

Population and Species Diversity Fluctuations in a Rocky Intertidal Community Relative to Severe Aerial Exposure and Sediment Burial

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Abstract

From a series of 10 quarterly assessments between October 1975 and May 1978 (inclusive), fluctuations in abundance were determined for macroinvertebrates and macrophytes of a rocky intertidal community on Santa Cruz Island, California, USA. During afternoon low tides in late fall and winter of the first 2 yr of study, organisms of the upper and middle intertidal zones were subjected to prolonged aerial exposure. Many species there tolerated this exposure, but die-backs occurred for a barnacle (*Chthamalus fissus*/*C. dalli*) and several algae (*Endocladia muricata*, *Pelvetia fastigiata* f. *gracilis*, *Corallina officinalis* var. *chilensis*, *Corallina vancouveriensis*, *Cylindrocarpus rugosus* and *Codium fragile*). These die-backs were succeeded by blooms of *Ulva californica* and *Porphyra perforata*. In the upper and middle intertidal zones, the major cover organisms that could tolerate prolonged aerial exposure were disproportionately prevalent and appeared to be maintained by the periodic repression of species intolerant to such exposure. In February 1978, heavy rainfall caused sediment inundation of the middle and lower intertidal zones. This event was followed by declines in abundance of a barnacle (*Tetraclita rubescens*) and several algae (*Pelvetia fastigiata* f. *gracilis* and *Corallina* spp.). Shannon-Wiener H' species diversity fluctuated from a high in October to a low the following May during both 1975–1976 and 1976–1977 in conjunction with the period of increased daytime aerial exposure in late fall and winter. A further decline in diversity following sediment inundation in February 1978 contributed to a long-term trend of declining H' species diversity (3.06 in October 1975 to 1.87 in May 1978). We hypothesize that predictable late fall to winter aerial exposure stresses, in combination with a random physical disturbance (sediment burial), exceeded an "optimal" intermediate level of disturbance predicted for maximal species diversity.

Introduction

The inhabitants of many rocky-intertidal communities on the Pacific Coast of North America are space-limited, and in the absence of external disturbance such communities will develop into an assemblage of the competitively-dominant species and their associated fauna and flora. In a habitat characterized by low disturbance, Paine (1966) removed a major predator (source of local disturbance) and, since other disturbances did not intrude, a monoculture of mussels and their associated biota developed. More often, however, frequent local disruptions make the limiting resource available to a pool of potential colonizers. In wave-exposed intertidal systems, patches are often generated within stands of the competitively-dominant species by wave-driven logs (Dayton, 1971), the shearing force of waves (Harger and Landenberger, 1971), movement of substrate (Osman, 1977), and the spontaneous death of older organisms (Levin and Paine, 1974).

Under conditions of extreme disturbance, species diversity should be low and communities should be composed mainly of opportunistic organisms. Although few data exist, Littler and Murray (1975) showed that sewage-induced disturbances resulted in a community dominated by opportunists with reduced overall diversity. Also, Dayton (1971) has clearly established that species diversity is low in localized areas of the Pacific Northwest that are pounded regularly by wave-driven logs. Thus, in accordance with the predictions of Levin and Paine (1974), Connell (1978) and Fox (1979), maximal species diversity tends to occur at intermediate levels of disturbance.

Factors structuring the rocky shore communities in southern California have been examined only to a limited extent and for relatively short periods. Substrate turnover in boulder fields near Santa Barbara resulted in a pronounced seasonal disturbance (Sousa, 1979). Similarly, sand inundation of a rocky intertidal community on San Nicolas Island produced a seasonal disturbance (Littler, 1980a). Storms were important in regulating densities of

mussels at a site near Santa Barbara (Harger and Landenberger, 1971). Finally, aerial exposure during extreme low tides in the late fall and winter subject southern California intertidal organisms to severe stresses (discussed by Seapy and Hoppe, 1973, and Littler, 1980a). Such exposure stresses increase greatly when low tides occur during the day and coincide with periods of hot and dry desert winds (Gunnill, 1980b).

The purpose of the present work is to present an overview of seasonal community dynamics for a rocky-intertidal system at Willows Anchorage, Santa Cruz Island, obtained from permanently-positioned quadrats assessed over a 3 yr period. The populational data that form the basis of this paper are detailed elsewhere (Seapy and Littler, 1977, 1978b, 1979a, b). The observed changes in abundances of the populations comprising this intertidal community suggest that (1) seasonal stresses due to desiccation produced a predictable yearly pattern of fluctuating diversity; and (2) such physiological stresses, apparently beyond an "optimal" intermediate level, in conjunction with a random physical disturbance (sediment burial), were associated with a long-term decline in community diversity.

Materials and Methods

Study Area

Santa Cruz Island (Fig. 1) is the largest island off the coast of southern California, USA (249 km² in area; about 40 km long and from 3 to 10 km wide), and is located about 40 km south of the mainland at Santa Barbara. Biogeographically, the island is in a transition zone (Hewatt, 1946; Seapy and Littler, 1980) between northern cold-water and southern warm-water biotas.

Because of private ownership and limited public access, the island has remained relatively undisturbed, aside from the ranch facilities and the effects of grazing livestock. Erosional problems in recent years have increased dramatically as a result of overgrazing by feral sheep (Brumbaugh, 1980).

The study site at Willows Anchorage (Latitude 33°57'38"N; Longitude 119°45'18"W) is centrally located on the southern shore (Fig. 1B, C) at the mouth of the overgrazed Willows Canyon. The anchorage consists of a sheltered sandy beach flanked on the east by a boulder field and on the west by a rocky shelf that extends toward the seaward opening of the anchorage as a gently-sloping platform about 25 m in width. The study area was located on this platform of highly irregular, mid-Miocene tuff-breccia (Fisher and Carlton, 1976). Surf does not generally break over the platform due to rapid depth increases immediately seaward; however, a substantial surge consistently rolled over the study area during times of heavy swells.

A mixed, predominantly semidiurnal tidal pattern is characteristic of the Pacific Coast of North America

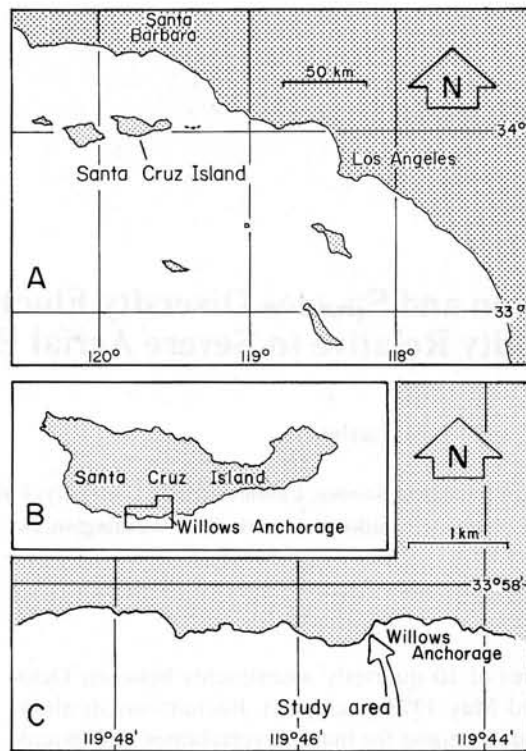


Fig. 1. (A) Southern California offshore region; (B) Santa Cruz Island; (C) location of study area at Willows Anchorage

(Ricketts *et al.*, 1968). Afternoon low spring tides occur during the late fall and winter months in southern California (Seapy and Hoppe, 1973; Gunnill, 1980a). These afternoon minus-tides subject the intertidal biota to aerial exposure stresses which may result in partial die-offs (Littler, 1980a). The effects of aerial exposure were most pronounced during the first winter period of the study. Strong, hot and dry desert winds (locally termed "Santa Ana" winds) were experienced throughout the 23–28 February 1976 site visit. These winds blew from the northeast across Santa Cruz Island and were diverted southward down Willows Canyon. Intertidal organisms exposed by afternoon low tides appeared to be severely stressed by the desiccating effects of this persistent wind pattern. The extreme nature of these wind conditions was documented (U.S. Navy, unpublished data) during the last 2 wk of January and the last week of February at the Naval Weather Station on Santa Cruz Island. Abrupt increases of up to 10°C in the mean daily maximum temperature accompanied these winds.

Superimposed on this predictable seasonal pattern of aerial exposure stress, a pronounced physical disturbance occurred during the winter months of the third year of the study. After unusually heavy rains in early February 1978, aerial observations and photographs recorded the transport of sediments down Willows Canyon and into Willows Anchorage, resulting in a sediment layer that completely inundated the substrate below about +2.0 m.

Standing Stock Measurements

Standing stock of the macrobiota was assessed 10 times between October 1975 and May 1978. The methods employed have been presented in detail elsewhere (Seapy and Littler, 1978a; Littler, 1980c), and a brief summary of these, including modifications used in the current study, is given below.

Two parallel transect lines, 23 and 24 m in length and 2.8 m from each other, were orientated perpendicular to the shoreline (56° magnetic). The lines extended down the shore from a tidal height of +4.0 to +0.3 m relative to mean lower low water (MLLW). Immediately beyond the last quadrat position on each transect line, the intertidal bench dropped off into deep water.

Assessments were made approximately every 3 mo. Labeled photographs of 44 to 54 permanently-marked 30×50 cm quadrats (0.15 m²) spaced at 1.0 m intervals were taken at right angles to the substrate with 35 mm cameras equipped with electronic flash units; also, detailed field notes of species composition and abundance were recorded. At least two photographs were taken of each quadrat, one with Kodachrome 64 color-slide film and the other with Ektachrome infrared-slide film. The infrared photographs permit the quantification of Cyanophyta, which may otherwise be indistinguishable from dark substrates. Moreover, unhealthy algae with bleached or reduced chlorophyll content (resulting from aerial exposure stress) are revealed; these would otherwise not be visible by color photography or to the unaided eye. In cases where sampling included multilayered macrophyte canopies, overstory species were moved aside and additional photographs were taken to measure stratification.

Percentage cover of the macroinvertebrates and macrophytes was determined in the laboratory for each quadrat by point-intercept analyses of the photographs, aided by the detailed field notes. Species observed in quadrats, but not abundant enough to be subtended by a point-intercept, were assigned a cover value of 0.1%.

The cover data for the macroinvertebrate and macrophyte taxa from all possible pairs of quadrats were compared by product-moment correlation and subjected to hierarchical cluster analysis (flexible sorting) by the weighted pair-group method (Sokal and Sneath, 1963). This technique enabled us to identify complex, multi-species quadrat groupings in an unbiased manner during each site visit. Cluster analysis resulted in dendrograms of assemblages based on correlation coefficients which, characterized by their cover dominants, were used to label the quadrats along each transect line and produce maps describing the prevalent zonal patterns during each visit.

Results

Assemblages and Zonation

The basic community structure for the intertidal biota at Willows Anchorage can be characterized from abundance

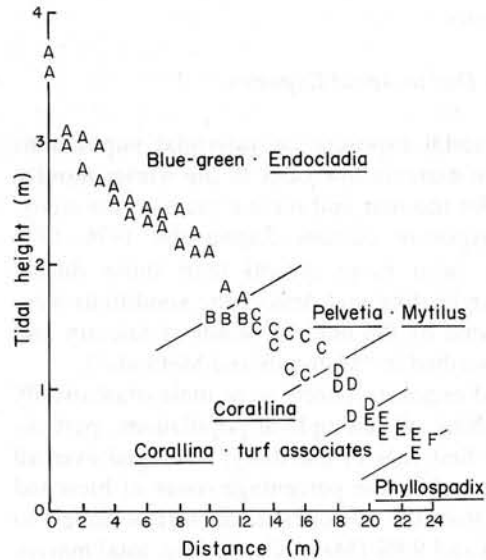


Fig. 2. Distributional patterns of cluster groups (A – F) in relation to tidal height and distance from shore. Cluster groups were determined from a dendrogram display of differential clustering of quadrats sampled during October 1975. (See text below for full description of predominant organisms)

data collected during the initial site visit in October 1975. Cluster analysis revealed the presence of 6 distinctive quadrat groups, which were characterized by one to several predominant organisms and described 5 zones (Fig. 2):

(1) A blue-green/*Endocladia* zone extended above, +1.6 m to +3.7 m and included high densities of *Littorina planaxis* and *L. scutulata*. While cover in the upper portion of this zone was greatest for blue-green algae, the lower portion was dominated by *Endocladia muricata* and *Lithophyllum proboscideum*.

(2) Between about +1.2 and +1.6 m, two quadrat groupings defined a *Pelvetia/Mytilus* zone, which was characterized by *Pelvetia fastigiata* f. *gracilis*, *Mytilus californianus* and *Corallina officinalis* var. *chilensis*. High densities of the barnacles *Chthamalus fissus/C. dalli* and *Tetraclita rubescens* were also recorded here.

(3) A *Corallina* spp. zone was located from about +0.8 to +1.2 m, and included high cover of both *C. officinalis* var. *chilensis* and *C. vancouveriensis*.

(4) A *Corallina*/turf-associates zone ranged downward from +0.8 to +0.5 m and contained a number of turf-forming red algae (*Laurencia lajolla*, *Gigartina canaliculata*, *Gelidium coulteri*, *Laurencia pacifica* and *Gastroclonium coulteri*), although the cover dominant was *C. officinalis* var. *chilensis*. *Strongylocentrotus purpuratus* was maximally abundant in this zone, as was *Anthopleura elegantissima*. Although *S. purpuratus* was limited to this zone, *A. elegantissima* ranged upward into the *Corallina* spp. and *Pelvetia/Mytilus* zones.

(5) The last zone identified by cluster analysis, the *Phyllospadix* zone, was characterized by *Phyllospadix torreyi*, with *Gigartina canaliculata* and *G. spinosa* as secondary species.

Seasonal Dynamics

Recurrent Stress Due to Aerial Exposure

The effects of aerial exposure on intertidal populations during afternoon extreme low tides in the winter months were apparent for the first and second years of the study. We consider exposure stresses during the 1976–1977 winter to have been more typical than those during 1975–1976, when heating and desiccating conditions were greatly accentuated by the hot, dry winds of January and February (as described in “Materials and Methods”).

Winter aerial exposure effects were most dramatically shown by bleaching of macrophyte populations, particularly during the first year of the study. Averaged over all tidal intervals sampled, the percentage cover of bleached algae increased from 0% (October) to 2.4% (December) to 8.4% (February) and 9.8% (May). Conversely, total macrophyte cover, averaged over the sampled tidal intervals and excluding the blue-green algae, declined steadily over this time period from 49.6% in October to 36.6% the following May.

Winter declines were pronounced among middle to upper intertidal species of macrophytes (Fig. 3). *Endocladia muricata*, a member of the uppermost zonal assemblage, declined substantially between December 1975 and February 1976, but then declined again by February 1977. Because the total cover by *Pelvetia fastigiata* f. *gracilis* was relatively low, its populational changes do not appear as marked as those of *E. muricata*. However, during the afternoons of the February 1976 site visit, *P. fastigiata* f. *gracilis* was observed to be severely stressed, as evidenced by the shrivelled and brittle thalli. Only a moderate degree of regrowth by this species had occurred by October 1976.

Corallina spp. exhibited a dramatic decline between December 1975 and February 1976, with erect thalli of *C. vancouveriensis* being eliminated (Fig. 3). Neither species had recovered by May 1976, but summer regrowth was extraordinary and resulted in dense cover by October 1976. The more moderate winter aerial exposure stresses of 1976–1977 were associated with less of a die-back by *C. officinalis* var. *chilensis* and the persistence of *C. vancouveriensis*.

Overall, the 5 red algal species comprising the *Corallina*/turf associates declined between October 1975 and February 1976 (Fig. 3). Upon closer inspection, however, it can be seen that the decrease in cover occurred above about +0.9 m and was attributable to *Gigartina canaliculata*, while below +0.9 m *G. canaliculata* cover increased. Although cover by this species was fairly constant from October 1976 to February 1977, the *Corallina*/turf associates above about +0.6 m decreased during this period.

The macrophytes *Cylindrocarpus rugosus* and *Codium fragile* declined steadily through the winter of 1975–1976, and then re-established at somewhat higher levels on the shore by October 1976 (Fig. 3: annuals). Both populations

underwent a similar pattern of decrease during 1976–1977, although *Cylindrocarpus rugosus*, the higher-dwelling species, was not decimated during the winter as was the case the preceding year.

Ulva californica and *Porphyra perforata* have been characterized (Littler, 1980b), as has *Colpomenia sinuosa* (Emerson and Zedler, 1978; Murray and Littler, 1978), as opportunistic colonizers. *U. californica* ranged broadly in low abundance in October 1975 and decreased steadily until February 1976 (Fig. 3: opportunists). Between February and May, however, it and *P. perforata* recruited strongly between +0.9 and +1.8 m. Colonization of the lower shore (below +0.9 m) by *C. sinuosa* was recorded in December 1976 and increased greatly in cover between February and May of 1977.

Among the sessile invertebrate populations, only *Chthamalus fissus*/*C. dalli* declined conspicuously during the winter period of aerial exposure stress between December 1975 and February 1976 (Fig. 4B). A similar seasonal decline was not shown by the other abundant barnacle, *Tetraclita rubescens*, whose densities remained relatively constant (Fig. 4C). This constancy was not caused by the presence of a long-lived, persistent adult population, but rather was the result of the steady addition of recruits into a population composed of a low number of large adults in which most of the juveniles died off. The mussel *Mytilus californianus* appeared resistant to aerial exposure stresses, as its numbers remained relatively constant through the winters of 1975–1976 and 1976–1977 and the population increased (due to recruitment) between February and May of each year (Fig. 4A).

Disturbance Due to Sediment Damage

Deposition of a sediment layer of terrestrial origin over the study area took place several weeks prior to the sampling period in February 1978. Between February and May 1978, total macrophyte cover, averaged over the sampled tidal intervals and excluding the blue-green algae, decreased from 45.3 to 37.3%. Declines in cover by the macroinvertebrates were even more pronounced; from 15.8% in February to 6.5% in May. A substantial decrease in cover occurred for *Corallina* spp. between February and May (Fig. 3). This decrease stands in contrast to *Gigartina canaliculata*, a major component of the *Corallina*/turf-associates zone, which declined only slightly from February to May. While *C. officinalis* var. *chilensis* formed a closely-adherent saxicolous turf at this level, *G. canaliculata* rose above the turf and, as a result, was much less affected by the layer of deposited sediment.

Pelvetia fastigiata f. *gracilis* maintained a relatively constant abundance until February 1978 (Fig. 3), when it was represented only by limited abraded remnants of upright thalli and holdfasts. By May 1978, only holdfast remnants were detected.

Between February and May 1978, mortality was recorded for *Tetraclita rubescens* and, above about

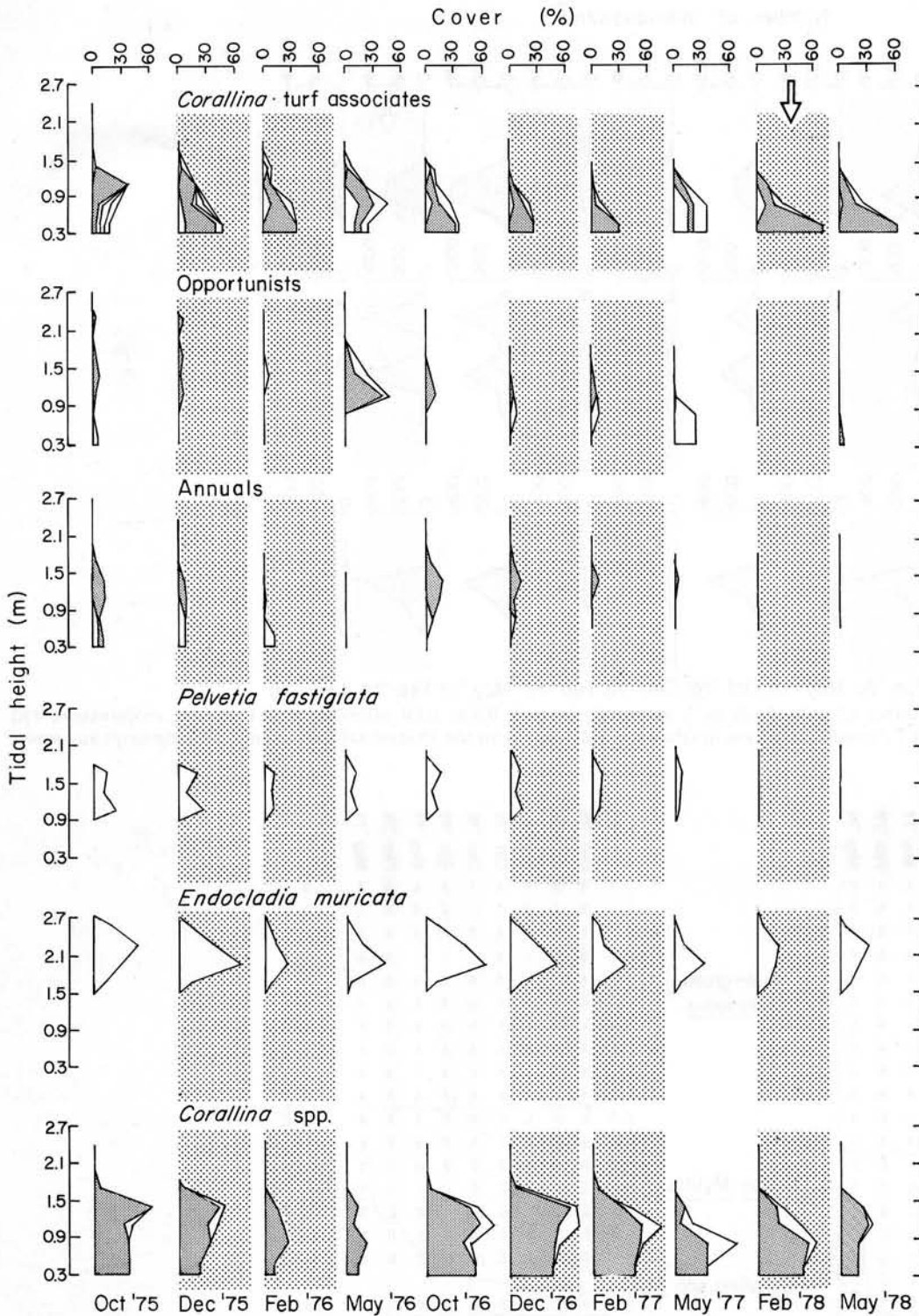


Fig. 3. Percentage cover (means of replicate quadrats for each 0.3 m tidal interval) of selected macrophyte species and functional groupings in relation to tidal height for the 10 seasonal assessments. Species comprising functional groupings from left to right in each distributional profile include – *Corallina*/turf associates: *Laurencia lajolla*, *Gigartina canaliculata* (shaded), *Gelidium coulteri*, *Laurencia pacifica* and *Gastroclonium coulteri*; opportunists: *Ulva californica* (shaded), *Porphyra perforata* and *Colpomenia sinuosa*; and annuals: *Cylindrocarpus rugosus* (shaded) and *Codium fragile*. *Corallina* spp. were represented by *C. officinalis* var. *chilensis* (shaded) and *C. vancouveriensis*. Times of aerial exposure are indicated by strips of lighter shading; arrow indicates time of sediment inundation over intertidal bench

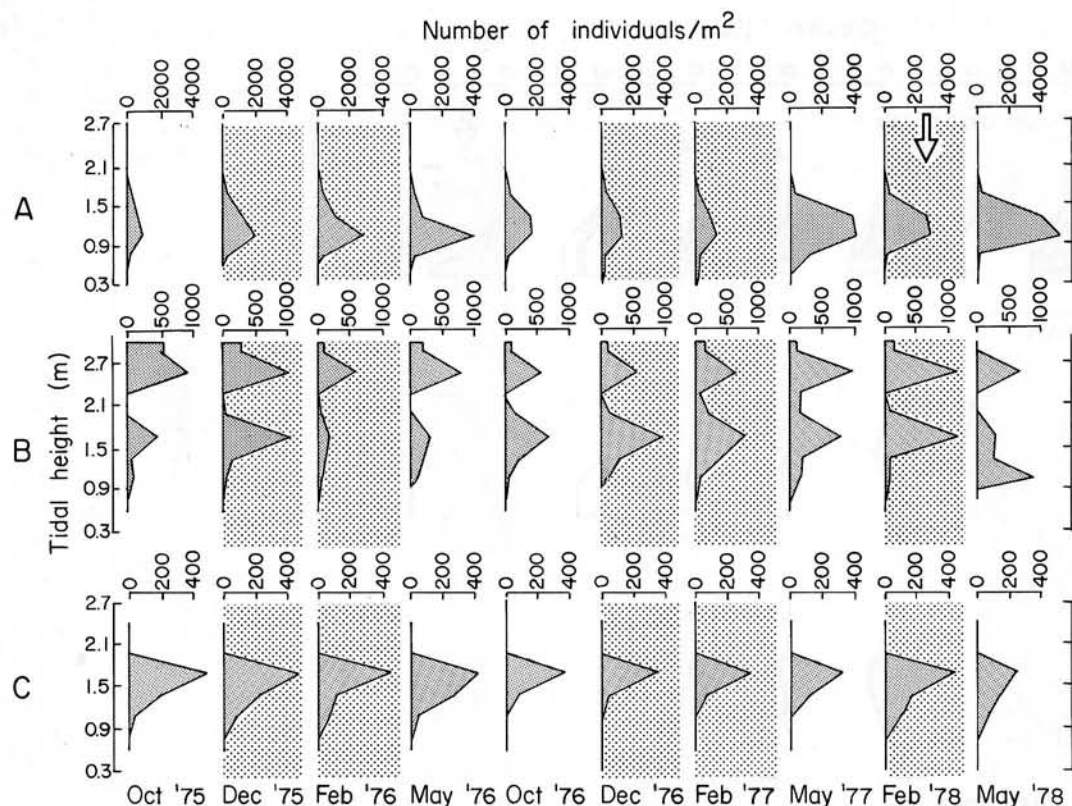


Fig. 4A - C. Density (mean number of individuals m⁻², averaged for each 0.3 m tidal interval) of (A) *Mytilus californianus*, (B) *Chthamalus fissus*/*C. dalli* and (C) *Tetraclita rubescens* in relation to tidal height for the 10 seasonal assessments. Shading strips and arrow as in Fig. 3

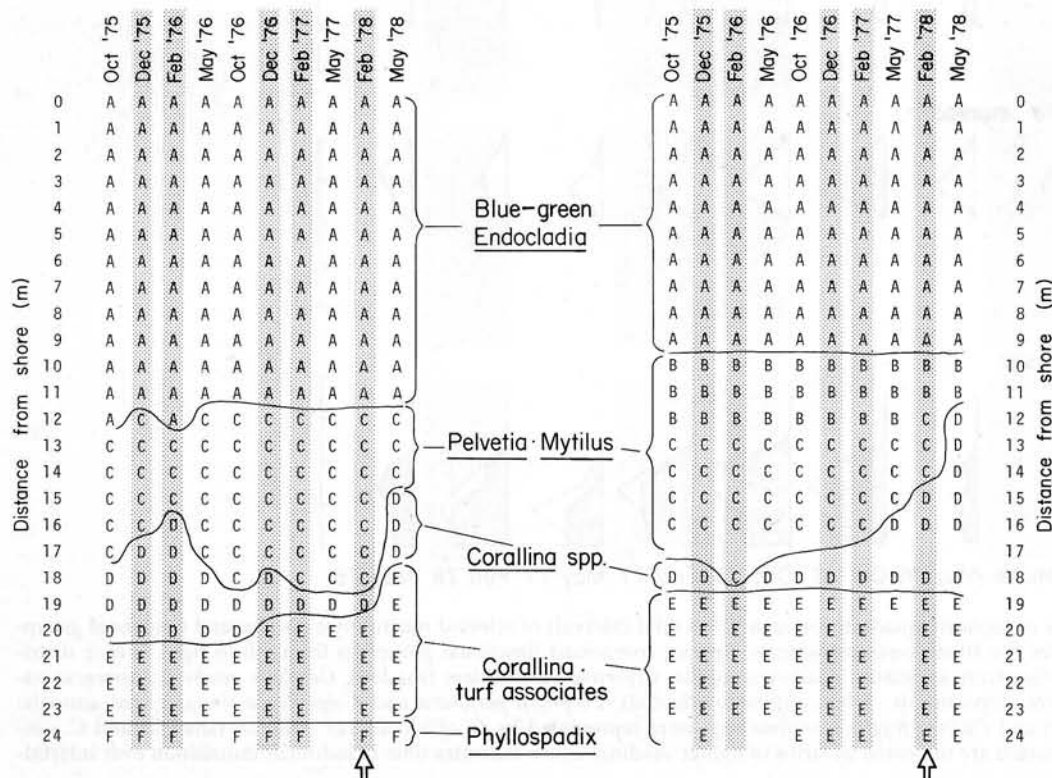


Fig. 5. Distributional pattern of species groups as determined by cluster analyses using percent cover data during the 10 seasonal assessments. Columns of letters represent line transects, with the most landward samples at the top and the most seaward samples at the bottom. Results are presented for south and north transect lines separately in left and right halves of the figure, respectively. Contour lines are drawn between sampling dates to denote locations of boundaries between clustered species groups. Approximate tidal heights corresponding to the quadrat locations (A - F) on the shore can be obtained by examination of Fig. 2. Shading strips and arrow as in Fig. 3

+1.5 m, for *Chthamalus fissus*/*C. dalli* (Fig. 4). Between these two dates, however, *C. fissus*/*C. dalli* successfully recruited below this level, as noted for *Mytilus californianus*, presumably in response to newly-cleared substrates.

Sediment damage also appeared to have affected zonal patterns. From October 1975 to May 1977, community structure remained quite constant (Fig. 5), with the exception of the boundary between the *Pelvetia*/*Mytilus* and *Corallina* spp. zones on the south transect line. However, between February and May 1978, the *Corallina* spp. and *Corallina*/turf-associates zones shifted upward on the south transect line, while on the north transect line only the *Corallina* spp. zone expanded upward. The upward shift by the *Corallina* spp. zone can be attributed to die-backs by *Tetraclita rubescens* (Fig. 4C) and, secondarily, *Pelvetia fastigiata* f. *gracilis* (Fig. 3). As a result of these die-backs, *Corallina officinalis* var. *chilensis* became the primary cover organism in these quadrats, where it had previously been subordinate to *T. rubescens* and *P. fastigiata* f. *gracilis*. The moderate expansion of the *Corallina*/turf-associates zone can be attributed to increased cover by the turf-associated red algae *Gigartina canaliculata*, *Gelidium coulteri* and *Laurencia pacifica*.

Diversity Trends

Two patterns (seasonal and long-term) of Shannon-Wiener H' diversity (Shannon and Weaver, 1963) were evident during the study (Fig. 6). Diversity fluctuated seasonally from a high in October to a low the following May during the first and second years. This decrease was in association with the period of daytime aerial exposure that occurs in the late fall and winter months each year throughout southern California. A recovery in diversity is indicated by the February 1978 values of H' , although decreases occurred for the third consecutive year between February and May.

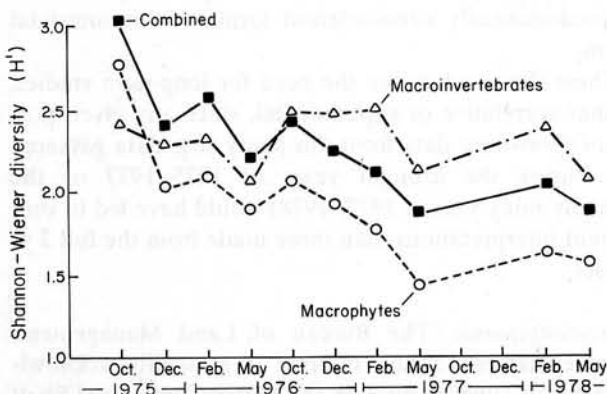


Fig. 6. Shannon-Wiener H' diversity values for macrophyte cover (circles), macroinvertebrate density (triangles) and combined macrophyte and macroinvertebrate cover (squares) for each of the 10 seasonal assessments

Superimposed on the seasonal pattern of fluctuating diversity was a long-term decline in diversity by the combined taxa (Fig. 6). This decline was heavily influenced by the macrophytes, which were the major cover organisms. The macroinvertebrates contributed only a small proportion of the total biotic cover and did not exhibit the same long-term decline. However, they did show seasonal (October to May) trends that were approximately parallel to the macrophytes.

Discussion

A three-strategy model of adaptive specialization has been proposed (Grime, 1977) for terrestrial plants, and has been applied to subtidal marine red algae by Shepherd (1981) and to marine organisms in general by Vermeij (1978). According to this model (as developed by Vermeij), species can be categorized as (a) opportunists; which exhibit high reproductive rates, a short life span, high dispersibility, reduced long-term competitive abilities, and occupy ephemeral or disturbed habitats, (b) stress-tolerant forms; which can tolerate chronic physiological stress, exhibit low rates of recolonization, tend to be long-lived with slow growth rates and, consequently, are generally poor competitors, and (c) biotically-competent forms; which generally live in physiologically-favorable environments, have long life spans, are good competitors and have evolved mechanisms to avoid predation. In the rocky intertidal zone, Vermeij identifies stress-tolerant forms as characteristic of the high intertidal, while biotically-competent taxa are prevalent in the low intertidal. Opportunistic forms would appear ephemerally on disturbed or newly-available substrates. This model represents a workable framework within which to interpret fluctuations of the algal and sessile invertebrate populations at Willows Anchorage.

The zonal assemblage dominants at Willows Anchorage (Fig. 2) are primarily characteristic of stress-tolerant and opportunistic strategists. The former group is most abundantly represented and, hypothetically, is maintained by the regular occurrences of aerial exposure stresses that are prevalent during the daytime minus tides of late fall and winter. Rocky intertidal areas generally, and southern California particularly, would be expected to be dominated by stress-tolerant strategists; however, we suggest that there is a disproportionate shift toward these forms at the Willows Anchorage site, with a general reduction in biotically-competent taxa. For example, the large brown algae *Egregia menziesii*, *Eisenia arborea* and *Halidrys dioica*, and the angiosperms *Phyllospadix* spp., which are abundant intertidally on most southern California islands such as Santa Catalina, San Clemente and Santa Barbara Islands (Littler, 1980a), were poorly represented in our quadrats (although they became more abundant on the outer margins at Willows Anchorage). This site seems to be highly susceptible to heating and desiccation stresses because of its southern exposure, black flow-breccia substrate and location at the mouth of a large canyon.

At Willows Anchorage, the blue-green/*Endocladia*, *Corallina* spp., and *Corallina*/turf-associates zones are characterized by algae that tend to form mats or turfs. This "turf morphology" has been shown (Hay, 1981) to ameliorate heat and desiccation stresses associated with aerial exposure, while also conferring resistance to herbivory. The *Pelvetia/Mytilus* zone located just below the blue-green/*Endocladia* zone is dominated by the rockweed *Pelvetia fastigiata* f. *gracilis*. Rockweeds of the order Fucales generally occur throughout temperate intertidal systems of the world at much higher tidal levels than do other fleshy algae (Stephenson and Stephenson, 1972). The fucoids are among the most desiccation-resistant groups of larger frondose algae (Schonbeck and Norton, 1978), and some require periodic aerial exposure (reviewed by Edwards, 1977). This zone also contained abundant *Mytilus californianus*, the potential competitively-dominant species in wave-exposed rocky headland habitats (Paine, 1966; Dayton, 1971). However, *M. californianus* is able to withstand considerable aerial exposure stress (Bayne *et al.*, 1976). Abundant populations of the barnacles *Chthamalus fissus/C. dalli* and *Tetraclita rubescens* occur on the upper shore (Fig. 4B, C). Intertidal barnacles tolerate high temperatures and desiccation (Foster, 1969, 1971), although they also are able to opportunistically colonize new substrates due to a prolific and nearly-continuous reproductive output (Hines, 1978).

The *Corallina*/turf associates zone and, to a lesser extent, the *Corallina* spp. and *Pelvetia/Mytilus* zones contained moderately high abundances of the sea anemone *Anthopleura elegantissima*. This species is clearly a stress-tolerant form, because it is behaviorally and physiologically well-adapted to desiccation. Desiccation resistance is provided by the behavior of attaching bits of gravel and shells by verrucae on the outer body wall (Hart and Crowe, 1977) which increases the boundary layer of high humidity. Physiological adaptations, such as high permeability of the body wall to oxygen, reduced energy demand and lowering of oxygen debt during aerial exposure, allow survival of *A. elegantissima* at relatively high intertidal levels (Schick *et al.*, 1979).

The thin sheet-like algae, mainly *Ulva californica* and *Porphyra perforata*, appeared abundantly but so ephemerally that they never resulted in the separate clustering of specific quadrats. However, they were conspicuously present following the seasonal periods of daytime low tides in winter (Fig. 3: opportunists), with blooms of *U. californica* appearing by May 1976 and *P. perforata* occurring by May 1977. These two species possess a number of characteristics associated with opportunism, including high productivity and low biomass per unit area (Littler, 1980c), and opportunistic colonization of disturbed substrates (Castenholz, 1967; Dayton, 1971; Murray and Littler, 1978).

The lowest zone sampled is dominated by *Phyllospadix torreyi*, an angiosperm that can be characterized as a biotically-competent species owing to its resistance to herbivores and its competitive ability (Littler, 1980a).

P. torreyi is always associated with sand that it traps by means of its rhizomatous root system, while maintaining its long, thin photosynthetic leaves well above the substrate. It is able to outcompete most algae by its invasive root system and its long wiry form that presumably allows it to whiplash and shade smaller species. We suggest that the susceptibility of the relatively large and biotically competent macrophytes (e.g. *Egrecia menziesii*, *Eisenia arborea* and *Halidrys dioica*) to recurrent aerial exposure stresses explains their paucity in our samples.

Willows Canyon was especially vulnerable to the heavy erosional rains of early February 1978 due to its long history of overgrazing by feral sheep (Brumbaugh, 1980). The flood and subsequent sediment inundation over the study site at this time appeared to have only augmented the long-term pattern of declining diversity. Following sediment inundation, *Pelvetia fastigiata* f. *gracilis* underwent a precipitous decline, while prior to this time it had maintained a relatively stable population (Fig. 3). At La Jolla, Gunnill (1980b) reported that *P. fastigiata* maintained a stable population throughout the period of the present study, and no such extreme disturbance took place. Although long-term declines by several of the other species of dominant algae were noted by Gunnill (1980a), these declines were interpreted as reflective of stressful environmental conditions during reproduction and recruitment, rather than due to an overall environmental trend.

Among the 6 island sites (on San Miguel, Santa Cruz, Santa Barbara, San Nicolas, Santa Catalina and San Clemente Islands) that were sampled with the present methods in the fall of 1975 (Littler, 1980a), the Willows Anchorage site had the highest H' diversity (3.06). By May 1977, however, Willows Anchorage had the lowest diversity (1.87) among the 6 sites, and remained lowest to the end of the study. Because of this decreasing trend in diversity, we are led to conclude that the levels of recurrent stress in combination with random disturbance exceeded an "optimal" intermediate level of disturbance. The fact that the inundation of the intertidal bench below +2.0 m did not cause a precipitous decline in H' diversity can be interpreted as a reflection of the pre-adaptations of the predominantly stress-tolerant forms of this intertidal system.

These data underscore the need for long-term studies, whether correlative or experimental, since any given portion of short-term data from this study (e.g. data gathered only during the drought years of 1975–1977 or the unusually rainy year of 1977–1978) would have led to very different interpretations than those made from the full 3 yr data set.

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Literature Cited

- Bayne, B. L., C. J. Bayne, T. C. Carefoot and R. J. Thompson: The physiological ecology of *Mytilus californianus* Conrad. 2. Adaptations to low oxygen tension and air exposure. *Oecologia* 22, 229–250 (1976)
- Brumbaugh, R. W.: Recent geomorphic and vegetal dynamics of Santa Cruz Island. In: The California Islands: proceedings of a multidisciplinary symposium, pp 139–158. Ed. by D. M. Power. Santa Barbara: Santa Barbara Museum of Natural History 1980
- Castenholz, R. W.: Stability and stresses in intertidal populations. In: Pollution and marine ecology, pp 15–28. Ed. by T. A. Olson and F. J. Burgess. New York: Wiley 1967
- Connell, J. H.: Diversity in tropical rain forests and coral reefs. *Science*, N.Y. 199, 1302–1310 (1978)
- Dayton, P. K.: Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41, 351–389 (1971)
- Edwards, P.: An investigation of the vertical distribution of selected benthic marine algae with a tide-simulating apparatus. *J. Phycol.* 13, 62–68 (1977)
- Emerson, S. E. and J. B. Zedler: Recolonization of intertidal algae: an experimental study. *Mar. Biol.* 44, 315–324 (1978)
- Fisher, R. V. and D. W. Carlton: Mid-Miocene Blanca Formation, Santa Cruz Island, California. In: Aspects of the geological history of the California continental borderland, pp 228–240. Ed. by D. G. Howell. Menlo Park: American Association of Petroleum Geologists 1976. (Misc. Publ. Am. Ass. Petrol. Geol., Pacif. Sect. No. 24)
- Foster, B. A.: Tolerance of high temperatures by some intertidal barnacles. *Mar. Biol.* 4, 326–332 (1969)
- Foster, B. A.: Desiccation as a factor in the intertidal zonation of barnacles. *Mar. Biol.* 8, 12–29 (1971)
- Fox, J. F.: Intermediate-disturbance hypothesis. *Science*, N.Y. 204, 1344–1345 (1979)
- Grime, J. P.: Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111, 1169–1194 (1977)
- Gunnill, F. C.: Recruitment and standing stocks in populations of one green and five brown algae in the intertidal zone near La Jolla, California during 1973–1977. *Mar. Ecol. Prog. Ser.* 3, 231–243 (1980a)
- Gunnill, F. C.: Demography of the intertidal brown alga *Pelvetia fastigiata* in Southern California, USA. *Mar. Biol.* 59, 169–179 (1980b)
- Harger, J. R. E. and D. L. Landenberger: The effect of storms as a density dependent mortality factor on populations of sea mussels. *Veliger* 14, 195–201 (1971)
- Hart, C. E. and J. H. Crowe: The effect of attached gravel on survival of intertidal anemones. *Trans. Am. microsc. Soc.* 96, 28–41 (1977)
- Hay, M. E.: Functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* 62, 739–750 (1981)
- Hewatt, W. G.: Marine ecological studies on Santa Cruz Island, California. *Ecol. Monogr.* 16, 186–208 (1946)
- Hines, A. H.: Reproduction in three species of intertidal barnacles from central California. *Biol. Bull. mar. biol. Lab., Woods Hole* 154, 262–281 (1978)
- Levin, S. A. and R. T. Paine: Disturbance, patch formation and community structure. *Proc. natn. Acad. Sci. U.S.A.* 71, 2744–2747 (1974)
- Littler, M. M.: Overview of the rocky intertidal systems of southern California. In: The California Islands: proceedings of a multidisciplinary symposium, pp 265–306. Ed. by D. M. Power. Santa Barbara: Santa Barbara Museum of Natural History 1980a
- Littler, M. M.: Morphological form and photosynthetic performance of marine macroalgae: tests of a functional form hypothesis. *Botanica mar.* 22, 161–165 (1980b)
- Littler, M. M.: Southern California rocky intertidal ecosystems: methods, community structure and variability. In: The shore environment, Vol. 2: Ecosystems, pp 565–608. Ed. by J. H. Price, D. E. G. Irvine and W. F. Farnham. New York: Academic Press 1980c. (Systematics Association Special Volume No. 17b)
- Littler, M. M. and S. N. Murray: Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Mar. Biol.* 30, 277–291 (1975)
- Murray, S. N. and M. M. Littler: Patterns of algal succession in a perturbed marine intertidal community. *J. Phycol.* 14, 506–512 (1978)
- Osman, R. W.: The establishment and development of a marine epifaunal community. *Ecol. Monogr.* 47, 37–63 (1977)
- Paine, R. T.: Food web complexity and species diversity. *Am. Nat.* 100, 65–75 (1966)
- Ricketts, E. F., J. Calvin and J. W. Hedgpeth: Between Pacific tides, 614 pp. Stanford: Stanford University Press 1968
- Schick, J. M., W. I. Brown, E. G. Dolliver and S. R. Kayar: Oxygen uptake in sea anemones: effects of expansion, contraction, and exposure to air and the limitations of diffusion. *Physiol. Zool.* 52, 50–62 (1979)
- Schonbeck, M. and T. A. Norton: Factors controlling the upper limits of fucoid algae on the shore. *J. exp. mar. Biol. Ecol.* 31, 303–313 (1978)
- Seapy, R. R. and W. J. Hoppe: Morphological and behavioral adaptations to desiccation in the intertidal limpet *Acmaea (Collisella) strigatella*. *Veliger* 16, 181–188 (1973)
- Seapy, R. R. and M. M. Littler: Biological features of rocky intertidal communities near Willows Anchorage, Santa Cruz Island, California. In: Spatial and temporal variations in the distribution and abundance of rocky intertidal and tidepool biotas in the Southern California Bight, pp 685–794. Ed. by M. M. Littler. Washington D.C.: Department of the Interior, Bureau of Land Management 1977
- Seapy, R. R. and M. M. Littler: The distribution, community structure, and primary productivity of macroorganisms from two central California rocky intertidal habitats. *Pacif. Sci.* 32, 293–314 (1978a)
- Seapy, R. R. and M. M. Littler: Variations in the rocky intertidal biota near Willows Anchorage, Santa Cruz Island, California. In: The annual and seasonal ecology of southern California rocky intertidal, subtidal, and tide pool biotas in the Southern California Bight, Chapter 1.1.9. pp 1–64. Ed. by M. M. Littler. Washington D.C.: Department of the Interior, Bureau of Land Management 1978b
- Seapy, R. R. and M. M. Littler: Assessments of the distribution, abundance and community structure of rocky intertidal organisms at Willows Anchorage, Santa Cruz Island, California. In: The distribution, abundance and community structure of rocky intertidal and tidepool biotas in the Southern California Bight, Chapter 1.1.1. pp 1–41. Ed. by M. M. Littler. Washington D.C.: Department of the Interior, Bureau of Land Management 1979a
- Seapy, R. R. and M. M. Littler: The impact of heavy sediment loading on the rocky intertidal biota at Willows Anchorage, Santa Cruz Island, California. In: Catastrophic surveys of

- rocky intertidal communities following natural disturbances. Chapter 3.4, pp 1–35. Ed. by M. M. Littler. Washington, D.C.: Department of the Interior, Bureau of Land Management 1979b
- Seapy, R. R. and M. M. Littler: Biogeography of rocky intertidal macroinvertebrates. *In: The California Islands: proceedings of a multi-disciplinary symposium*, pp 307–323. Ed. by D. M. Power. Santa Barbara: Santa Barbara Museum of Natural History 1980
- Shannon, C. E. and W. Weaver: The mathematical theory of communication, 111 pp. Urbana: University of Illinois Press 1963
- Shepherd, S. A.: Ecological strategies in a deep water red algal community. *Botanica mar.* 24, 457–463 (1981)
- R. R. Seapy and M. M. Littler: Intertidal Community Fluctuations
- Sokal, R. R. and P. H. A. Sneath: Principles of numerical taxonomy, 359 pp. San Francisco: W. H. Freeman & Co. 1963
- Sousa, W. P.: Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60, 1225–1239 (1979)
- Stephenson, W. A. and A. Stephenson: Life between tidemarks on rocky shores, 425 pp. San Francisco: W. H. Freeman & Co. 1972
- Vermeij, G. J.: Biogeography and adaptation: patterns of marine life, 332 pp. Cambridge: Harvard University Press 1978
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Population and species diversity fluctuations in a rocky intertidal community relative to severe aerial exposure and sediment burial. *Marine Biology* 71: 81-96.