( $P < .05$ , Wilcoxon test). The large initial increase of *H. decipiens* represents an artifact because this crustose alga was obscured to a large extent by *A. elegantissima* when the initial assessments were made.

Following the initial increase in recruitment and growth of the opportunistic algal taxa in exclosures during December 1977 through June 1978, these species showed declines coincident with the influx of grazing molluscs (Fig. 4) and the settlement and growth of *Phragmatopoma californica* (Fig. 5A). While cover values for total macroalgae and some of the more abundant algal taxa (*Cladophora columbiana*, *Chaetomorpha linum*, Ralfsiaceae, *Hydrolithon decipiens*; Fig. 3) remained relatively constant from June 1978 to April 1979 in both control treatments (no significant change;  $P > .05$ , Wilcoxon test), exclosures showed significant decreases in cover for these taxa ( $P < .05$ ). *Cladophora columbiana* exhibited a subsequent increase, beginning in April 1979, growing on *P. californica* as secondary substrate. *Corallina vancouveriensis* exhibited little net change over this period but exhibited wide variations with season (Fig. 3); the exclosure fluctuations were also more extreme throughout, exhibiting the greatest net decrease in cover following the heavy winter 1977–1978 sand inundation.

Changes in macroinvertebrate densities and cover occurred after *Anthopleura elegantissima* removal.

Taken as a group, the guild of grazing molluscs (chitons, *Mopalia muscosa*, *Cyanoplax hartwegii*, and *Nuttalina californica/fluxa*; littorines, *Littorina planaxis* and *L. scutulata*; limpets, *Collisella digitalis*, *C. limatula*, *C. pelta*, *C. scabra*, *C. strigatella*, *Fissurella volcano*, and *Lottia gigantea*; *Tegula funebris*) showed a tenfold density increase (Fig. 4,  $P < .05$ , Wilcoxon test) in exclosures after the sand-burial period. This increase primarily involved the three acmaeid limpets, *C. scabra*, *C. limatula*, and *C. strigatella* (all showing increases,  $P < .05$ , Wilcoxon test). The densities of *Tegula funebris*, a common associate of *A. elegantissima* aggregations (Francis 1973b) actually decreased ( $P < .05$ , Wilcoxon test). Both control treatments experienced lesser increases into June 1978 followed by declines (Fig. 4), while in exclosures, the increases were maintained until the onset of heavy *Phragmatopoma californica* recruitment (October 1978). A similar although delayed relationship was apparent for the barnacles (*Tetraclita squamosa rubescens* and *Chthamalus fissus/dalli*). The removal of *A. elegantissima* yielded a greater than tenfold increase ( $P < .05$ , Wilcoxon test) of barnacles in exclosures during June to October 1978 (Fig. 4), contrasting with relatively constant low numbers in both control treatments. This elevated density in exclosures was eliminated with the subsequent recruitment and growth of *P. californica* from October 1978 to July 1979 (Fig. 5A). No significant changes in abundance of carnivores (predatory gastropods) were apparent following the experimental alteration of the community.

The most dramatic structural change attributable to the absence of *Anthopleura elegantissima* involved the sand tube building polychaete, *Phragmatopoma californica*. During this investigation and a 3-yr seasonal study of the same site (Littler 1979), *P. californica* showed very low abundances between +0.6 and +1.1 m, where it occurred singly or in small aggregations (cf. Wilson 1971) prostrate on the substrate between *A. elegantissima* individuals. This contrasts with the large, reeflike aggregations found at lower intertidal and subtidal elevations throughout the study area (all aggregations are formed by the settlement of sexually produced larvae). Furthermore, Kendall rank-order correlation analysis (Nie et al. 1975) of *P. californica* and *A. elegantissima* abundances in this community (Fig. 6; data from community structure studies) revealed a significant negative relationship ( $\tau = -.19$ ,  $P < .001$ ); in this analysis abundance (cover) values only from quadrats ( $N = 233$ ) with <30% sand were used because sand above these values made cover determinations difficult.

After the experimental removal of *Anthopleura elegantissima*, *Phragmatopoma californica* colonized the newly opened primary space. Between October and December 1978, a dense recruitment of *P. californica* occurred, resulting in a significant increase in cover

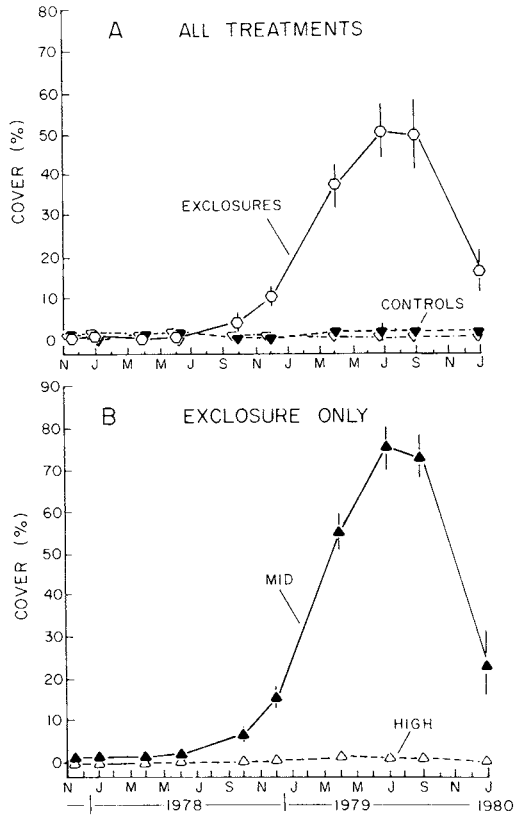


FIG. 5. Percent cover of *Phragmatopoma californica* following removal of *Anthopleura elegantissima*. A. All tidal heights of each treatment combined. Open circles = fenced exclosures, open triangles = unmanipulated controls, and closed triangles = fence controls ( $N = 6$  per treatment). B. Exclosure treatment only with quadrats separated into two tidal zones. Open triangles = high zone (+1.1 m to +1.3 m,  $N = 2$ ) and closed triangles = mid-zone (+0.7 m to +1.0 m,  $N = 4$ ). Bars represent standard errors of means.

(to  $10.4 \pm 4.4\%$ ;  $P < .05$ , Wilcoxon test) in the exclosure treatments (Fig. 5A), while neither control treatment exhibited such an increase. Between April and July 1979, recruitment and growth continued to  $50.9 \pm 16.7\%$  mean cover in exclosures, while between September 1979 and January 1980, *P. californica* showed a decline to  $16.2 \pm 6.2\%$  mean cover (Fig. 5A).

The success of *Phragmatopoma californica* in colonizing and maintaining free space varied with tidal height. In Fig. 5B, the exclosure quadrats are divided into an upper group ( $N = 2$ , +1.1 to +1.3 m above MLLW) and a lower group ( $N = 4$ , +0.7 to +1.0 m). *Phragmatopoma californica* recruited only into the lower area (mean cover in July 1979 was  $75.7 \pm 8.9\%$ ), while in the upper region, its cover remained  $<1.0\%$ , consisting of prostrate solitary individuals and small aggregations (as was the case in control treatments in both zones). Significant ( $P < .05$ , Mann-Whitney  $U$

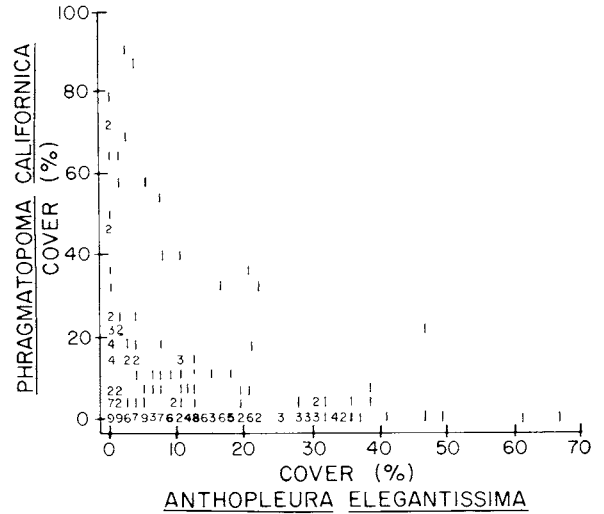


FIG. 6. Percent cover relationships of *Phragmatopoma californica* and *Anthopleura elegantissima*. Data are for quadrats with *P. californica* or *A. elegantissima* present. Quadrats with  $>30\%$  sand cover were excluded due to difficulties in determining biotic cover. Numbers indicate quantity of individual data points; 9 refers to nine or greater points with similar values for both species. The abundances of the two taxa show a significant negative correlation ( $P < .001$ , Kendall rank-order analysis,  $N = 233$ ).

tests) differences were indicated in *P. californica* recruitment between upper and mid-level areas in the secondary succession studies (see below). In the lower exclosure quadrats, aggregations attained considerable size and three-dimensionality, similar to those in the lower intertidal and subtidal regions. However, these new large aggregations did not persist through the winter of 1979–1980 but decreased to  $24.0 \pm 1.0\%$  mean cover in January 1980 (Fig. 5B).

Similar successional events occurred following the removal of the total biota. *Phragmatopoma californica* did not settle in quadrats from the high zone (above +1.1 m) though free space was readily available (Fig. 7); *Anthopleura elegantissima* regained pre-manipulation abundance levels there within 2 yr ( $P > .05$ , Wilcoxon test). This postremoval increase was considerably more rapid than that reported by Sebens (1977), presumably because of greater fission or migration rates. In the mid-zone (0.7 to 1.0 m above MLLW), *P. californica* settled and grew in quadrats where it was absent before the disturbance (Fig. 7). *Anthopleura elegantissima* attained near pre-manipulation cover values after 2 yr ( $P > .05$ , Wilcoxon test). In the low zone (below +0.5 m), where *P. californica* can be locally abundant and *A. elegantissima* is less common, *P. californica* quickly attained and exceeded predisturbance levels (Fig. 7) after  $<12$  mo. *Anthopleura elegantissima* was essentially unsuccessful at acquiring available free space below +0.5 m.

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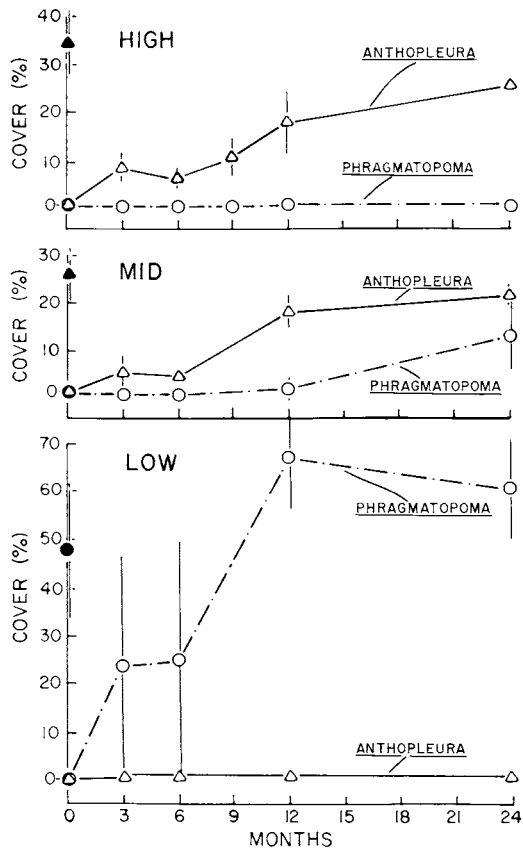


FIG. 7. Percent cover of *Anthopleura elegantissima* (triangles) and *Phragmatopoma californica* (circles) following total removal of the biota. Solid symbols represent the pre-removal cover. High zone is above +1.1 m ( $N = 4$ ); mid-zone is +0.7 m to +1.0 m ( $N = 4$ ); low zone is below +0.5 m ( $N = 4$ ). Bars represent standard errors of means.

where *Phragmatopoma californica* is dominant does not experience the seasonal deposition of sand found at the higher levels dominated by *Anthopleura elegantissima*, we investigated the possibility that sand burial is important in the distribution of *P. californica*. There was a significant negative correlation in the seasonal data (Kendall rank-order correlation analysis,  $\tau = -.49$ ,  $P < .001$ ,  $N = 233$ ) between sand cover and *P. californica* abundance. The inverse nature of the relationship, when quadrats with both *P. californica* and sand present at any sampling period were grouped, is shown in Fig. 8. During the laboratory experiment, >95% of the worms died when buried in sand for 5 d; control groups showed significantly ( $P < .05$ , ANOVA) lower mortality (mean = 17.0%). In the field, *P. californica* showed significantly greater decreases in cover ( $P < .03$ , Mann-Whitney  $U$  test; from  $89.6 \pm 5.2\%$  to  $7.8 \pm 5.9\%$ ) following burial than did unburied controls (from  $56.9 \pm 7.1\%$  to  $45.5 \pm 12.2\%$ ).

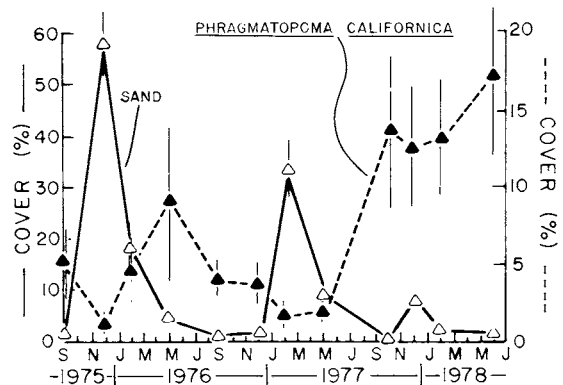


FIG. 8. Seasonal percent cover patterns for *Phragmatopoma californica* (right axis) and sand (left axis). Data represent mean values for quadrats with *P. californica* at any sampling visit ( $N = 233$ ). Bars represent standard errors of means.

#### DISCUSSION

*Anthopleura elegantissima* plays an important role in the distribution and abundance of macroalgae in this community. Its removal increased the mortality of some macroalgae, especially erect and crustose coralline forms, including *Corallina vancouveriensis*, the most abundant macroalga in the community (Fig. 3). This was most likely a result of increased desiccation stress in the absence of the water-retaining *A. elegantissima* clonal aggregations. The sensitivity of coralline algae to desiccation stress was demonstrated during earlier studies at this site and others on San Nicolas Island, correlating heavy macroalgal mortality with the occurrence of the hot and dry "Santa Ana" wind conditions (Littler 1978, P. Taylor, *personal observation*). Lebednik (1973) reported similar mortalities of coralline algae following minor (10 cm) uplifting of an intertidal beach in Alaska.

The presence of *Anthopleura elegantissima* also greatly influences the invertebrate composition of the community. *Tegula funebris*, a grazing gastropod which sometimes co-occurs with *A. elegantissima* clonal aggregations (Francis 1973b), exhibited decreased densities when the anemones were removed, as did the predatory *Acanthina* spp., *Epitonium tinctum*, and *Opalia funiculata*. It is not clear to what extent this may be due to desiccation stress, since *T. funebris* can be found at higher intertidal levels not associated with anemones, and *E. tinctum* and *O. funiculata* are considered predators of *A. elegantissima* (Ricketts et al. 1968).

Newly available free space was colonized by opportunistic or fugitive algal taxa such as *Chaetomorpha linum*, *Cladophora columbiana*, and Ralfsiaceae (cf. Northcraft 1948, Castenholz 1961, Dayton 1975, Murray and Littler 1978) and by the barnacles, *Tetra-*



*clita squamosa rubescens* and *Chthamalus fissus/dalli* and the tube worm *Phragmatopoma californica* (Figs. 3, 4, 5). When new space is provided in relatively small patches, recruitment by adult immigration of mobile species may be important, as demonstrated here by the influx of grazing gastropods after algal recruitment (Fig. 4).

The most dramatic alteration in community structure following the removal of *Anthopleura elegantissima* was the colonization and subsequent domination of space by *Phragmatopoma californica*, a phenomenon confined to tidal heights below +1.0 m. At the end of 20 mo in the enclosure samples, *P. californica* had achieved an average of >75% cover in the mid-region, while remaining at <1% in the upper area (Fig. 5). Associated with this domination of space was a concomitant reduction in other macroinvertebrate and macroalgal abundances (Figs. 3 and 4) presumably by exploitation (of space) or interference (overgrowing) interactions, a phenomenon reported for another sabellariid polychaete by Wilson (1971).

Above +1.1 m, *P. californica* was rare and occurred mainly as separate individuals or very small prostrate assemblages within the moist mats of the cover dominant, *A. elegantissima* (see Wilson 1971 on another related and ecologically similar sand tube building polychaete). Removal of *A. elegantissima* at these levels did not result in an increase in the abundance of *P. californica*, indicating a probable desiccation/thermal limitation (Fig. 5). Predation on *P. californica* apparently was not important and would have resulted in the reverse of the pattern measured; i.e., a reduced lower intertidal abundance of *P. californica*, such as that shown for *Mytilus californianus* (Paine 1974), would be expected if predation from a mobile subtidal organism were influential. Also, no differences were found in the abundances of macroinvertebrate predators between the high and mid-areas. Bird predation on *P. californica* was never observed.

*Anthopleura elegantissima* is well adapted to existence in the upper-intertidal areas. The tendency to aggregate increases contact between individuals, thereby decreasing effective surface area, which minimizes evaporation (Francis 1973a, 1979) and helps hold water between the individuals. Further desiccation resistance is provided (Hart and Crowe 1977) by the attachment of gravel and shells to the outer body wall verrucae, creating a larger boundary layer of high relative humidity. Shick et al. (1979) have indicated that other factors, including the permeability of the body wall to oxygen, reduction of energy demand, and relative lack of oxygen debt during emersion represent adaptations to an intertidal existence in *A. elegantissima*. These authors further suggest that the clonal form shows a morphological adaptation to higher intertidal areas, being less reliant on the tentacles and coelenteron flushing for oxygen uptake. These addi-

tional factors also are advantageous for withstanding sand burial as is *A. elegantissima*'s ability to extend above shallow layers of sand by body wall elongation. The mode of vegetative reproduction (binary longitudinal fission, Hand 1955, Francis 1976, Sebens 1980) may also enhance the survival of *Anthopleura elegantissima* in stressful intertidal habitats. Juvenile anemones resulting from sexual reproduction are relatively more sensitive to desiccation (Ottaway and Thomas 1971, Ottaway 1973, Griffiths 1977), presumably due to their small size, a factor that limits the upper distribution of the anemone *Actinia tenebrosa* (Ottaway 1973). Because clonal *A. elegantissima* reproduce by fragmentation, recruitment into upper areas can be achieved by movement of individuals from lower zones. These recruits have the advantage of larger initial size and decreased surface : volume ratios. It may also be important that *A. elegantissima* employs binary longitudinal fission rather than pedal laceration in asexual reproduction, a mode that will yield the largest products, presumably with the greatest desiccation resistance.

Other features may result in adaptation of *Anthopleura elegantissima* to periodic burial which can last for 3 mo or more (K. Sebens, *personal communication*; P. Taylor, *personal observation*). Schlichter (1975, 1978) indicated the ability of another intertidal anemone, *Anemonia sulcata*, to actively take up dissolved organic matter from seawater in the form of carbohydrates and amino acids. Such an energy source could be of importance during prolonged periods of sand cover because interstitial water generally has higher concentrations of dissolved organic materials than surface waters (Clark 1969, Stephens 1975). Symbiotic zooxanthellae may have a significant but secondary nutritional role for *Anthopleura elegantissima* (Muscatine 1961, Taylor 1969, Sebens 1980, Fitt and Pardy 1981) via the translocation of photosynthates, a factor of potential importance if sand burial depth is low enough to allow adequate light transmission. Additionally, digestion of symbionts cannot be ruled out as being nutritionally important. Metabolism of body tissue (Sebens 1980) may be the primary explanation of survival following prolonged burial.

Experimental (laboratory and field) and correlative evidence from the present study indicate a relative inability on the part of *Phragmatopoma californica* to withstand sand burial (Fig. 8). Wilson (1971) reported a similar intolerance to sand burial in the sand tube worm *Sabellaria alveolata* in Great Britain. The manipulative, successional, and seasonal data, however, suggest that *Phragmatopoma californica*, by way of its opportunistic life history (probable continuous occurrence of viable gametes and presence in the plankton [J. Blake, *personal communication*] and relatively rapid colonizing ability) is adept at utilizing space made available by unpredictable disturbances. *Phrag-*

*matopoma californica* appears to fit many of the criteria for r-selected species (Pianka 1970) or the ruderal strategist of Grime (1977), i.e., adapted to make use of disturbed habitats. In the relatively benign conditions (with regard to desiccation and sand-burial stress) of the lower-intertidal (below +0.5 m) and shallow subtidal regions, *P. californica* is predominant over *Anthopleura elegantissima*. *P. californica* aggregations are relatively constant, persisting when contiguous with *A. elegantissima*, and are capable of actually overgrowing individual anemones as they can other organisms (e.g., erect algae and urchins; P. Taylor, *personal observation*). *Phragmatopoma californica* may be capable of responding to unpredictably available free space more quickly than *A. elegantissima* (Fig. 7) which appears to gain space by a primarily fragmentive, asexual reproductive mode in the areas studied (no evidence of larval recruitment was observed in our quadrats but larval recruitment may be important into other areas, e.g., mussel beds; cf. Sebens 1977). Larval selectivity (cf. Wilson 1968) of adult sand tubes and continuous reproduction in *P. californica* may facilitate its domination of space once acquired and may provide a further advantage in larval recognition of suitable free space. After physical disturbance has removed *P. californica*, portions of old sand tubes usually remain on the substrate and appear to stimulate larval settlement and rapid recolonization (cf. Wilson 1978). This remaining sandy material, likely an unstable substrate in the absence of maintenance by living worms, may inhibit use by other space occupiers including *A. elegantissima*.

While predation effects cannot be ruled out as affecting the distribution of *A. elegantissima*, some evidence suggests that these may not be as important as elsewhere (e.g., subtidally in Washington, Sebens 1977). First, large subtidal clones of *A. elegantissima* occur off the rocky point studied. Nudibranch predators and the batstar, *Patiria miniata* are not common at this location (Littler 1979). Second, while *Epitonium tinctum* and *Opalia funiculata* are common, it is uncertain if these macroparasites are influencing distributions greatly.

*Anthopleura elegantissima*, because of mentioned morphological, behavioral, physiological, and reproductive features, is well adapted to desiccated and sand-influenced mid- to high-intertidal regions (+0.7 to +1.3 m). It corresponds to the stress-tolerant strategist of Grime's (1977) three-strategy model. *Anthopleura elegantissima* is capable of maintaining space in the mid- to high regions once established, and patches of space provided by small-scale disturbance nearby can be utilized by movement or division of individuals. *Phragmatopoma californica*, contrastingly, is sensitive to aerial exposure at high levels (above +1.1 m) and therefore cannot persist in the face of infringing *A. elegantissima* aggregations except in temporary refugia between anemones. At mid-levels,

*P. californica* may flourish with the provision of new space by local physical or biological disturbance (Figs. 5 and 7). This occurred in one fence control quadrat between September 1979 and January 1980 (to 21% cover), accounting for the increase noted in Fig. 5. Without the provision of space by disturbance, *P. californica* appears unable to acquire space from *A. elegantissima*. Thus, *Phragmatopoma californica* is susceptible to compensatory mortality (via desiccation and sand) which negates the competitive advantages it has in less stressful regions. A similar interplay of environmental factors and species tolerances may exist between *A. elegantissima* and other space-occupying organisms (e.g., coralline algae) that are more sensitive to sand- and aerial-exposure influences. The importance of sand scouring in this community, particularly to *P. californica*, appears to be relatively minor. None of the evenly eroded worm aggregations and rocks evident at other locations were apparent at the San Nicolas Island study site.

The findings of the present study may be framed in light of current theory on community development (Drury and Nisbet 1973, Connell and Slatyer 1977). The latter authors have proposed three alternative mechanisms producing a sequence of species in succession. These mechanisms, simply stated, stem from differential abilities of species to colonize space and the effect of earlier colonists on the success or ability of themselves or other species to recruit and mature. Earlier colonists may make the environmental conditions more suitable (facilitation model) or less suitable (inhibition model) for later colonists, or they may leave environmental suitability unaffected (tolerance model). In the facilitation and tolerance models the early colonists lose out in competition for resources with the later colonists, whereas, in the inhibition model, as later species cannot recruit and mature in the presence of earlier colonists, disturbance- (or stress-) related vectors are required for succession to proceed.

The mechanics of succession in this community (which is simple in that relatively few species are very abundant) is a complex issue depending on the environmental parameters of stress and disturbance, as well as adaptive characteristics of the important space occupiers. For this model, we separate the organisms that occupy primary space into four functional groups: *Anthopleura elegantissima*, *Phragmatopoma californica*, long-lived macroalgae (e.g., *Corallina vancouveriensis* and *Hydrolithon decipiens*), and opportunistic macroalgae (e.g., *Cladophora columbiana*, *Chaetomorpha linum*, and Ralfsiaceae).

In benign habitats (low tidal levels), free from sand and desiccation stresses, the rapidly colonizing *Phragmatopoma californica* has a more important role. It can inhibit the invasion of *Anthopleura elegantissima* and macroalgae. Resident *P. californica* (or its remains) may encourage subsequent use by its

own juvenile stages rather than rendering the environment less suitable for further recruitment (contrast with the facilitation model, Connell and Slatyer 1977). Continuous reproduction and larval selectivity may help maintain early successional stages in this self-facilitating strategy, even in the event of disturbances that destroy the resident *P. californica*.

In the periodically stressed (sand-inundated) mid-intertidal region, the dominant *Anthopleura elegantissima* facilitates the survival of small perennial macroalgae while inhibiting recruitment of opportunistic macroalgae. *A. elegantissima* also inhibits the formation of large aggregations of *Phragmatopoma californica*. Disturbance, however, allows *P. californica* to form such colonies, while periodic stress of sand inundation prevents the persistence of these aggregations. This compensatory mortality favors invasion by *A. elegantissima* which can ultimately prevent reestablishment of large *P. californica* colonies. The more stressful environmental conditions (desiccation in addition to sand burial) of the upper intertidal result in much the same pattern, though *P. californica* is incapable of forming large colonies there, even in the absence of *A. elegantissima*.

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