Bull. Southern California Acad. Sci.
86(2), 1987, pp. 95–106

Effects of Stochastic Processes on Rocky-Intertidal Biotas: An Unusual Flash Flood near Corona del Mar, California

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Abstract.—A localized storm on 9 May 1977 produced deluge-level quantities of rain (2.56 cm within 3 h) causing flooding of the rocky shoreline at Corona del Mar, California. Unlike the patterns observed throughout 1975 and 1976 and at a comparable site 40 km to the north during the same time period, the sea urchin *Strongylocentrotus purpuratus* experienced a significant decrease in cover (from about 2.0% to less than 0.1%, $P < 0.05$, ANOVA) in the lower intertidal zone (MLLW to +0.3 m) and disappeared entirely within the +0.3 to +0.6 m interval. Belt transects documented an average of 90.5% mortality, whereas a census of the total area between the two permanent transect lines revealed 93.6% of the *S. purpuratus* to be dead. A biotically similar area beyond the periphery of the region flooded (20 m north of the north transect line) experienced only 1.1% mortality of *S. purpuratus*. Ephemeral macrophytes characteristic of disturbed environments, *Ulva californica*/*Enteromorpha* sp. (combined) and Ectocarpaceae, increased significantly in mean overall cover (14.6% and 8.9%, respectively) following the flood, as did newly recruited barnacles. However, the majority of persistent macrophytes, such as *Hydrolithon decipiens,* blue-green algal crusts, and *Gelidium coulteri*/*pusillum,* showed slight (but not significant) declines in mean cover (1.3%, 7.8%, and 5%, respectively). Therefore, stochastic events can have highly-localized species-specific catastrophic effects on intertidal populations which may set in motion subsequent changes to overall community structure that would be difficult to understand if a program of infrequent sampling was used.

The goal of this study was to assess changes in rocky-intertidal biotas as a direct consequence of a freshwater flood. Replicated nondestructive analyses (see Littler and Littler 1985) were contrasted during mid-March (prior to the flood of 9 May 1977) and late May 1977 near the mouth of Morning Canyon, Corona del Mar, a system intensively studied by us since July 1975 (Littler 1977, 1978, 1979). The first assessment of the rocky-intertidal biota in the vicinity of Corona del Mar (0.4 km northwest of the area sampled here, Fig. 1) was performed by Dawson (1959, 1965) in an attempt to compile baseline data on the intertidal macrophytes of Southern California. Dawson concluded that a general reduction in macroalgal species had occurred throughout Southern California since the 1895–1913 collections of W. A. Setchell and N. L. Gardner. Subsequent to Dawson's surveys (1959, 1965), Corona del Mar was reinvestigated during three separate studies (Widdowson 1971; Nicholson and Cimberg 1971; Thom and Widdowson 1978). Nicholson and Cimberg (1971) recorded a 68% reduction of algal taxa since 1959, including a shift toward turf-forming species. Widdowson (1971) also concluded

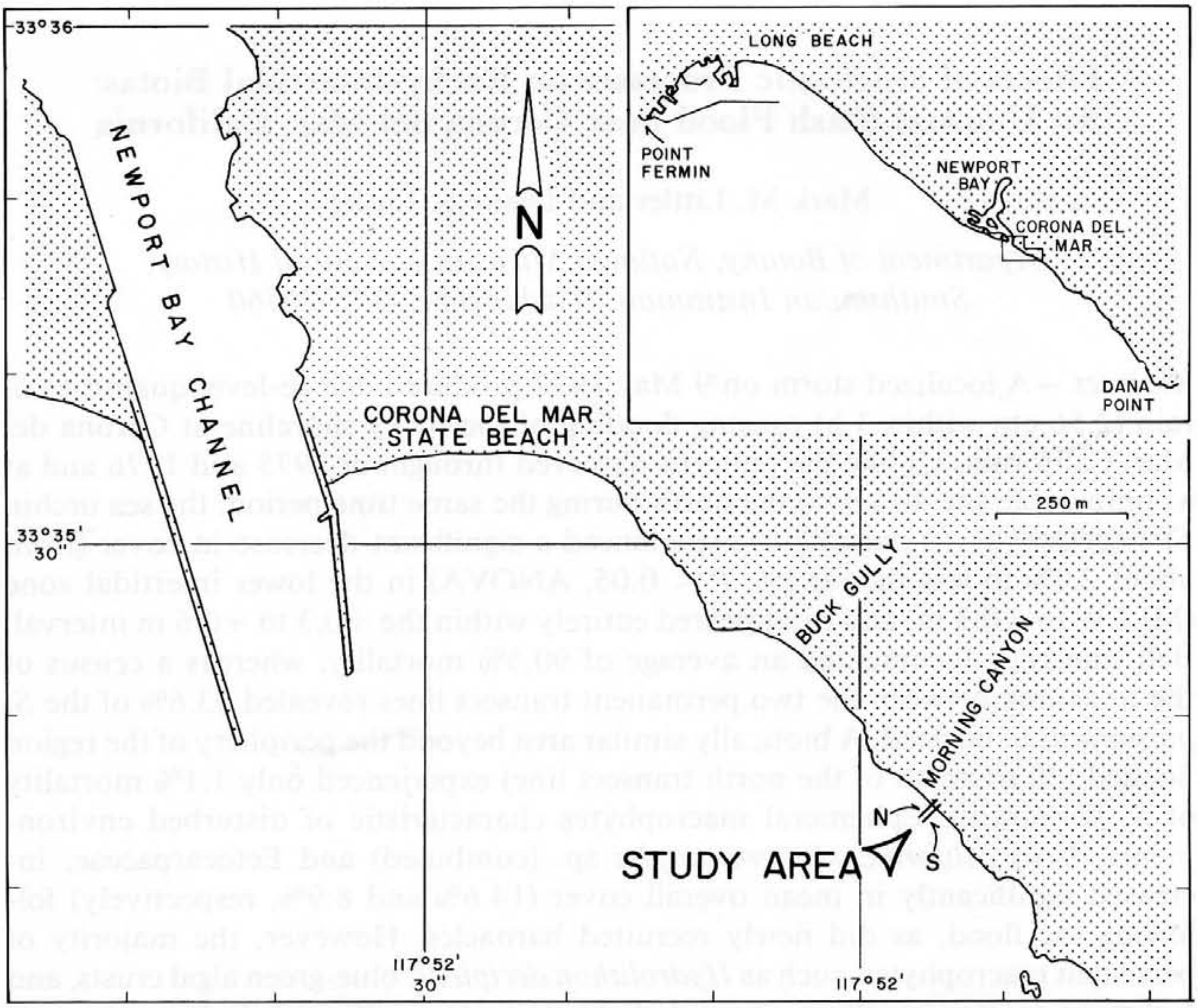

Fig. 1. Location of the Corona del Mar study site and permanent transect lines.

that considerable decreases had occurred, with Corona del Mar ranking third in greatest percentage of species lost relative to other regions of Southern California. In agreement, Thom and Widdowson (1978) noted that massive and foliose intertidal algae in the area had been replaced by turf-like forms (along with articulated corallines).

Information exists concerning the effects of various physical/chemical disturbances such as sewage pollution (e.g., Borowitzka 1972; Munda 1974; Littler and Murray 1975; Murray and Littler 1978, 1984), sand scouring and sediment burial (e.g., Daly and Mathieson 1977; Seapy and Littler 1982; Taylor and Littler 1982; Littler et al. 1983), substratum instability (e.g., Sousa 1979, 1980; Littler and Littler 1984), extreme aerial exposure (e.g., Seapy and Littler 1982), and sediment inundation (Seapy and Littler 1982; Stewart 1983; Littler et al. 1983) on the population dynamics and diversity of intertidal seaweeds. However, the impact of freshwater flooding in the intertidal has not been measured.

On 9 May 1977, a localized rainstorm occurred in which deluge-level quantities of rain fell ($2.56\ \mathrm{cm} \cdot 3\ \mathrm{h}^{-1}$) causing Morning Canyon to flood and produce torrents, which eroded a large gully in the sandy beach (Figs. 2A and B) and flooded the study site. No accumulation of sediments occurred anywhere in the intertidal zone. We suspected that the stresses imposed by such a large freshwater inundation

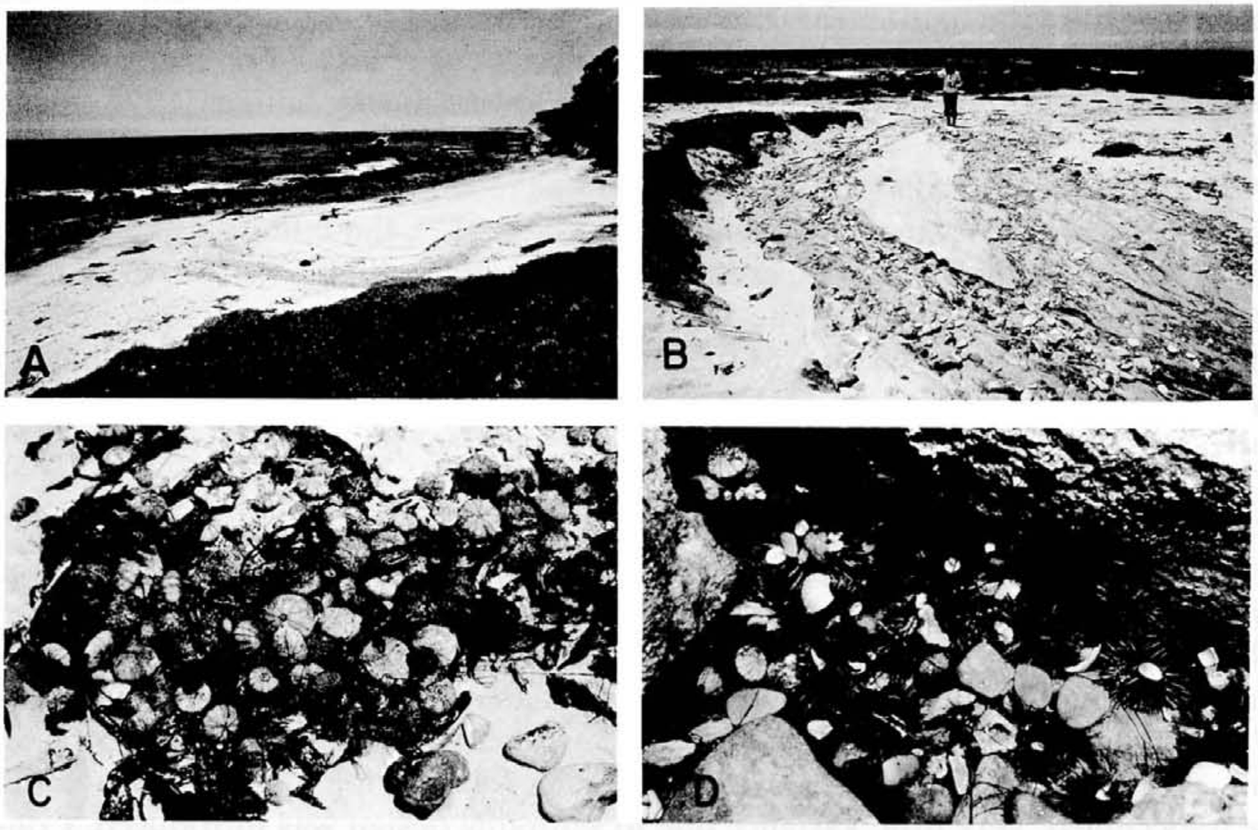

Fig. 2. (A) View of study site from Morning Canyon. (B) Beach above study site showing erosional path of the flash-flood. (C) Windrows of recently killed *Strongylocentrotus purpuratus* tests cast onto beach two days after the flood. (D) Population of healthy *S. purpuratus* in deep lower shore pool in the path of inundation.

would kill the more stenohaline populations. Indeed, two days after the storm, windrows of recently killed sea urchins were cast up on the shore, but only above the study site near the eroded portion of the beach (Fig. 2C). Consequently, we documented the effects of this stochastic disturbance on a rocky-intertidal biota for which an extensive historical baseline of descriptive information was available.

Study Area

The site selected for study at Corona del Mar, California (Figs. 1 and 2A) lies near the mouth of Morning Canyon (approximately 33°35′14″N and 117°51′54″W), located 1.4 km southeast of the entrance channel to Newport Bay. The intertidal zone extends over a horizontal distance of about 25.0 m with a slope of 3.4 degrees. Although spring tides at the site have an amplitude greater than 1.5 m, the tidal range of our quadrats was MLLW to +0.9 m levels. A sandy beach covered the upper intertidal zone. The rocky portion studied consists of siltstone and conglomerate, covered almost entirely by granitic boulders (0.5 to 1.0 m in diameter).

Environmental Data

Long-term records of mean monthly air and seawater temperatures (12 to 21°C and 15 to 19°C, respectively) reflect a reasonably constant system, with January to February being the coldest and August the warmest periods of the year (Kimura 1974; U.S. Department of Commerce 1970). Records of seawater salinity near the study site are available for 1961 (Scripps Institution of Oceanography 1962) and show little fluctuation (33.3 to 33.7 ppt). Physical data recorded during the course of the study were consistent with the previous records. For example, seawater temperatures and salinities were always lowest during January 1976 (mean of 13.6°C and 32.0°C), while the highest temperature (19.4°C) occurred in July 1975 and the maximum salinity (33.5 ppt) was recorded for March 1976. At the time of the first post-storm assessment (11 May 1977), the salinity was 23.5 ppt, the lowest measured. The temperature of both water and air was 18.0°C and the relative humidity was 72%. The shoreline near Corona del Mar is exposed to moderate wave action, because of the ameliorating effects of the offshore Channel Islands on the prevalent southerly swell, and has been classified as a protected outer coast (see Ricketts et al. 1968).

Methods

The survey methods employed were identical to those used during the previous two years (a total of eight quarterly assessments) at the same site. Undisturbed photogrammetric sampling of the rocky intertidal and tidepool habitats was conducted during all site visits using the same permanently marked 0.15-m^2 quadrats. This method is accurate and reproducible with ±5% of the cover (% absolute) values scored for abundant taxa (Littler 1980a). Because the identical plots could be re-occupied, very little variance due to sampling design was introduced. Consequently, the changes documented for species occurring in more than trace amounts are within ±5% of the actual cover present. Similar taxa that could not be visually distinguished in the field were combined in the analyses of data.

Undisturbed Samples

Two parallel transect lines 25 m long and 5.0 m apart were established. The upper and lower ends of each line were permanently marked by drilling and cementing eyebolts into the substratum, with the highest point (+0.9 m) being that containing epilithic marine organisms, the lowest position (MLLW) being delimitated by the lowest substrata exposed to air during the initial site visit (July 1975). Each line was laid perpendicular (205° from magnetic north) to the shore by means of a sighting compass, and corners of quadrats were permanently marked at 1.0-m intervals with hard-rock cement. A total of 43 emergent-rock quadrats was provided by this means with 4 located in the upper (+0.6 to +0.9 m) interval, 23 between +0.3 to +0.6 m, and 16 between MLLW to +0.3 m; 8 quadrats fell within tidepools and were not analyzed. The densities and/or cover for the various taxa in each quadrat were averaged and analyzed by ANOVA (Sokal and Rohlf 1981) to detect statistically significant changes at the populational level.

The 2 identical transects and 43 quadrats assessed by nondestructive techniques (Littler and Littler 1985) during 13–18 March 1977 were re-occupied on 20 May 1977. Sampling consisted of photographing each quadrat during low tide in infrared and color with 35-mm cameras equipped with electronic strobes. The species composition, locations, and visual estimates of cover were recorded in the field. These field notes were then used with the photographs in the laboratory to determine percent cover and density (number of individuals$\cdot m^{-2}$).

In addition to the above analyses, two 50 cm-wide belt transects (25 m^2 total area) were run (11 May 1977) centered on each of the permanent transects to quantify mortality effects on *Strongylocentrotus purpuratus* (Stimpson). Also, the total area between the two lines was searched and scored for *S. purpuratus* and compared with an equal-sized area (125 m^2) of the same intertidal system just 20 m to the north of the freshwater-impacted region. A parallel study conducted 40 km to the north at Whites Point (Murray and Littler 1984) provided comparative data.

Results

General observations two days after the flood indicated that: (1) all beach drift sea urchins were recently killed (tests mostly intact and pigmented, Fig. 2C), (2) all *Strongylocentrotus purpuratus* among crevices on emergent rock beyond 20 m from the flood site and in large-volume tidepools were healthy (Fig. 2D), (3) the coralline alga *Hydrolithon decipiens* (Foslie) Adey throughout the intertidal was mostly dead or dying (bleached), (4) the brown alga *Sargassum muticum* (Yendo) Fensholt in the large upper intertidal pool was in poor health and becoming extensively overgrown by the green algae *Ulva californica* Wille and *Enteromorpha* sp., (5) the anemone *Anthopleura elegantissima* (Brandt) experienced no mortality and several had ingested small *S. purpuratus,* and (6) the sea star *Pisaster ochraceous* (Brandt) appeared healthy, but of 15 examined none were feeding even though surrounded by dead and dying *S. purpuratus.*

Species normally present in samples but absent 11 days after the flood included four mobile gastropods (*Haliotis cracherodii* Leach, *Hipponix cranioides* Carpenter, *Littorina planaxis* Philippi, and *Opalia funiculata* (Carpenter)), the mobile crab *Pugettia producta* (Randall), and an unknown bryozoan. Also absent was the bivalve *Glans carpenteri* (Lamy), which had been present during the three preceding periods of study. All of these were present in their characteristic abundances both to the north and south (20 m distant) of the flooded habitat.

Macrophyte taxa characteristic of disturbed environments, *Ulva californica/ Enteromorpha* sp. (combined) and Ectocarpaceae, showed significant ($P < 0.05$, ANOVA) increases in absolute cover on former sea urchin territories (overall mean increases of 14.6% and 8.9%, respectively) following the disturbance (cf. Fig. 3). However, the majority of macrophytes, such as *Hydrolithon decipiens,* blue-green algae, and *Gelidium coulteri* Harvey/*G. pusillum* (Stackhouse) Le Jolis remained similar in absolute cover (slight declines not significant, $P > 0.05$) following the rainstorm. Abundances of these algae 20 m to the north and south of the transect site were also visually similar to those recorded during March 1977.

Few changes in absolute macroinvertebrate cover patterns were evident (Fig. 4) except that *Strongylocentrotus purpuratus* decreased dramatically from about 2.0% to less than 0.1% cover in the lower intertidal (MLLW to +0.3 m) and disappeared entirely from the +0.3 m to +0.6 m interval (significant at $P < 0.05$). Although not shown graphically because of their high abundances, the barnacles *Chthamalus fissus* Darwin/*C. dalli* Pilsbry (combined) and *Tetraclita rubescens* Darwin had some mortality of established individuals, but this was offset by large cover increases (66.1% and 85.1%, respectively, relative to their previous values) in the upper intertidal due to recruitment of juveniles. Adult *Anthopleura elegantissima* did not change ($P > 0.05$) following the runoff.

Density is perhaps the most sensitive measure of changes in mobile macroinvertebrate populations over short periods of time and the patterns of density for

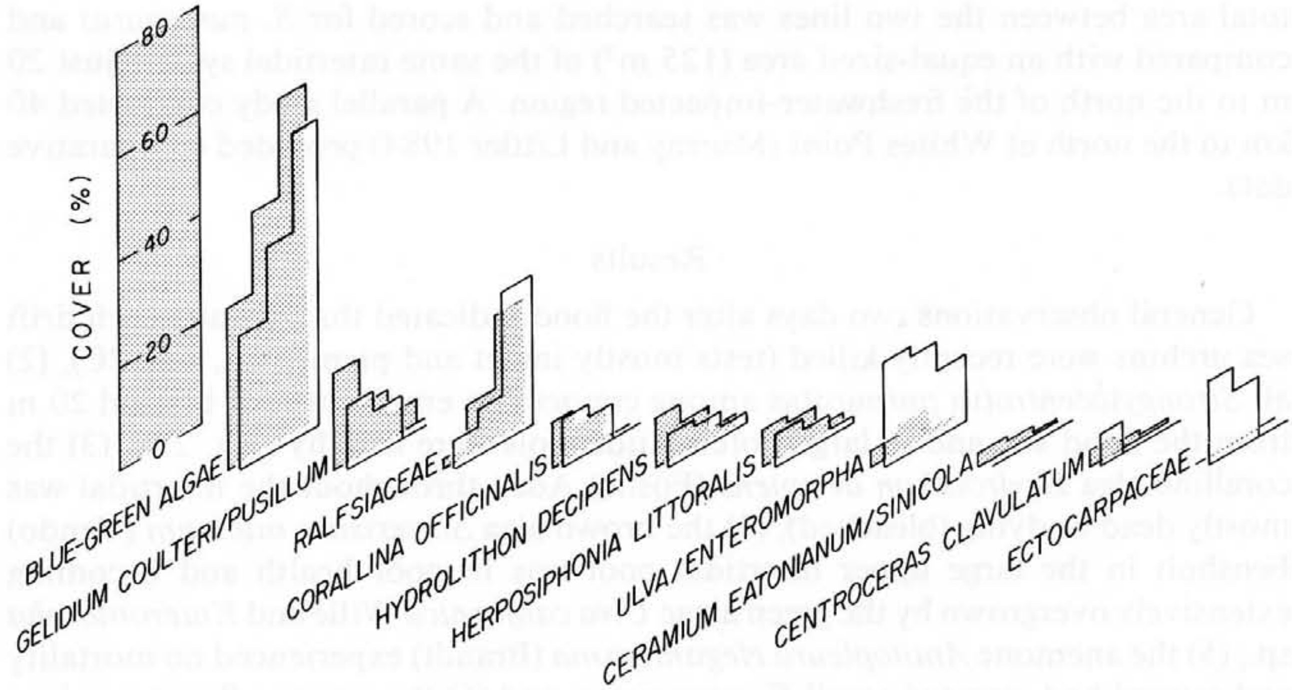

Fig. 3. Macrophyte cover on emergent substrata plotted over three tidal intervals before (shaded histograms in rear) and after the flash flood. From left to right (and front to back), the first third of each histogram indicates the mean for mean-lower-low-water (MLLW) to +0.3 m, the middle third = +0.3 to +0.6 m, and the last third = +0.6 to +0.9 m.

March 1977 and May 1977 (Fig. 5) showed some important differences. Macroinvertebrates that increased in numbers (significant at $P < 0.05$, ANOVA) throughout all intervals were the mobile species: *Collisella limatula* (mean increase of $27 \cdot m^{-2}$), *Pagurus samuelis* (increase of $22 \cdot m^{-2}$), *C. conus/C. scabra* (increase of $49 \cdot m^{-2}$), and the sessile barnacle *Tetraclita rubescens* (increase of $1500 \cdot m^{-2}$); the last clearly related to recruitment of juveniles on the upper shoreline. The two species showing pronounced decreases (significant at $P < 0.05$, ANOVA) in terms of both cover and density (cf. Figs. 4 and 5) were *Eupomatus* (*Hydroides*) *gracilis* (Bush) (mean decrease of $74 \cdot m^{-2}$) and *Strongylocentrotus purpuratus* (decrease of $60 \cdot m^{-2}$) in the interval from MLLW to +0.3 m.

The most dramatic effects over relatively broad areas of the intertidal (Fig. 5) were revealed by the density counts of *Strongylocentrotus purpuratus* immediately following the storm. Our belt transects documented an average of 90.5% mortality (19 recently killed out of 21 urchins), whereas a census of the total area between the two permanent transect lines revealed 96.3% of the *S. purpuratus* to be dead (52 dead out of 54 urchins). An equal area just beyond the region flooded (20 m north of the north transect line) contained only 1.1% dead *S. purpuratus* (6 dead out of 539 urchins). As mentioned, there were several hundreds of *S. purpuratus* tests cast in windrows on the beach above the study lines (Fig. 2C). The deepest tidepools on the lower portions of the shore (Fig. 2D), although lying in the direct path of the flood waters, contained abundant populations of healthy *S. purpuratus.*

Discussion

Information is scanty on the effects of unpredictable catastrophic events on rocky intertidal biotas; in particular, the effects of freshwater inundations are largely undocumented. There is a burgeoning literature on the role of generalized

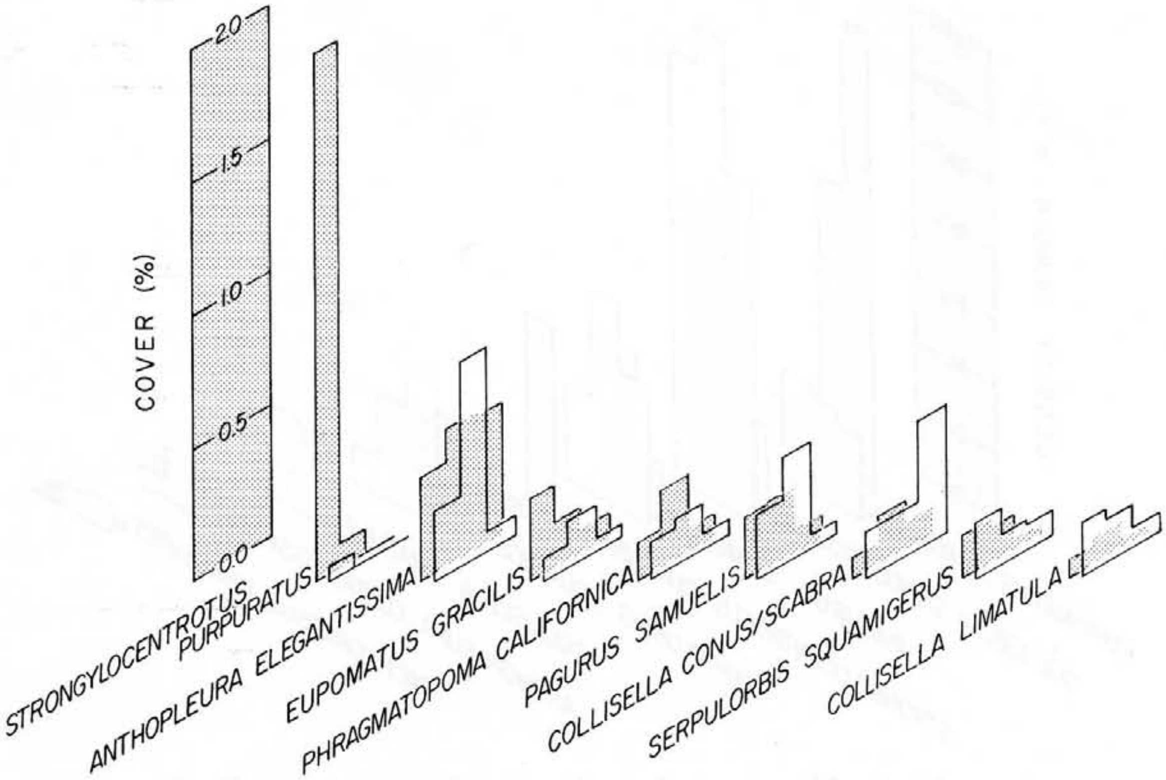

Fig. 4. Macroinvertebrate cover (features are the same as those given in Fig. 3).

disturbance gradients relative to the maintenance of species diversity. However, the phenomenon documented here is relatively species selective, although presumably not an isolated occurrence (cf. Sousa et al. 1981).

It would have been optimal if we had been able to compare the transect area affected by the flood with an identical control area unaffected by the flood (both before and after). However, since this was not possible, we used (1) an adjacent unflooded control area (visually similar) established after the flood, (2) a comparable but not identical control area 40 km to the north (i.e., Whites Point, Murray and Littler 1984), and (3) the previous two years of detailed seasonal data at Corona del Mar in which no flooding occurred. Our method of nondestructive sampling, by utilizing the identical sampling locations that were precisely relocated and reassessed, provided a powerful tool for the quantification of natural changes in the intertidal standing stocks, because variance due to sampling design was virtually eliminated.

Throughout the two years of quarterly sampling at this site prior to the flood, seasonal patterns tended to be both minor and predictable (Littler 1977, 1978). Historically, plant cover at Corona del Mar increased annually during spring to late summer followed by slight declines in late fall and early winter associated with aerial exposures during daytime low tides and some rock tumbling due to storm waves. Animal cover typically showed little seasonal change, except for vertical migratory movements of mobile limpet species (Seapy and Hoppe 1973) and a sporadic winter to spring recruitment of barnacles (Littler 1980a), that appeared to be minimally affected by the flood. Intertidal standing stocks of other Southern California systems (Gunnill 1980; Littler 1980a; Seapy and Littler 1982; Littler et al. 1983; Murray and Littler 1984) tend to follow a similar trend.

Unlike the patterns observed during 1975 through 1976 (Littler 1977, 1978) and at nearby Whites Point (where no comparable rainstorm occurred, Murray

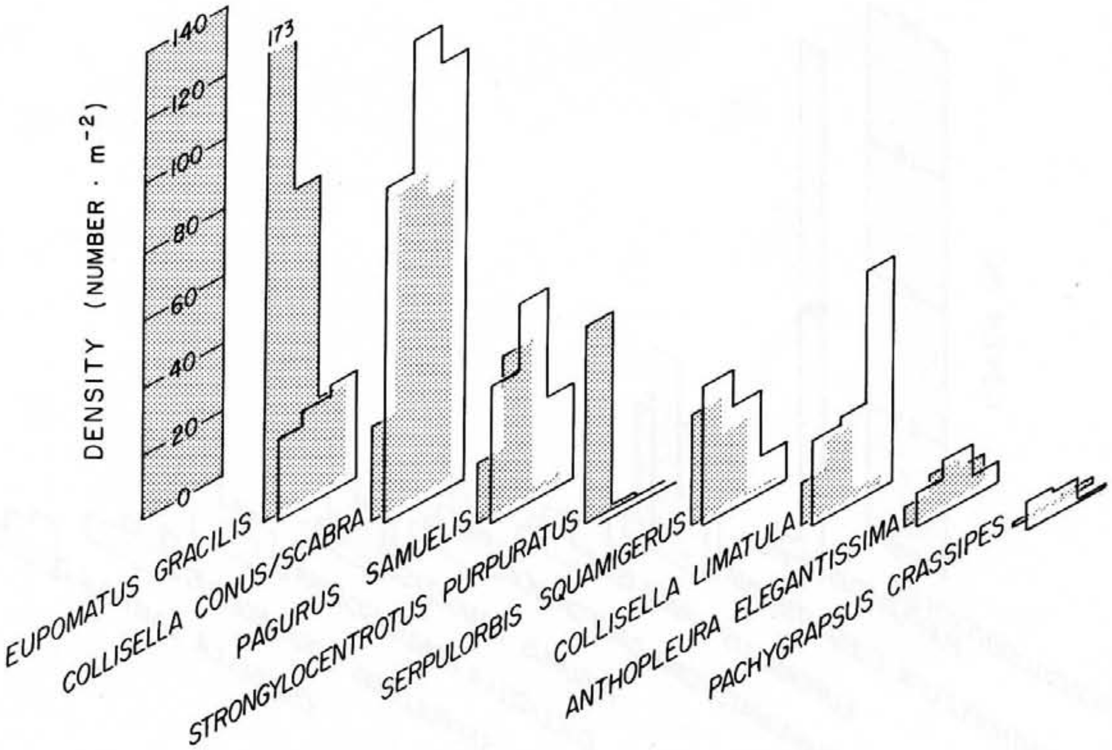

Fig. 5. Macroinvertebrate densities (features same as Fig. 3).

and Littler 1984), the thin sheet-like and microfilamentous algae, mainly *Ulva/Enteromorpha* and Ectocarpaceae, appeared abundantly in former sea urchin territories following the mass mortality of *Strongylocentrotus purpuratus.* Such algal forms have been shown (Sousa et al. 1981) to be maintained in low abundances by *S. purpuratus* when populations of the herbivore remain at high levels. From early February to late May 1977, *S. purpuratus* populations were assessed (Murray and Littler 1984 at a comparable intertidal study site just 40 km to the north, Fig. 1) by the identical methods used here and showed very little variability (0.2% cover and $16 \cdot m^{-2}$ density in February versus 0.8% cover and $13 \cdot m^{-2}$ density in late May, not significant, $P > 0.05$, ANOVA). The sheet form *Ulva californica* was uncommon at Whites Point and increased only slightly (from <0.01% to 0.6% absolute cover, $P > 0.05$), whereas Ectocarpaceae and *Enteromorpha* sp. consistently remained at only trace levels. The three persistent perennial taxa *Hydrolithon decipiens,* blue-green crust, and *Gelidium coulteri/pusillum* that decreased slightly at Corona del Mar, underwent a combined relative increase of one third during the same period at Whites Point (0.9 to 1.2%, 22.9 to 23.8%, and 0.4 to 6.3% absolute cover, respectively).

Dawson (1959, 1965) analyzed groups of intertidal organisms and reported a decline in leafy red algal forms and increased growth of jointed calcareous corallines in Southern California near sites of sewage discharge. Since then, changes in terms of gross morphological groupings of algal taxa have been evaluated (Widdowson 1971; Thom and Widdowson 1978; Sousa et al. 1981; Murray and Littler 1984) subsequently for the same regions of Southern California. Shifts from biotically competent strategists (sensu Grime 1979) in favor of stress-tolerant and opportunistic forms have been reported (Seapy and Littler 1982; Littler et al. 1983) for rocky intertidal communities subjected to extreme heating and desiccation stresses as well as to extensive sand inundation. Biotic patterns within sewage-polluted rocky intertidal communities (Littler and Murray 1975; Murray and Littler 1984) also showed similarities in terms of the adaptive strategies of the dominant forms.

Sheet and filamentous algae such as *Ulva/Enteromorpha* and Ectocarpaceae possess a number of characteristics associated with opportunism, including high productivity and low biomass per unit area (Littler 1980b; Littler and Arnold 1982; Littler et al. 1983) and rapid colonization of disturbed substrata (Castenholz 1967; Crapp 1971; Dayton 1971; Littler and Murray 1975; Murray and Littler 1978; Sousa 1979; Littler and Littler 1981). Opportunistic reproductive strategies have been indicated for both *Enteromorpha* sp. (Fahey 1953) and *Ulva* sp. (Littler and Murray 1974). In this regard, free space, experimentally cleared throughout several seasons next to the same transects studied here (Murray and Littler 1979), was first colonized by these same species of opportunistic algae. *Enteromorpha, Ulva,* Ectocarpaceae, and Ralfsiaceae (cf. Northcraft 1948; Dayton 1975; Littler and Murray 1978; Dethier 1981) as well as the barnacles *Chthamalus fissus/dalli* and *Tetraclita squamosa* (Hines 1978; Taylor and Littler 1982) have high and nearly continuous reproductive output.

Opportunistic forms are typically delicate and susceptible to mechanical removal by grazers (Littler and Littler 1980; Sousa et al. 1981). However, such rapidly growing algae have the potential (Hay 1981; Taylor et al. 1986) to be competitively superior to long-lived herbivore resistant species in the absence of grazing. It has been shown that perturbations occurring at different times of the year in Southern California can profoundly alter subsequent patterns of community recovery (Emerson and Zedler 1978). When *Strongylocentrotus purpuratus* was experimentally removed in Southern California (Sousa et al. 1981), opportunistic Ulvaceae and Ectocarpaceae also rapidly increased their abundances. However, sea urchin removals during August ultimately led to mature communities containing abundant, long-lived, turf-forming Rhodophyta that recruit between September and December (Sousa 1979); whereas, the same perturbation conducted in December led to significantly greater coverages of the brown algae *Egregia* and *Halidrys* (Sousa et al. 1981).

In summary, the natural elimination of a predominant grazer such as *Strongylocentrotus purpuratus* at Corona del Mar quickly resulted in a localized increase of delicate high producing macrophytes (Littler 1980b; Littler and Littler 1980) and highly-reproductive macroinvertebrates (e.g., barnacles) that correspond to the opportunistic strategists documented in successional studies (Murray and Littler 1979). The population census, in support of the community cover and density data, indicates that freshwater inundation of the intertidal zone can result in highly localized catastrophic effects on intertidal organisms (*S. purpuratus* in particular). Therefore, stochastic events that acutely disturb specific intertidal populations may set in motion subsequent changes to overall community structure that would be difficult to interpret from a program of infrequent sampling.

Acknowledgments

Gratitude is extended to P. J. Geddis as well as team photographers R. K. Mizusawa and S. D. Gaines. Additional personnel assisting at this site were: C. A. Curtis, P. Y. Ha, A. C. Kindig, M. M. McGlynn, M. P. Schildhauer, and R. H. Sims. We thank our colleagues S. N. Murray and R. R. Seapy, who verified most of the algal and invertebrate identifications, respectively. Without a large cooperative effort in responding rapidly to the tasks involved during the field and laboratory operations at Corona del Mar, this study would not have been completed. Support for the research originated from the Bureau of Land Management (now Minerals Management Service), United States Department of the Interior through their Outer Continental Shelf Research Program (Contract No. AA550-CT6-40).

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Accepted for publication 25 August 1986.

Citation:

Littler M. M. & Littler D. S. 1987.
Effects of stochastic processes on rocky-intertidal biotas:
an unusual flash flood near Corona del Mar, California.
Bulletin of the Southern California Academy of Science
86(2): 95-106.