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OCS Study
MMS 85-0049

Causes of Spatial and Temporal Patterns in Rocky Intertidal Communities of Central and Northern California

Volume 2 of 2
Literature Review

MMS U. S. Department of the Interior
Minerals Management Service
Pacific OCS Region

CAUSES OF SPATIAL AND TEMPORAL PATTERNS IN ROCKY INTERTIDAL COMMUNITIES OF CENTRAL AND NORTHERN CALIFORNIA

VOLUME 2 OF 2

LITERATURE REVIEW

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This study was funded by the Pacific Outer Continental Self Region of the Minerals Management Service, U.S. Department of the Interior, Los Angeles, California, under Contract No. 14-12-0001-30057.

September 1986

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PREFACE

This literature review and analysis on "Causes of Spatial and Temporal Patterns in Rocky Intertidal Communities of Central and Northern California" represents one segment of a three part report comprised of an annotated bibliography, literature review, and recommendations for design of an intertidal field studies program. The report has been prepared for the Pacific OCS Region, Minerals Management Service in support of a long-term project on study of "Successional and Seasonal Variation of the Central and Northern California Rocky Intertidal Communities as Related to Natural and Man- Induced Disturbances" (Contract No. 14-12-0001-30057). The primary focus of this report has been a review of the literature on the rocky intertidal communities of the central and northern California coast, supplemented by information relevant to the region; extending from British Columbia to Baja California, and by relevant studies conducted on other coasts. An executive summary is provided as a separate volume.

ABSTRACT

Literature relevant to understanding the causes of variation in distribution, abundance, and species composition of rocky intertidal plants and animals along the coastline of central and northern California is reviewed. Spatial variations in populations are discussed within and between vertical zones and on a geographic scale, and temporal variations are discussed within and between years for both plant and animal assemblages. The effects of natural disturbances including effects investigated by experimentation in the field, are contrasted with the effects of pollution.

In the absence of pollution and major storms, populations are generally more variable in space than in time. At any one site and time, disturbances caused by grazing, predation, and wave action are of special significance. Community succession following disturbance is a complex phenomenon that varies with the mode, degree, and history of disturbance, the life history characteristics of the organisms disturbed, dispersal, recruitment, and a variety of possible interactions among species. The importance of dispersal and recruitment to recovery from disturbance and the predictability of rate and outcome of recovery are still largely unknown. Impacts resulting from point sources of pollution may cause gradients of disturbances that are reflected in complex changes in distribution, abundance, and species composition. Under relatively constant gradients of stress, succession is broadly predictable. In the absence of biological disturbance (e.g., grazers and predators), opportunistic ephemeral species may persist. In the presence of intermittent stress or catastrophic perturbations, succession is less predictable.

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> ". ..As the years go by I have been more and more impressed by this factor of variation in marine habitats. ..it is the change, in other words, the variation shown by these animal communities and the individuals that comprise them which make them so interesting."
>
> G.E. MacGinitie, 1938

I. INTRODUCTION

The objective of this review is to examine the causes of variation in species composition, distribution, and abundance of rocky intertidal plants and animals along the coastline of northern and central California. Examination of such variation, both in space and time, has been the subject of numerous studies for over 50 years, and the shores of central and northern California have received their share of attention. However, these studies have been concentrated in areas near marine research stations; areas which are not necessarily typical of the coast. Indeed, most of the coastline of western North America is remote and inaccessible, and decidedly unsuitable as sites for research facilities. Our generalizations about intertidal communities of central and northern California, therefore, must be read with caution, and with full appreciation of the restricted nature of the primary research.

A second caveat is that even within the areas where most descriptive and experimental research has been conducted, such work is usually done in selected microhabitats. Flat, gentle inclines, although uncommon overall in California (Woodward-Clyde 1982; Hardin et al. in prep.), often best display intertidal zonation patterns and are the most suitable for setting up experiments that demand replication. Irregular rocky outcrops and boulder fields, which are more typical of California rocky intertidal coasts (Woodward and Clyde 1982; Hardin et al. in prep.), are rarely examined except for particular species that occur within them [outstanding exceptions are Seapy and Littler's (1978) and Sousa's (1979a,b, 1980) work on intertidal boulder fields].

A final condition that should be set on our discussion of the region reviewed is that, with important exceptions (e.g., Sutherland 1970, 1972; Haven 1973; Wolcott 1973; Doering and Phillips 1983; Fawcett 1984; Sousa 1984), the major experimental work on factors determining spatial and temporal patterns of intertidal organisms has not been done in central or northern California. Rather, it has focused on areas of southern California (e.g., Harger 1972; Dixon 1978; Sousa 1979a, 1980; Taylor and Littler 1982) and Washington State (e.g. , Connell 1970; Dayton 1971, 1975; Paine 1974, 1976, 1984; Suchanek 1978, 1981; Quinn 1979; Paine and Levin 1981). Other important experimental work includes that done in New England (e.g., Menge 1976, 1983; Lubchenco and Menge 1978), Great Britain (Connell 1961a,b; Lewis 1977), and southeast Australia (e.g. , Denley and Underwood 1979; Underwood 1980, 1981; Branch and Branch 1981; Underwood et al. 1983). We will attempt to incorporate this work into our discussion below, evaluating how conclusions drawn from it apply to the rocky intertidal of central and northern California.

Variation in plants is discussed in Section II, and variation in animals in Section III. A general consideration of types and effects of natural and human disturbances on rocky intertidal community structure follows in Sections IV and V, respectively. Variations in space and time are discussed separately within the sections on plants and animals. Relatively little is known about variation in time, and this is reviewed in the appropriate sub-sections, subdivided into scales of within-year (seasonal) and between-years (greater than one year).

The causes of spatial patterns are reviewed at three scales: geographic, vertical (zonation), and within-zone (microhabitat). Patterns at the geographic and within-zone scales are described in the text. However, because much of the extensive intertidal literature, particularly that published before the 1970's, is devoted to describing patterns of vertical zonation and associated tidal changes, we will only summarize this descriptive information in the following paragraphs, and restrict our review in later sections to the causes of zonation. Ricketts and Calvin (1968) and Carefoot (1977) provide detailed discussions of zonation patterns, tides, and climate in the northeastern Pacific, Lewis (1964) does the same for the British Isles and Stephenson and Stephenson (1972) review such patterns for coasts throughout the world.

Several schemes of subdividing rocky shores into horizontal bands have been proposed, and the major ones have been reviewed in Ricketts and Calvin (1968). Included in their discussion of intertidal zonation is Ricketts' own scheme, and it is his that we have adopted as a basis for comparison. We use his not because it is inherently better than any other, but because its development was based primarily on observations from the central California coast. A second reason for the adoption of this scheme is that we were "brought up" with it and are therefore familiar with its strengths and weaknesses.

The generalized scheme of intertidal zonation of rocky shores of Ricketts and Calvin is based on the extent of tidal exposure. According to this scheme there are four well-defined horizontal bands, zones, or associations. The highest or splash zone, Zone 1, is only infrequently wetted by storm waves and spray. It is mainly bare rock or blue-green algae, but green (*Enteromorpha* or *Ulva*) or red algae (*Porphyra*, *Bangia*), and diatoms may be present, especially in the winter or spring (Cubit 1984). The few animals which occupy this zone include the gastropod *Littorina keenae*, the isopod *Ligia* spp., and limpet *Collisella digitalis.* Zone 2 is the high intertidal, and is usually exposed to air for a long period at least once a day. It is characterized by dense populations of barnacles, *Balanus glandula*, and is frequently referred to as the barnacle zone. In addition to barnacles, the algae *Pelvetia fastigiata*, *Endocladia muricata* and *Gigartina papillata* are conspicuous and characteristic members of this zone. The tiny snail *Littorina scutulata/plena*, the turban snail *Tegula funebralis*, and several species of limpets also occupy this zone. Zone 3, often called the mussel zone, is the middle intertidal. It is generally exposed to air for relatively short periods twice a day, and its most conspicuous members are mussels (predominantly *Mytilus californianus*) and gooseneck barnacles (*Pollicipes polymerus*). Other characteristic species are the predatory snail *Nucella emarginata*, the chitons *Katharina tunicata* and *Nuttallina californica*, and the alga *Iridaea flaccida.* Zone 4 is the low intertidal and is only uncovered by the lowest tides; it may be covered with water most days of each month. This zone typically is easily identified by dense carpets of the surfgrass *Phyllospadix*, upright laminarian algae, and a variety of red algae. Although these plants are the most conspicuous indicators of this zone, it is here that one also finds sponges, hydroids, and ascidians, most of which do not occur higher on the shore.

Many studies of vertical zonation of intertidal organisms carried out along the west coast of North America have turned up a pattern similar to that of Ricketts'. In Table 1 we present seven zonation patterns reported from the Pacific Coast of North America from British Columbia to southern California.

Table 1. Patterns of Zonation

Ricketts & Calvin 1968 Pacific Coast, N. America	Carefoot 1977 Vancouver Island, B.C.	Pearse 1980 Ano Nuevo island	Stephenson & Stephenson 1972 Pacific Grove, California	Ferguson 1984 Big Sur Coast	Seapy & Littler 1978 Cayucos, CA (sea stack)	Caplan 8 Boolootian 1967 San Nicolas Island, CA
LITTORINA KEENAE Porphyra Cladophora Enteromorpha Ligia Balanus glandula	**PORPHYRA**	SPLASH ZONE Blue-green algae Lichens Porcellio scaoer Ligia pallosii Littorina keenae	**SUPRALITTORAL FRINGE** Littorina planaxis Ligia Pachygrapsus	SPLASH ZONE Littorina keenae Littorina scutulata Ligia		**LITTORAL FRINGE** Chthamalus fissus Littorina keenae
	BARNACLE ZONE Balanus glandula Chthamalus					
BALANUS GLANDULA Pelvetia Littorina scutulata Tegula funebralis	MIXED **BARNACLES/SEAWEEDS** Balanus glandula Gigartina Fucus/Pelvetiopsis	HIGH ZONE Porphyra spp. Gigartina papillata Endocladia muricata Pelvetiopsis limitata Balanus glandula Chthamalus dalli Mytilus californianus Phragmatopoma californica Pollicipes polymerus Anthopleura elegantissima Collisella digitalis Collisella scabra Tegula funebralis Littorina scutulata/plena Nuttallina californica	UPPER HID-INTERTIDAL Balanus glandula Tetraclita	HIGH **ZONE** Porphyra Pachygrapsus Collisella digitalis/ austrodigitalis Collisella scabra Lottia	**BALANUS/CHTHAMALUS**	UPPER **EULITTORAL** Littorina scutulata Collisella digitalis
MYTILUS Pollicipes Nucella californica Katharina Nuttallina	**MUSSELS/GOOSE** BARNACLES Mytilus californianus Pollicipes	MID-ZONE Iridaea flaccida Anthopleura elegantissima Anthopleura xanthogrammica Dodecaceria fewkesi Collisella digitalis Collisella pelts Collisella scabra Notoacmea scutum Tegula funebralis Tegula brunnea Pisaster ochraceus	LOHER **MID-INTERTIDAL** Chthamalus dalli Tegula funebralis Thais Nuttallina	HID ZONE Pagurus Tegula funebralis Anthopleura elegantissima Haliotis Lottia Katharina Mytilus/Pollicipes (only on offshore rocks)	**MYTILUS/POLLICIPES**	**MIDDLE EULITTORAL** Mytilus californianus Lottia Collisella scabra
					ENDOCLADIA	
	BARNACLES/ALGAE Balanus cariosus Ulva Halosaccion Whelks Limpets		**INFRALITTORAL** FRINGE Alaria Lessoniopsis	LOW ZONE Sponges Bryozoans Tunicates Mopalia Tonicella Leptasterias Phyllospadix	**EGREGIA/LITHOPHYLLUM** **CORALLINA/PHYLLOSPADIX**	**LOWER EULITTORAL** Corallina Lithothamnion Nuttallina Strongylocentrotus
PHYLLOSPADIX Laminarians	**HEDOPHYLLUM** Chitons Sea stars Phyllospadix	LOW ZONE Phyllospadix Laminaria spp. Egregia menziesii Sponges Bryozoans Tunicates			**MIXED REDS/PHYLLOSPADIX** **MIXED** REDS	

Species assemblages or zones are indicated in capitals. If a species is capitalized, it typifies or characterizes the assemblage. These species may or may not have been explicitly given by the authors. Within each column the assemblages are grouped vertically in their order of occurrence on the shoreline, without reference to tidal level since the studies are from several different locales with different exposure to surf. The order of species within a group does not necessarily reflect their vertical position in that group. Common to all seven studies are four distinct zones: a high splash or littorine zone [littorines were absent from this zone in Seapy and Littler (1978)], a *Balanus* zone, a mussel zone, and a low *Phyllospadix* zone. Stephenson and Stephenson (1949) did not include a mussel zone, and Seapy and Littler (1978) and Carefoot (1977) show additional assemblages between these common zones. These additional zones could be due to differences in the level of detail at which the study was carried out, the method used to lump or categorize assemblages, or to actual differences in the structure of the intertidal communities examined. The similarities among the seven sites could be misleading, however, because all the studies in Table 1 were done on massive rocky shores exposed to moderate to severe wave action. The variation in the kinds of shoreline found between British Columbia and Baja California has not been described, and we will address the issue of the way shoreline topography modifies vertical zonation in the sections below.

In addition to the traditional descriptive analyses, zonation has also been studied by assemblage characteristics and mathematical association analyses (Chapman 1974). Den Hartog (1959) characterized zones along the Dutch coast in terms of life form, stratification, successional patterns and positions in relation to other zones. From his work in central Chile, Santelices (1981) has also suggested zonation of algal morphologies rather than strict species zonation. Russell (1972) defined a two-zone shore on Hilbrae Island using cluster analyses on common species, and showed a strong negative correlation between twoassemblages. Such correlations remove the subjectivity of traditional descriptions. The general lack of continued work along these lines may indicate a satisfaction with the description of zones and a shift of interest to studies considering the causes of zonation.

One prominent hypothesis regarding the causal agents which lead to such distinctive assemblages, centers around the concept of critical tidal levels. Critical tidal levels are levels of the shore where some parameter such as time of exposure to air changes abruptly with a small change in tidal height. That zonation patterns are caused by these changes in exposure is intuitively appealing, because limits to distribution of intertidal organisms are also abrupt. Colman (1933) working British shores, and Hewatt (1937) and Doty (1946) working on the Pacific coast of the United States, correlated the vertical distributions of intertidal organisms to critical levels in the tidal cycles associated with abrupt changes in the hours of exposure to air. Shotwell (1950) correlated the upper limits of distribution of *Collisella* to critical tidal levels responsible for extremes in desiccation. The critical tide level hypothesis has been criticized by Cornell (1972) largely because the correlation between critical tidal levels and vertical limits of distribution of organisms is not objectively assessed and, looking at the data published by these workers, not very precise. Underwood (1978) refuted the critical tide level hypothesis for British shores on two counts. First, re-calculation of the annual emersion times against height on the shore yielded a smooth, monotonic curve without sharp increases in emersion time. Second, boundaries of species' distributions on British shores were found to be randomly distributed, not clumped as would be expected if they were associated with critical tidal levels. In addition, much recent work has shown that biological interactions are also important in controlling the vertical distribution of intertidal organisms, a concept which was not widely acknowledged in the early intertidal literature. Colman (1933) did, however, point out that behavioral responses of gastropod are probably important in explaining their vertical distribution, and that interspecific competition probably explained how extremely distinct boundaries between pairs of algal species could occur without declining abundances of either one near their common borders.

The concept of critical tidal levels has not been entirely discarded, however. Swinbanks (1982) identified several different orders of critical tidal levels which coincided with various cycles of the tide (e.g., daily, monthly, annually), resulting in identification of many more critical tidal levels than proposed earlier by Colman (1933) or Doty (1946). Swinbanks provided examples in which the upper limits of distribution of many intertidal organisms coincided with these critical tidal levels.

The distributions of some intertidal organisms do appear to be directly determined by changes in the abiotic environment associated with tides. Numerous experimental studies, however, have shown that biotic factors may also directly affect distributions in the field. Thus, as a general hypothesis, critical tide levels has been rejected, although it may apply to a specific distribution in a particular place. The available information now suggests the working hypothesis that a variety of phenomena can affect spatial patterns of distribution. We review this information in the sections that follow.

II. PLANTS

This section reviews the temporal and spatial patterns of algal distribution, abundance and reproduction. As will be seen, a synthesis of spatial pattern such as that provided for northern New Zealand kelp communities by Cheat and Schiel (1982) or for British shores by Lewis (1964) is impossible for the northeastern Pacific because of the lack of comprehensive, quantitative surveys at numerous sites. Moreover, surveys that are available generally do not consider temporal variation, and do not include a great range of spatial scales. We will use the available information to piece together as complete a picture as possible, and fill in some of the gaps with speculation.

A. Spatial Variation

1. Geographic Distribution

The presence or absence and the abundance of a species on a geographic scale is the result of general oceanographic conditions and large-scale dispersal, including that by humans (Druehl 1981). Although numerous correlations have been made between the latitudinal distribution of intertidal plants and various environmental factors (e.g., Murray et al. 1980), few of these correlations have been experimentally tested. Moreover, the patterns themselves are often questionable for algae because of incomplete or missing records for particular areas , the difficulty of proving absence, and the use of different taxonomic criteria by different investigators (Druehl 1981).

Given these difficulties, it has been established that the distribution of intertidal seaweeds changes with latitude between British Columbia and Baja California. These changes have been discussed by Scagel (1963) and recently reviewed in detail by Murray et. al. (1980) for marine macroalgae in California. Distributional end points for northern and southern species are particularly common along the California coast, producing a rich and diverse flora (Abbott and Hollenberg 1976; Murray et al. 1980). Various biogeographic provinces have been established for the northeastern Pacific (Section III) but, with the exception of the region around Point Conception and perhaps Monterey, changes in the flora with latitude are gradual (Scagel 1963; Murray et al. 1980).

The relatively rapid changes in species composition around Point Conception are associated with changes in oceanographic conditions, particularly temperature (Murray et al. 1980). To our knowledge, no one has suggested a correlation with oceanographic conditions for the observed floral break around Monterey; perhaps it is correlated with the diversity and extent of rocky habitats in the area, and with the intensity of collection.

These geographic studies are largely based on presence or absence data, and could be used to construct probable intertidal floras for a particular section of coast. In the context of this review, however, one would also like to know whether such latitudinal changes in one species causes indirect changes in others. To even speculate about this, some indication of relative abundance is needed, along with information about the functional consequences of a species presence. Table 2 lists algal species or groups that vary in abundance with latitude in California, and which are known to affect other species. Of the species or groups listed, only the effects of latitudinal variation in algal turfs have been examined. Sousa et al. (1981) found that when sea urchins were removed from the low intertidal zone in southern California, red algal turfs developed that could displace juveniles of large brown algae. This is

Table 2. Algal Species or Groups of Known Ecological Importance that Vary in Abundance With Latitude in California. Distributions are from Abbott and Hollenberg (1976).

Species	Distribution	Ecological Importance	Reference
RED ALGAE			
Algal turfs	[1]More abundant south of Pt. Conception.	Trap sediment, provide sites for epiphytes, preempt space.	Sousa et al. 1981 Stewart 1982
Gigartina canaliculata	[2]Baja Calif. to south Oregon, declining abundance north of Pt. Conception.	Can exclude other species in boulder fields.	Sousa 1979a
Gigartina leptorhynchos	[2]Baja Calif. to Humboldt Co., Calif. declining abundance North of Pt. Conception.	Can be very abundant south of Pt. Conception	Sousa 1979a
Rhodoglossum affine	British Columbia to Baja Calif., but uncommon south of San Luis Obispo Co., California.	Can form turfs north of Pt. Conception.	Foster, pers. ohs.
BROWN ALGAE			
Hedophyllum sessile	Alaska to Monterey, rare in Calif.	Can displace or provide microhabitat for other species.	Dayton 1975
Lessoniopsis littoralis	Alaska to Monterey.	Can displace other species.	Dayton 1975
Postelsia palmaeformis	British Columbia to San Luis Obispo Co., California.	Can produce primary substratum when dislodged.	Dayton 1973 Paine 1979
Sargassum muticum	Introduced, patchy, British Columbia, San Francisco, Santa Barbara, San Diego, Santa Catalina Island.	Can displace at least one other common alga.	DeWreede 1983
Fucus distichus	Washington to Pt. Conception.	Can be very common north of Pt. Conception, can provide shelter or displace other species.	Foster, pers. ohs.

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[1] Stewart 1982

[2] Foster, pers. ohs.

In contrast to similar removals in Washington where turfs do not grow in abundance in the low intertidal zone and where urchin removal results in a persistent cover of large brown algae (Paine and Vadas 1969; Dayton 1975; Paine 1977). Sousa et al. (1981) suggest disturbance as a major cause of these community differences. Many of the algal turf species in southern California are, however, rare or absent to the north (Abbott and Hollenberg 1976; Stewart 1982), and many of the northern large brown algae (e.g., *Hedophyllum sessile*) are rare or absent in southern California (Abbott and Hollenberg 1976). Thus, latitudinal differences associated with sea urchin removal may be simply a result of the natural history characteristics of the species available in an area. Additional experiments in areas where northern and southern species overlap are necessary before the importance of latitudinal variation on local community patterns can be more thoroughly evaluated.

In addition to direct changes in algal species composition, other factors may contribute to the latitudinal variation in the distribution and abundance of algae. Latitudinal changes in grazers may influence local community patterns (Gaines and Lubchenco 1982). Sousa et al. (1981) speculate that large scale changes in disturbance contribute to local pattern. They suggest that more frequent disturbances by waves and logs in the more exposed intertidal areas north of Point Conception reduce grazer abundance and clear space more frequently, contributing to the maintenance of local stands of large, canopy forming algae. On the other hand, disturbances associated with shifting sand (Daly and Mathieson 1977; Taylor and Littler 1982) may be more prevalent along the mainland south of Point Conception where sandy beaches are common.

2. Vertical Zonation

The general patterns of intertidal zonation were discussed in the Introduction. Below we examine the causes of algal zonation, and divide these causes in the the general categories of physical and biological factors.

a. The Effects of Physical Factors

Experimental work on physical factors affecting the vertical distribution of algae on the shore has concentrated on the effects of desiccation in terms of both physiological processes and simple survival. Observations of mortality after intertidal uplifting by earthquakes (Johansen 1972) and nuclear bomb testing (Lebednik 1973) dramatically demonstrate the sensitivity of algae to their position on the shore. More classical examples suggesting the importance of desiccation are the raising of zones in areas of high wave exposure and moist air conditions, in areas of drainage from tide pools, and in areas where shade is produced by canopy species or where the substratum faces away from the sun (for review of examples see Lewis 1964; Connell 1972; Carefoot 1977).

Schonbeck and Norton (1978, 1979a, 1979c) thoroughly investigated the effects of desiccation on some fucoid algae, and found that tissue damage was highly correlated with long exposure during extreme drying conditi ens. Tolerance to dessication varied with season and with the position of an alga on the shore (Schonbeck and Norton 1979c). Though growth in apical tips of some fucoids increases during short periods of desiccation (Stromgren 1977) it is generally accepted that abiotic environmental conditions become less favorable to algae as intertidal height increases (Foster 1982), and that the upper limits of these plants are set by desiccation (Connell 1972, 1975; but see qualifications below). Descriptive work by Druehl (1967a) in a British Columbia inlet suggests that intolerance to high temperatures and low salinity may lower the upper limits of some low intertidal algae.

Transplanting algae vertically on the shore, as done by Schonbeck and Norton (1978), Hodgson (1981), and Foster (1982) can be a powerful method of determining the distributional limits of an alga. If the transplanted alga is unable to grow, this simple field experiment will give more conclusive results than countless correlations based on laboratory experiments. However, the results of transplantation may be cologically meaningless at a particular site if the juveniles never reach or are not able to grow in the area of transplant (Underwood and Denley 1984).

Laboratory studies have suggested that some algae are physiologically best adapted to their Position on the shore. Quadir et al. (1979) found that *Fucus distichus*, a representative upper intertidal alga, had maximum net photosynthesis when 20% desiccated. Quadir et al. (1979) and Hodgson (1981) found that lower intertidal species such as *Iridaea cordata* and *Gastroclonium coulteri* always had higher net photosynthesis when submerged than when emerged. Bidwell and Craigie (1963) distinguish between the effects of''emergence" and desiccation, and Schonbeck and Norton (1979b) found that increasing nutrient concentrations could compensate for slow growth under conditions of only occasional, brief submergence.

b. The Effects of Biological Factors

In addition to biological attributes of the plants themselves, the biological factors that have been identified as important to the vertical distribution of intertidal algae are competition, grazing andmutualism. Grazing andmutualism have been shown to directly affect the upper and, in one case, lower limits of interidal algae. Competition has only been shown to affect the lower limits.

Robles and Cubit (1981) showed that algal growth could be limited by grazing dipteran larvae in an upper rocky intertidal community. After removing larvae by hand and using insecticides with appropriate controls, microalgae and small foliose algae were able to grow at higher levels than previously observed. Careful observation reveals that insects and amphipods are prominent throughout the intertidal zone in central and northern California (Glynn 1965; Robles 1982). As more techniques are developed to manipulate these organisms in field experiments, their potentially important effects on algal distribution may be more thoroughly elucidated.

Macroscopic molluscan grazers have been manipulated to determine their effect on algal distribution. Castenholz (1961) found that littorine snails could set the upper limit for intertidal diatom mats during the summer season in southern Oregon, and limpets in this same locale can nearly eliminate ephemeral algae (e.g., *Bangia*, *Porphyra*, *Ulva*) in the summer (Cubit 1984). Hay (1979) removed intertidal limpets and found a low intertidal kelp was able to colonize 1.6m higher than with limpets present. In a similar experiment, but where conditions were dryer, colonization did not extend upward. Raffaelli (1979) found little or no effect after removing grazers from the mid-intertidal in New Zealand, but Underwood (1980) suggests that the removal techniques may have been insufficient.

In an exemplary study of grazing effect on mid-intertidal algae using well designed experiments and considering alternative hypotheses, Underwood (1980) found that foliose algae were able to colonize in areas of grazer removal, but only grew to maturity in unnaturally shaded areas. In a more recent study, Underwood and Jernakoff (1984) examined the effects of tidal height, wave exposure, and seasonality as well as grazing. Algae again were found to grow best when desiccation was reduced, and no plants established in the high intertidal if grazers were present. Underwood (1980) concludes that grazing prevents the establishment of algae in the high intertidal but, in the absence of grazers, physical factors control their abundance.

From the above examples it seems that the upper limits of algae can be set by grazers but only under relatively harsh physical conditions. The above studies were done in areas inhabited almost exclusively by ephemeral algae (e. g., *Ulva, Porphyra,* diatoms). Processes may be different for long-lived species. Other factors that should be considered in evaluating the effects of molluscan grazers are their densities, ability to feed effectively under all environmental conditions (e.g., high wave shock conditions), and method of feeding. Scanning electron microscope observations indicate that some species graze rock very thoroughly, while others only crop thalli, having no measurable impact on rates of colonization (Underwood and Jernakoff 1981).

Much less work has been done on the molluscan grazer-algal interactions in the lower intertidal. Underwood and Jernakoff (1981) found that limpets were not able to survive in the lower intertidal because algae generally grew fast, covering the substratum so that these animals could not attach. Lubchenco (1980) and Foster (1982) found that grazing by molluscs can retard but not prevent the establishment of macroalgae at their lower limits of distribution. Moreno and Jaramillo (1983) indicate that the *Iridaea* zone in Chile extended downward if grazers were removed. This manipulative experiment is interesting because it is the first to find that the lower intertidal limits of algae can be set by grazers. Unfortunately, the experiment was pseudoreplicated (Hurlbert 1984) and the measurement of zone width does not indicate direction of zone expansion. Plant-herbivore interactions can be very complex leading to a variety of patterns at different spatial scales (Lubchenco and Gaines 1981).

Competition with other plants can have significant effects on their lower distributional limits. Competition theory (reviewed by Chapman 1974) has yet to contribute significantly to our understanding of the role of competition in intertidal algal zonation. This may be largely due to the biologically unrealistic assumptions of the models. Pielou (1974), for instance, assumes a balance in nature, considers only a few environmental variables, and uses a model that has never been tested. Field experiments, on the other hand, have been useful. By removing plants from lower intertidal zones (Hruby 1976), making partial clearings, performing transplant experiments, or a combination of the above (Hodgson 1980; Lubchenco 1980; Schonbeck and Norton 1980; Foster 1982), interspecific competition has been shown to set the lower limits of some macroalgae. In contrast, Dayton (1975) has shown that overstory algae may modify the environment such that other plants may extend their range upward beneath overstory algal canopies (mutualism). Competition may include direct interference (whiplash) or exploitation of light or space. These factors have not yet been separated and tested in the field. Lubchenco (1980) and Foster (1982) found that removing only the upright parts of potential competitors still prevented a downward extension of higher intertidal algae, suggesting inhibition (preemption of spaceon the substratum) alone can prevent colonization.

Thus, we find that Cornell 's (1972) generalization that physical factors are important in setting the upper limits, while biological relationships are more important for setting lower limits of organisms in rocky intertidal systems, should be modified. Several studies have indicated that the upper limits of ephemeral algae are set by grazing, a biological interaction. Underwood and Denley (1984) provide a series of alternative hypotheses, mainly dealing with faunal planktonic stages and settlement, that may also modify Cornell's generalization. They also point out the importance of developing generalizations, but emphasize that these should be critically tested.

3. Variation Within Zones

At a specific latitude and within one zonal assemblage, species abundance and distribution can be quite variable. This spatial variation may occur on scales from meters to millimeters, and is caused by physical and biological factors, or a combination of both.

Disturbances create new space for colonization, resulting in patches at different stages of succession within an assemblage (Sousa 1979b, 1984; Paine and Levin 1981; Section IV). Colonization within a cleared area may be limited by spore availability because of limited spore production or short dispersal distances causing variability between patches (Dayton 1973; Sousa 1984), The timing of a disturbance can also determine the composition of the algal community in the disturbed area (Emerson and Zedler 1978). The coincidence of harsh insolation with low tides also causes localized changes within assemblages. Loss of pigments in algae during such times is commonly observed, and Schonbeck and Norton (1978) have noted changes at the upper limits of fucoid zones due to such weather conditions.

At a larger scale, water motion affects species composition. This is commonly noted when comparing the species composition of exposed and sheltered rocky shores (e.g., Ricketts and Calvin 1968). The most obvious possible cause of the differences is ability of adults to withstand wave forces, but this does not explain why plants characteristic of exposed sites are generally not found in quiet water. Druehl (1967b) found that around Vancouver Island, the long form of *Laminaria groenlandica* is found in areas of heavy surf, the short form in areas of moderate surf, and *L. saccharin* is only found in calm areas. Experiments indicated this was due to different abilities to withstand water motion and the ability of *L. saccharin* to grow and reproduce in the reduced salinities associated with the calm water sites. After making partial clearings, Dayton (1975) found that recovery rates of *Hedophyllum sessile* were much more rapid at exposure sites. More complex interactions may also affect species composition along exposed gradients. Paine (1979) proposed that moderate wave intensity creates space in mussel beds, and that this was necessary for the local persistence of *Postelsia palmaeformis*. Lubchenco and Menge (1978) discuss other factors that have variable importance along a gradient of wave exposure in New England. For instance, the abundance of grazers (littorines) were lower at exposed sites, allowing for a greater abundance of ephemeral algae, which in turn compete with *Chondrus crispus*. Thus, a series of interactions slows the succession rate in exposed areas, Additional mechanisms affecting spatial variation along exposure gradients are discussed in Section III, A.4.

Tide pools also cause species variation within an assemblage. Underwood and Jernakoff (1984) found that during dry seasons foliose algal growth increased in artificially made tide pools but declined on adjacent rock platforms. Lubchenco and Gaines (1981) report different herbivore taxa in pools than outside, and Lubchenco (1982) found that fucoids can be excluded from protected pools by the joint action of herbivores and algal competitors. However, in areas with a high frequency of physical disturbance, Dethier (1984) contends that herbivory, competition and predation are less important than physical factors in structuring tide pool communities.

Substratum type, in terms of composition and relief, can create different microhabitats. *Fucus* growing on barnacles are more easily detached than when growing on rock (Barnes and Topinka 1969), plant loss during storms is higher on unstable substratum (Gunnill 1985), and algal zones are raised to much higher level son limestone than on basalt (Den Hartog 1959). Harlin and Lindbergh (1977) have determined that surface relief can regulate the development of an algal community. Using settling plates made of acrylic discs with layers of different diameter particles, they found that macroalgae generally preferred to colonize areas with greater surface relief. Greater relief may provide refuges from grazing (see below) and help prevent desiccation (Jernakoff 1983).

Algal patchiness can also be caused by localized size or spatial refuges from grazing. Lubchenco (1983) found that grazing gastropod prevented the establishment of *Fucus* on smooth rock, but only very high snail densities could prevent establishment of this plant in areas where crevices and barnacles were present. A similar interaction occurs between littorines and *Enteromorpha* (Petraitis 1983). Jernakoff (1983) suggests that the patchy distribution of algae within the barnacle zone reflects areas where spores have escaped grazing in the past. He indicates this is an escape by chance, because grazers were found to be effective in all microhabitats. Algae may find refuge from grazing by growing on the shells of herbivores. Where surrounding rock surfaces are barren of macroalgae, *Ulva* can be found growing on limpets, and perennial algae are found on some black abalone in the Monterey Bay area and on San Nicolas Island (De Vogelaere, pers. ohs.). Gaines (1985) found that local patchiness in *Iridaea cordata* was related to the distribution of the grazers *Katharina tunicata* and *Strongylocentrotus purpuratus*. At his study sites in Oregon, *I. cordata* abundance was greatly reduced on horizontal surfaces where these grazers were most abundant. When the grazers were experimentally reduced, the alga' s distribution became more uniform. Grazers can also create patchiness- by accelerating succession (Lubchenco and Menge 1978; Sousa 1979a) and, in the case of the territorial limpet *Lottia gigantea*, grazing creates large patches free of upright organisms (Stimpson 1970), while its mucus local ly enhances diatom growth (Connor and Quinn 1984).

Grazing may also generally alter algal abundance and species composition. Duggins and Dethier (1985) removed the chiton, *Katharina tunicata*, from a low intertidal site in Washington that was dominated by the kelp, *Hedophyllum sessile* and considerable bare space. Algal abundance and diverstiy rapidly increased after removal, resulting in a low intertidal kelp bed. In the continued absence of grazing, patchiness in this new assemblage was maintained by physical disturbance.

Disease caused by a variety of pathogens has frequently been noted in intertidal algae (Andrews 1976, 1977; Goff and Glasgow 1980), but little is known about the effects of disease on natural populations (Andrews 1977). A fungus alters the morphology of *Blidingia minima* (Abbott and Hollenberg 1976), and we have noted large (-15-20 cm dia.), black patches in stands of this species presumably caused by fungal infection. Anderson (pers. comm.) noted mites to graze patches in stands of the high intertidal green alga, *Prasiola meridionalis*. Epiphytes may also be common on intertidal algae and can be important in successional 'processes (Sousa 1979a).

Finally, certain species provide microhabitats for other organisms. Obligate understory algae are considered an ecological category of algae by

Dayton (1975). They die when the overstory canopy species are removed. Death is caused either from desiccation, exposure to excessive light intensity, or from physical battering. These obligate understory algae may be intertidal representatives of otherwise subtidal species that only extend their distribution upward when physically protected. Numerous animals are also associated with particular plants (Glynn 1965; Borden et al. 1975; Hill 1980; Gunnill 1983; Section III).

In summary, algal variability within zones at the microhabitat scale can be caused by physical disturbances, dispersal limitations, pools, substrate types and relief, grazing and interactions between grazers and substrate type, and particular associations, especially between understory algae and the overstory of larger perennial algae.

B. Temporal Variation

1. Within Years

As pointed out in the introduction, early work on intertidal ecology was primarily concerned with vertical patterns of distribution, while more recent work has focused on factors affecting these and other patterns. An assumption in most of this work is that temporal variation is low. To our knowledge, this assumption has never been explicitly tested in the northeastern Pacific, but natural history observations suggest it is true, as do data from control quadrats used in various experimental studies in this region (British Columbia and Washington: DeWreede 1983; Dayton 1975; Oregon: Turner 1983a,b; central California: Abbott 1980; Foster 1982; southern California: Sousa 1979a,b; Littler 1980a; Stewart 1982; Emerson and Zedler 1978). Neither Ricketts and Calvin (1968) nor Carefoot (1977) have sections on temporal variability, and it is not discussed in the review by Lewis (1964) of British shores, or by Stephenson and Stephenson (1972) in their review of the shores of the world. Based on his multi-site seasonal surveys in southern California, Littler (1980a) concluded that "local or even site-specific conditions tended to predominate more often and obscured any broad climatic effects (overall seasonal patterns)."

This apparent temporal stability in the northeastern Pacific might be expected as the more common intertidal algae are perennial and perhaps long lived. As discussed by Connell and Sousa (1983), however, if variability were scaled to lifespan, these plants may vary as much as annuals. Thus, stability remains a question until ages are known and demographic studies are done over the appropriate time scales. There are few published observations that observed seasonal differences in the abundance of these species are related to individual mortality. However, some of these perennials vary in the abundance of vegetative parts. *Hedophyllum sessile*, a large brown alga that can be abundant in areas of moderate wave exposure, may drop from 100% cover in summer to 50% in winter due to defoliation (Dayton 1975). The red algae *Iridaea cordata* and *I. flaccida* have perennial holdfasts and generally annual blades. Blades begin to grow in late winter, reach their maximum size in mid-summer, and then reproduce and senesce in the fall (Hansen and Doyle 1976; Hansen 1977; Foster 1982). Long term records of *I. flaccida* abundance at a site near San Luis Obispo clearly show this regular cycle (Figure 1). Hansen (1977) suggests that light may limit growth of *I. cordata* in winter, and that maturation is genetically controlled. Emerson and Zedler (1978) found that the perennial articulated coralline, *Lithothrix aspergillum*, declined in cover during the summer at a site near San Diego as a result of increased temperatures and desiccation during low tides. Occasional wide-spread loss of the blades of perennial

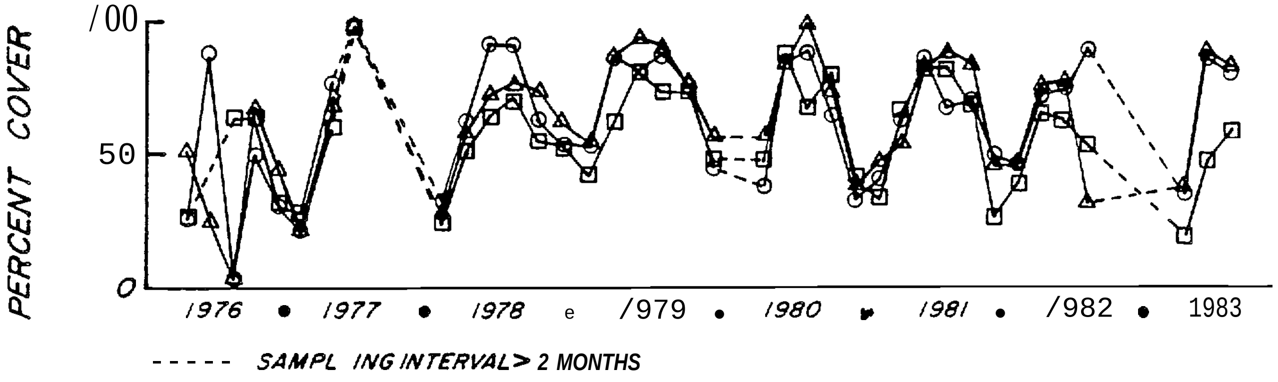

Figure 1. *Iridaea flaccida* abundance (at +3 ft above MLLW) near San Luis Obispo, CA. Data from three (triangle, circle, square) fixed 0.25-m^2 quadrats at one site. Quadrats sampled by noting cover under 60 randomly placed points (metal rod). Data are mean cover per quadrat (from PG&E 1984).

species occurs in Monterey when hot weather (no fog) coincides with summer low tides (Foster, pers. ohs.).

The general lack of observed seasonal changes may to some extent reflect the gross level of sampling (visual estimates of cover, bias towards large, canopy species) and the relatively short term nature of most studies. In those studies using more detailed sampling over longer periods, or that have followed individual or cohorts of plants, within year changes in abundance are usually found. In a particularly thorough study of reproduction, recruitment, and standing stocks of one green (Cot/ium *fragile*) and five brown (*Eisenia arborea, Egregia laevigata [= E. menziesii* in Abbott and Hollenberg 1976], *Sargassum muticum, Halidrys dioica* and *Cystoseira osmundacea*) algae, Gunnill (1980a) found clear seasonal variation in numbers of individuals in almost all species in his study sites near San Diego. Variation was largely due to variation in recruitment. Recruitment was most common in spring-summer, and appeared related to changes in reproduction. Similar trends were identified for the brown-alga, *Pelvetia fastigiata* (Gunnill 1980b). Gunnill (1980a) concluded that these population fluctuations were related to a complex of environmental factors including cloud cover, temperature, and wave action. Stewart (1983) has shown distinct seasonal patterns of abundance in several algal turf species. These patterns are correlated with seasonal changes in sand accumulation.

Probably the longest, most thorough observations of intertidal plants and animals come from monitoring programs done by companies with coastal power plants in California. Environmental monitoring around the Diablo Canyon nuclear power plant near San Luis Obispo has revealed seasonal patterns in almost every species examined (PG&E 1984). In addition to *Iridaea flaccida* (Figure 1), the perennial red algae *Endocladia muricata*, *Gigartina canaliculata* and G. *papillata* all change abundance seasonally, usually with maximum cover in summer and early fall and minimum cover in winter and early spring (Figure 2). Much of this change appears related to a cycle of winter storm damage followed by new growth (PG&E 1984), but seasonal variation in recruitment could also be important (Gunnill 1980a,b). We stress again that Figures 1 and 2 represent changes in cover. How much of this variation is due to individual death and recruitment is unknown.

Annual species or relatively large, annual stages in the life histories of heteromorphic plants do often undergo distinct seasonal changes in abundance (Mumford 1975; Lubchenco and Cubit 1980; Cubit 1984). *Porphyra* spp., *Bangia fuscopurpurea* and *Urospora penicilliformis* are particularly common in winter and spring in Oregon, growing on established plants and animals or bare space (Lubchenco and Cubit 1980; Cubit 1984). Related plants, including some brown algae, go through similar cycles in the northeastern United States (Lubchenco and Cubit 1980), and in southeastern Australia (Underwood and Jernakoff 1984). In both areas in the United States, the winter algal blooms appear related to more favorable abiotic conditions for the algae which allow their growth to exceed the ability of grazers to remove them (Lubchenco and Cubit 1980; Castenholz 1981; Cubit 1984). Similarly, Underwood and Jernakoff (1984) found that a reduction in grazing further increased algal cover in winter. This temporal escape from grazing by growth is analogous to the spatial escape suggested for algae in the low intertidal zone (Underwood and Jernakoff 1981; Foster 1982).

As demonstrated by Gunnill (1980a,b), some of the seasonal variation in abundance is a consequence of seasonal variation in reproduction. However, recruitment is not necessarily correlated with peaks in reproduction. For example, *Iridaea* sp. at a site near Monterey recruited in high densities in quadrats cleared in fall and spring, while spore production was highest in

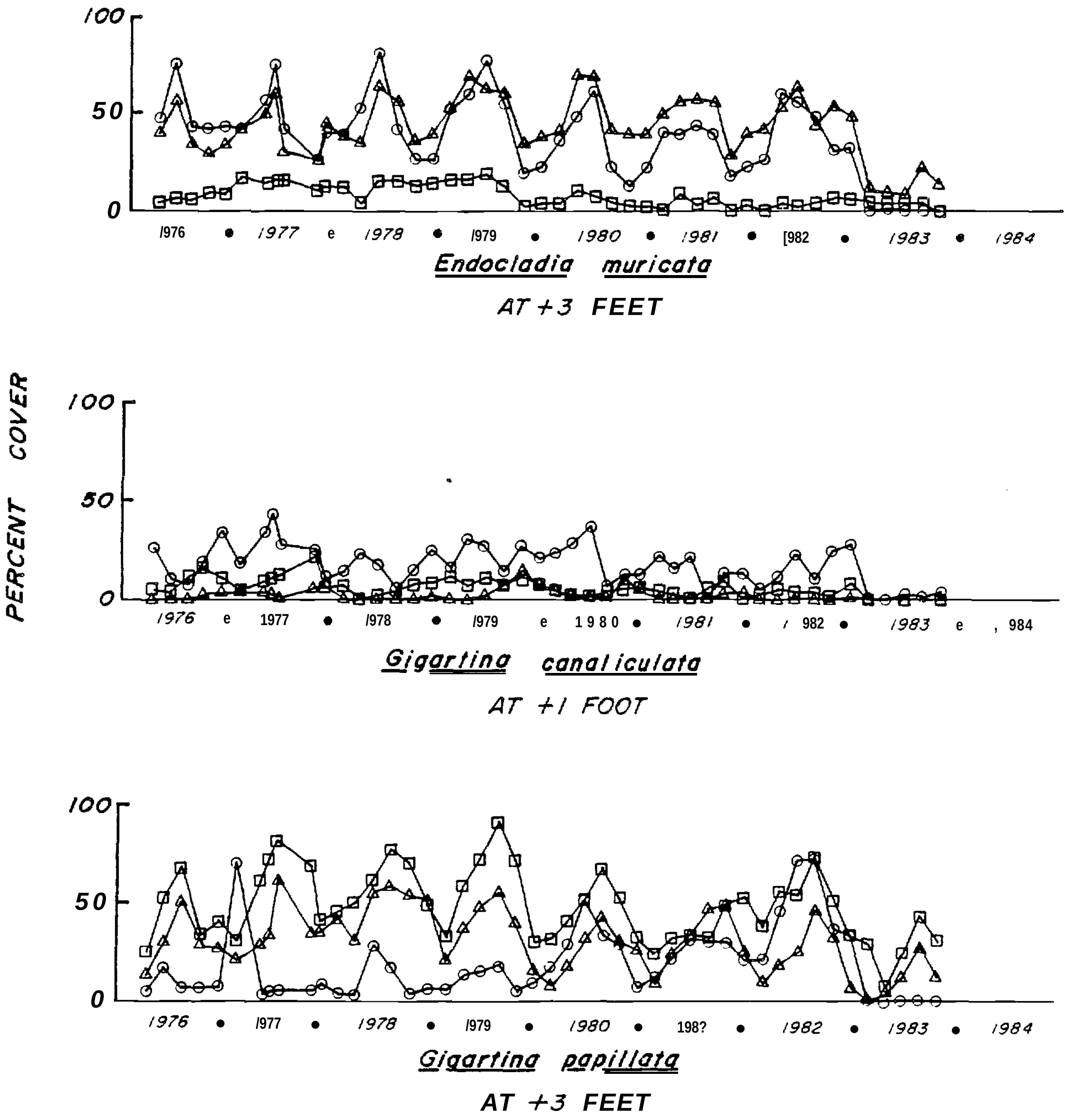

Figure 2. Year-to-year variation in three perennial algae near San Luis Obispo, CA (from PG&E 1984). Data are mean results from three (triangle, circle, square) fixed 0.25-m^2 quadrats at one site. Quadrats were sampled by noting cover under 60 randomly placed points (metal rod).

late summer and fall (Foster 1982). As indicated in Table 3, of those algae in the northeastern Pacific for which there are data on reproduction, most have a seasonal reproductive period or are continually reproductive but show seasonal reproductive peaks. Peak reproductive periods occur at various times for various species, but reproduction seems to be most common in fall, and to a lesser extent in summer and winter. However, there is little information available that relates reproduction to adult abundance patterns (but see Gunnill 1980a,b; Foster 1982). This is not a simple task because the presence of reproductive structures does not necessarily mean spores are being released. Moreover, as suggested by Gunnill (1980a), variation in adult abundance results from acomplex interactionof reproduction, avail ability of space for recruitment, and proper environmental conditions for growth. A demographic approach to seasonality in perennial intertidal algae is clearly necessary to unravel this complexity. In contrast to most animals, perennial algae appear to have very reduced planktonic stages (Dayton 1973; Sousa 1984) and thus a more complete understanding of their population dynamics may be easier to achieve.

2. Between Years

Most of the difficulties mentioned above in assessing seasonal patterns are even more applicable to between-year patterns. Long term temporal changes associated with various kinds of pollution (e.g., Widdowson 1971; Harris 1983; Section V) and the introduction of exotic species (DeWreede 1983) have been documented. However, the overall impression from natural history observations is a lack of long term temporal change. This conclusion is supported by the 1976-1983 time series near San Luis Obispo (Figure 2). The declines in the abundance of most species in 1983 was associated with the extreme 1982-83 winter storms. Gunnill (1980a,b) found considerable year-to-year variation in recruitment, superimposed on seasonal trends, for most species he studied in southern California. This variation in recruitment was often site specfic, as was the variation in cover at the sites near San Luis Obispo (PG&E 1984). Gunnill (1985) also found that mortality of low intertidal kelps increased at a southern California site during the recent “El Nine” warm water period.

When adequate sampling methods are used over proper periods of time, temporal variation in intertidal algal abundance is clearly evident (PG&E 1984). However, it is generally more subtle than changes in space (e.g., zonation), and we have only begun to sort out this variation and the factors responsible for it.

Table 3. Time of Spore or Gamete Production For Algal Species in the Northeastern Pacific.

Species	Time of Reproduction	Reference
RED ALGAE		
Gigartina canaliculata	All year with summer-fall peak	Abbott 1980
Gigartina leptorhynchos	All year with summer-fall peak	Abbott 1980
Gigartina papillata	All year with winter peak	Northcraft 1948
Iridaea cordata	All year with summer-fall peak	Hansen and Doyle 1976
Iridaea flaccida	All year with winter peak All year with summer fall peak	Northcraft 1948 Foster 1982
Rhodoglossum affine	All year with winter peak	Northcraft 1948
Rhodomela larix	All year with spring-summer peak	DeWreede 1983
BROWN ALGAE		
Cystoseira osmundacea	Fall-winter but variable	Gunnill 1980a
Eisenia arborea	Late fall-spring	Gunnill 1980a
Egregia laevigata	Late fall-spring	Black 1974 Gunnill 1980a
Halidrys dioica	Spring-summer	Gunnill 1980a
Hedophyllum sessile	Early winter	Widdowson 1965
Pelvetia fastigiata	Winter-spring	Gunnill 1980b
Postelsia palmaeformis	Spring-fall	Dayton 1973 Paine 1979
Sargassum muticum	Late spring-early summer	Gunnill 1980a
GREEN ALGAE		
Codium fragile	Winter-spring	Gunnill 1980a

III. ANIMALS

This section is organized in a manner similar to Section II. We will first review overall latitudinal and microhabitat distributional patterns, and how they vary (vertical zonation was discussed in the Introduction); then we will treat current knowledge of both within-year and between-year variation of these patterns. Our concern is mainly with macroscopic sessile, sedentary or slow-moving animals that can be noted easily and studied during low tides, primarily because these are the animals most commonly studied. There have been virtually no studies of microscopic organisms in the rocky intertidal, even though such organisms must be abundant and important in the system. Indeed, most marine macroscopic animals pass through a juvenile stage that places them within the meiofauna, and their survival there is crucial if they are to appear as larger adults (Thorson 1966; Highsmith 1982; Watzin 1983). Moreover, we will not treat “visitors” to the intertidal, such as birds and mammals during low tides, and fishes during high tides, even though predation and other forms of disturbance by these animals may be of paramount importance to the more permanent residents (e.g., Boal 1980: Castilla 1981; Frank 1982; Moreno et al.’ 1984; Warheit et al. 1984).

A. Spatial Variation

1. Geographic Distribution

The coastline from British Columbia to Baja California includes three of the four major faunal zones: cold-temperate, warm-temperate, and tropical. Several faunal provinces have been suggested in this area, the precise number depending upon the investigator. The boundaries between the provinces are based upon distributional patterns of several major taxonomic groups, and their precise locations are still a matter of debate and research. Over a dozen different schemes for dividing the west coast of North America into faunal provinces have been proposed over the past 120 years and the scheme one employs is mostly a matter of personal choice. Hall (1964), Valentine (1966), and Briggs (1974) each reviewed previous schemes of faunal provinces and each proposed their own. Recognizing that there are points of contention in all biogeographic schemes, the one that we use in this review (Figure 3) is based on that of Briggs (1974). Under this scheme, the coast between Alaska and Baja California includes three zoogeographic provinces which reflect the three major faunal zones. The Oregonian Province extends from Dixon Entrance in southeast Alaska to Point Conception in California. The San Diego Province extends south from Point Conception to Magdalena Bay on the Pacific side of the Baja Peninsula. The tip of the Baja Peninsula south of Magdalena Bay is a spatially isolated portion of the Mexican province, which extends south to Tangola-Tangola Bay, southern Mexico.

Generally, provincial boundaries are established by examining the distributions of specific animal groups. Echinoderms, nemerteans, ascidians, hydroids, bryozoans, fishes, and molluscs have all been used as the basis for establishing biogeographic regions. Areas that include the termini of many species ranges are considered as faunal boundaries. Areas where there is a high degree of endemism, that is, areas characterized by species which occur only in that area and nowhere else, are considered faunal provinces. The precise locations of provincial boundaries remain topics of debate and research because it is difficult to establish objective and non-arbitrary criteria for defining them. How much endemism is required for an area to qualify as a province, or how many range termini must occur in a region for it to be considered a boundary?

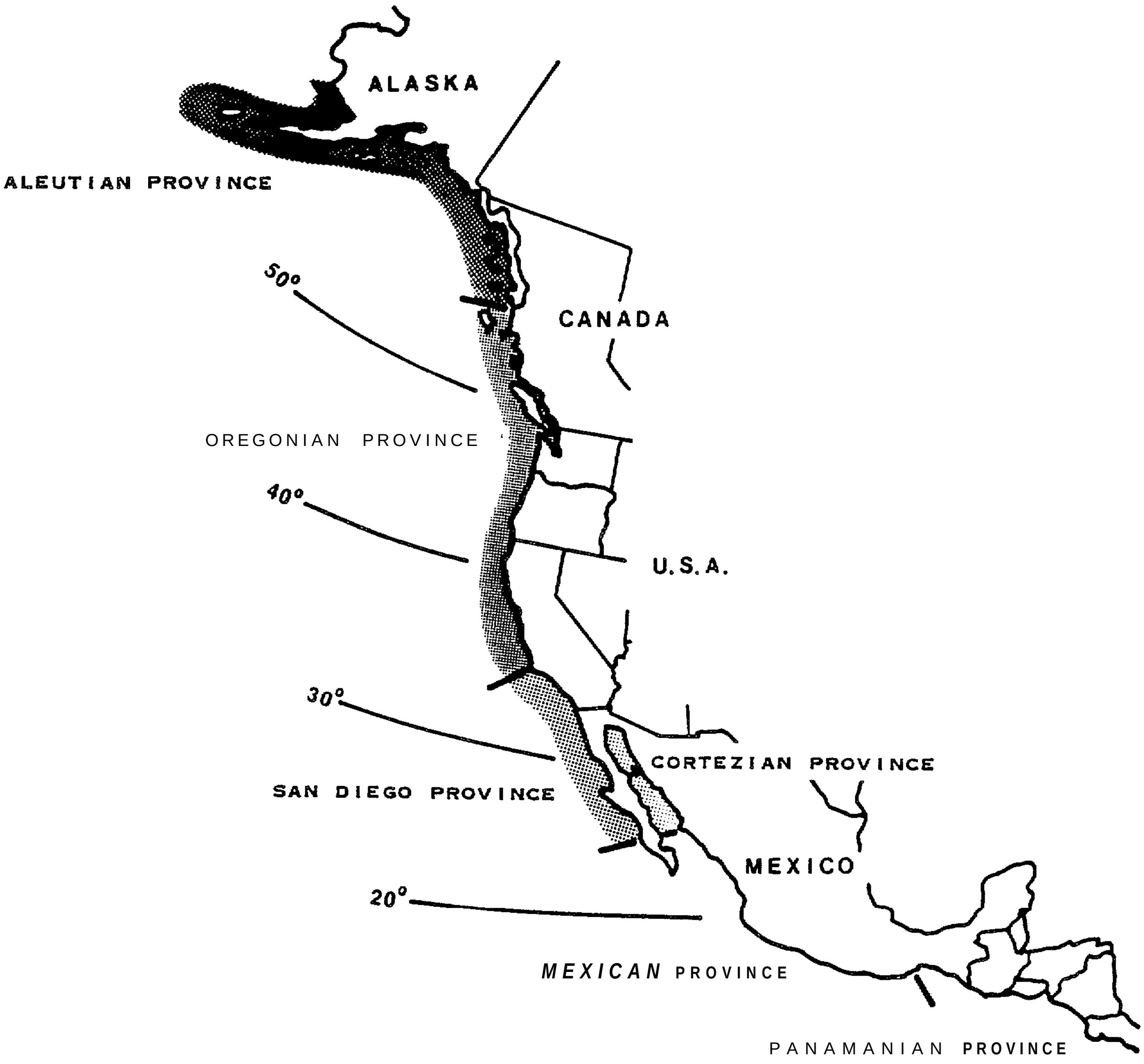

Figure 3. Zoogeographical provinces of the Pacific coast of North America (modified from Briggs 1974).

Valentine (1966), Hayden and Dolan (1976), and Seapy and Littler (1980) have utilized computer assisted techniques such as cluster analysis to provide more objective criteria in describing faunal provinces. It is encouraging that, in general, their proposed biogeographic schemes agree with those of previous workers.

Species populations within faunal provinces are not uniformly distributed but often exhibit large-scale spatial variation. Seapy and Littler (1980) suggested that due to current flow patterns and eddies, some islands in the San Diego Province (which they called the California Province) are populated with animals characteristic of the Oregonian Province while others are populated by species characteristic of the San Diego Province. Kanter (1980) found the species composition of mussel communities was highly variable throughout the Southern California Bight, and that patterns of similarity among mussel communities at different geographical locations were related to patterns of planktonic larval dispersal by prevailing currents.

What are the underlying factors responsible for biogeographic patterns? Temperature is the most often cited causal agent (Hutchins 1947, for example), but a direct correlation between faunal distributions and temperature has not yet been shown. Valentine (1966) attributed this difficulty to the fact that no single criterion for a "temperature factor" can be found, and concluded that overall, provincial and sub-provincial patterns are controlled by thermal regimes but not everywhere by the same thermal attribute. Fritchman (1962), summarizing his extensive study of reproductive cycles of limpets in central California, concluded that the ranges of the limpets studied are determined by failure of reproduction at unsuitable temperatures, and these temperatures are different for different species. Death of adults is probably not involved. Similarly, Hall (1964) suggested that the number of consecutive days or months that shallow sea temperature is appropriate for reproduction and early growth may be the critical factor limiting molluscan distributions. Hayden and Dolan (1976) defined marine climate boundaries based on the distribution of water masses and current flow within the masses which integrates temperature, salinity, and large-scale advection of waters, and found that provincial boundaries agreed well with the distribution of these marine climates. Mokyevsky (1960) suggested that latitudinal variation in species distributions was related not only to temperature but also to moistening of intertidal organisms, which is influenced by tidal range, surf conditions, and seasonal and sporadic changes in sea level. Wethey (1985) argues that the geographic distribution of mid and low intertidal species that are large, long-lived and slow to reproduce is related to catastrophic mortalities caused by sea ice.

The provincial boundaries shown in Figure 3 coincide with positions of changes in the flow of major current systems. The northern boundary of the Oregonian Province at Dixon Entrance coincides with a transitional area where the eastward-flowing West Wind Drift splits into a northward-flowing current and the south-flowing California Current (Briggs 1974). The boundary between the Oregonian and San Diego Provinces at Point Conception is well-defined and coincides with the departure of the California Current from the coastline. The California Current continues its southerly flow while the coastline veers eastward south of Point Conception. The southern California coastline and inner Southern California Islands are bathed by the warm, northwesterly-flowing Southern California Eddy (Seapy and Littler 1980). Point Conception thus represents a point of abrupt change in water temperature. The "temperate/ tropical boundary between the San Diego and Mexican Provinces probably arises from the declining influence of the California Current as it turns westward away from the coastline just south of the boundary. Some workers have suggested the presence of a distribution boundary at Monterey Bay, central California (Hall 1964; Valentine 1966; Hayden and DoIan 1976) but Hartman and Zahary (1983) found no evidence supporting this view. It may be, as we also suggest for algae (Section II), that such a boundary is an artifact of the intense sampling in this region.

The coastline from Alaska to southern California is thus inhabited by species which have arctic, cold- and warm-temperate, and tropical affinities. Although each province has characteristic assemblages of species, provincial boundaries are not distinct and considerable species overlap occurs, even across such well-defined boundaries as Point Conception. Also, the degree of overlap will change with time. Many species of warm-water fishes are known to find their way as far north as Monterey Bay during periods of extreme warm water, such as the 1982-1983 El Nine. If such anomalies are sufficiently long-lasting, overlap will also show up in the invertebrate fauna as well.

To our knowledge, the extent to which latitudinal variation in the distribution of intertidal organisms contributes to variation in other organisms has not been examined. Several species which are potentially important space occupiers in rocky intertidal communities have distributional boundaries within the geographic area considered in this review (Table 4). The polychaete *Phragmatopoma californica* inhibits both anemones (*Anthopleura elegantissima*) and macroalgae in the low intertidal zone in southern California (Taylor and Littler 1982). Likewise, *Tetraclita rubescens* can be abundant in the mussel zone and may influence associated species. *Chthamalus fissus* is ecologically very similar to C. *dalli* and it is unlikely that its absence north of San Francisco would result in differences in other species north and south of its distributional boundary.

2. Vertical Zonation

In the Introduction we briefly described the patterns of vertical zonation that have been found on the west coast of North America. Here we discuss mechanisms which have been found to contribute to these patterns in animal distribution.

a. Causes of Zonation

For sessile animals, Connell (1972) suggested the generalization that upper limits tend to be set by physiological tolerance to physical parameters such as desiccation, temperature, and salinity, and lower limits tend to be set by biological interactions such as competition and predation. In addition, the vertical distribution of motile animals may be regulated by behavioral mechanisms, which will be covered later in this section.

The most commonly reported factor responsible for setting the upper limits of intertidal animals is desiccation (Broekhuysen 1940; Shotwell 1950; Connell 1961a,b; Kensler 1967; Foster 1971a,b; Wolcott 1973; Dixon 1978; Peterson 1979). This is usually based on the correlation between the ability of an organism to withstand desiccation stress (often determined in the laboratory) and the position of its upper limit in the intertidal zone, but there are obvious problems with assuming cause and effect from such correlation. Wolcott (1973) provided more rigorous criteria for accepting the hypothesis that desiccation was responsible for the upper limit of intertidal limpets, and found that desiccation was responsible for the upper limits of limpets in Zone 1 but not

Table 4. Latitudinal Distribution of Eight Species Which Can Be Important Occupiers of Primary Space in Rocky Intertidal Communities. Distributional data are from Morris et al. 1980.

Species	Northern Boundary	Southern Boundary
Anthopleura elegantissima	Alaska	Baja California
Phragmatopoma californica	Central California	Ensenada (Baja California)
Balanus glandula	Aleutian Islands	Bahia de San Quintin (Baja California)
Chthamalus dalli	Alaska	San Diego, California
Chthamalus fissus	San Francisco	Baja California
Semibalanus cariosus	Bering Sea	Morro Bay, California
Tetraclita rubescens	San Francisco	Cabo San Lucas (Baja California)
Pollicipes polymerus	British Columbia	Punta Abreojos (Baja California)

in Zone 2, where behavioral adaptations prevent upward migration of limpets into potentially lethal environmental conditions. Compelling evidence for the role of desiccation in setting the upper limits of distribution of sessile organisms comes from chance observations of mass mortality at the upper limit of distribution under unusually dry conditions in the field (Connell 1961a; Frank 1965; Foster 1971b; Seapy and Littler 1982).

Other factors have been implicated in setting upper limits to species distributions. An animal's upper limit of distribution may be set by its tolerance to thermal stress independent of desiccation stress, though this has not been frequently reported (Connell 1961a,b; Foster 1969, 1971a). The vertical distribution of adults may also redetermined by patterns of larval recruitment. Denley and Underwood (1979) studied the zonation patterns in two barnacle species in Australia, and found no settlement of cyprids above the zone of adults. Grossberg (1982) found that the vertical distribution of the late planktonic stages of two barnacle species in central California, *Balanus glandula* and *B. crenatus*, corresponded almost exactly with the vertical distribution of adults on the shore. Similarly, Strathmann and Branscomb (1979) found that although the upper limit for adult *Semibalanus cariosus* is determined by mortality of juveniles from drying or high temperature, and occasionally large numbers of cyprids settle too high, most of the time the cyprids successfully use cues to avoid settling above the zone in which they can survive. Underwood (1972) rejected the idea that physical factors set the upper limit of distribution of four species of trochid gastropod because in the laboratory they were able to withstand far longer periods of emersion than they experienced in their natural habitat on British shores. He suggested that food availability may set the upper limit to their distribution. Salinity may potentially limit the upper distribution of intertidal invertebrates, but studies have generally shown that it is unimportant (Broekhuysen 1940; Bock and Johnson 1967; Foster 1971b; Wolcott 1973) . In Greenland, however, where seasonal ice formation and subsequent icemelt runoff are dominant physical attributes of intertidal existence, the vertical distribution of *Semibalanus balanoides* is determined by the sensitivity of settling larvae to the salinity of the icemelt (Petersen 1962). Luckens (1970) observed extensive mortality in New Zealand barnacles when heavy rain coincided with low tides. Frank (1965) found increased mortality in a population of *Colisella digitalis* in Coos Bay, Oregon, during two winter periods with exceptionally severe frosts.

Finally, biological factors cannot be ruled out as determinants of upper distributional limits. Cheat (1977) experimentally demonstrated that interspecific competition between *Collisella digitalis* and C. *paradigitalis* confined the latter species to lower intertidal levels. Dixon (1978) reported that the upper limit of one of four species of intertidal limpets in southern California was determined by exploitative competition for food with species higher on the shore.

The idea that lower limits of distribution are set by biological interactions first gained widespread exposure by the now classic work of Connell (1961a). In Scotland, the barnacle *Chthamalus stellatus* occurs higher on the shore than *Semibalanus balanoides*. Connell (1961a) found that when the two species came into contact, S. *balanoides* grew faster than its higher intertidal counterpart and killed them by lateral crushing, smothering, or undercutting. Experimental removal ofS. *balanoides* resulted in lowering of the lower distributional limit of *C. stellatus*, providing strong support for the idea that competition with S. *balanoides* set the lower distributional limit of C. *stellatus*. More recent examples of competitive interactions setting lower limits of animal distribution include studies by Menge (1976) and Peterson (1979).

Predation has also been shown to limit the lower distribution of intertidal animals. Perhaps the best known example of this phenomenon is the work of Paine on the outer coast of Washington state. By experimentally removing the predatory sea star *Pisaster ochraceus* he showed that predation by sea stars upon the mussel *Mytilus californianus* prevented mussels from occupying lower reaches of the intertidal zone (Paine 1966, 1974). Working in the same area, Connell (1970) also showed the importance of predation in setting lower distributional limits of barnacles. On the coast of Washington state, *Balanus glandula* occurs as a distinct narrow horizontal band. Cyprids settle in a wider band than the adults but those in lower areas are consumed by predators (Connell 1970; Dayton 1971; Strathmann and Branscomb 1979). Predation has also been shown to set the lower distributional limits of other intertidal organisms by Menge (1976) and Fawcett (1984).

The vertical distribution of motile invertebrates may be determined by the same kinds of factors that regulate the distribution of sessile species (Branch and Branch 1981; Creese 1982). In addition, behavioral responses of motile invertebrates can prevent them from encountering physiological stressful conditions above their normal range and predators and competitors below. Frank (1965) reported that the vertical distribution of *Collisella digitalis* in Coos Bay, Oregon, was determined behaviorally, and that movement patterns were related to moisture conditions. Wolcott (1973) found that although desiccation stress appeared to set the upper limit of vertical distribution for limpets in the high intertidal, limpets from lower on the shore possessed behavioral adaptations which prevented upward migration into potentially lethal microhabitats. At Bodega Head, central California, the ability of *Littorina keenae* and *L. scutulata/plena (see* Mastro et al. 1982 for discussion of the taxonomic distinctions between these two sibling species) to withstand desiccation, freshwater, and temperature was correlated with their respective tidal heights. Their upper and lower limits, however, are set by positive and negative geotaxic responses which can be reversed in responses to cues from the habitat (Bock and Johnson 1967). Haven (1971) indicated that active behavioral choice was the proximate cause of observed distributional patterns in *Collisella scabra* and C. *digitalis* in Pacific Grove, central California. Mitchell (1980) could find no correlation between tolerance to thermal stress, continuous submergence, or rate of water loss and tidal height in six species of New Zealand gastropod, and suggested that behavioral selection for distinct microhabitats explained the vertical separation of these six species. Defensive responses of marine gastropod to sea star predators are well known, and it is possible that they may explain the vertical distribution for some intertidal species. For example, at Cabrillo Point, central California, the limpets *Notoacaea scutum* and *Collisella limatula* move upward in the presence of the predator, *Pisaster ochraceus*, that occurs lower in the intertidal zone (Phillips 1976). Fawcett (1984) found that the lower limit of the distribution of *Tegula funebralis* on the shore is due to the snails' defense behavior. Moreover, behavioral differences in snails in northern versus southern California explained a latitudinal difference in the lower limits in this species' distribution. Thus, behavioral responses elicited by predators, rather than predation per se, 'can control the lower limit of some gastropod' distribution.

b. Modifications of Vertical Zones

It has long been recognized that zonational patterns are often modified by a variety of factors, the most important of which is exposure to the impact of breaking waves. This factor has been considered by several investigators

(Lewis 1964, 1968; Connell 1972; Southward 1958; Seapy and Littler 1978; Tsuchiya 1979; and others), and the central idea is that increased frequency of wave action, increased height of the waves, and raising of the level reached by spray are accompanied by raised boundaries of a majority of littoral species (Lewis 1964, Figure 53; Ricketts and Calvin 1968, Figure 4). Because upper shore species respond more to upward extension of the damp zone than lower shore species, the intertidal zones or belts are often differentially broadened (Lewis 1968). This has been extensively documented by Lewis (1964, 1968) for European shores and more recently by Tsuchiya (1979) in Mutsu Bay, Japan. The latter investigator found that the upper limits of the three major zones at a protected site were depressed below those at a nearby exposed site.

Topography and substratum can also modify patterns of vertical zonation. Topography can reduce the impact of breaking waves, resulting in the same effects mentioned above. Gently sloping benches may drain more slowly, resulting in extension of the upper boundaries of lower intertidal forms. Low intertidal/ shallow subtidal forms can inhabit higher level tidepools formed by depressions in the substratum. For example, Menge (1976) found that crevices extended the upper limit of mussels to higher than usual levels. Seapy and Littler (1978) compared patterns of vertical zonation at two adjacent intertidal sites in central California differing in the degree of exposure, slope of the shoreline, and type of substrate. The sea stack site was directly exposed to the prevailing seas and had a slope of 22.4 degrees. Zonation patterns of plants and animals were vertically distinct with little or no horizontal variation. From high to low tide levels, the zones were: *Balanus/ Chthamalus; Mytilus/Pollicipes; Endocladia*; and various algae (Table 1). The adjacent boulder field was protected from the sea by offshore rocks and had a slope of less than 4.4 degrees. At this site, the zones were vertically indistinct and were the product of tidal height and horizontal beach slope and breadth. Going horizontally from the shore to sea, the "zones" were: *Hesperophycus/Endocladia* and *Chthamalus; Pelvetia/Endocladia* and *Chthamalus*; and *Endocladia/Gigartina papillata*.

The presence of sand in rocky intertidal areas can modify vertical zonation. Frank (1965) found that the lower limit of limpets was determined by sand movement at a site in Oregon. The lower boundary of mussels and barnacles in New Hampshire was associated with the highest summer level of sand burial (Daly and Mathieson 1977). Cimberg (1975) found that sand burial set the lower limit of distribution of mussels in northern California, and Littler et al. (1983) found that on Santa Cruz Island in southern California, the lower limits of mussels, black abalones, and owl limpets (*Lottia gigantea*) were determined by the physical smothering action of sand, rather than by the kinds of biological factors documented for other rocky intertidal habitats. Finally, aspect, or the degree of insolation, can influence patterns of vertical zonation; lower shore species may be uplifted on shaded surfaces (Lewis 1964).

3. Horizontal Zonation

In sharp contrast to the voluminous literature on vertical zonation of rocky shores, there is very little published information on horizontal zonation patterns on rocky shores except for descriptions of exposed versus sheltered areas (e.g., Ricketts and Calvin 1968). This is unfortunate because shores that have horizontal gradients are common and because understanding mechanisms leading to horizontal zonation may yield new insights into mechanisms which regulate species distributions in marine systems in general.

Distinct zonation patterns have been found on horizontal shores but they were unrelated to vertical height. Rather. boundaries between assemblages were correlated with horizontal distance along the bench. Factors associated with horizontal distance included wave exposure (Marsh and Hodgkin 1962) and bench topography (Lebednick et al. 1971; O'Clair and Chew 1971).

4. Variation Within Zones

We have organized this section by mechanisms responsible for observed patterns of within-zone spatial variation, but recognize that such organization is arbitrary and artificial because patterns in nature are hardly ever attributable to a single factor. Indeed, in almost every study of within-zone vari ation that we reviewed, patterns were due to several factors interacting with one another in often complex ways. Nevertheless, to simplify the presentation of such a diverse topic we divide this section into four types of factors which can result in within-zone spatial variation: 1) biological interactions; 2) wave exposure; 3) disturbance; and 4) microhabitat variation. Clearly there is overlap among these categories (waveshock is a form of disturbance) but they do provide a workable framework for discussion. For the remainder of this section the phrase "spatial variation" refers to spatial variation within intertidal zones.

a. Biological Interactions

We previously discussed the degree to which predation and competition contributed to vertical zonation in rocky intertidal communities and concluded that both types of interactions were important. They also play an important role in creating spatial variation within intertidal zones, either by themselves or together, and are often modified by or act in concert with numerous other factors.

Menge (1983) has made a case for the overriding importance of predation in structuring rocky intertidal communities in New England, and argues that different levels of diversity observed within and among communities structured by predation and biotic disturbances represent equilibria determined by factors which enhance predation intensity versus those which inhibit it. In southeast Australia, predation was responsible for local reduction in densities of the limpet *Patelloida latistrigata* in areas of otherwise high densities (Creese 1982). Frank (1982) found that five species of limpets at Cape Arago, Oregon, occupied distinct microhabitats but at low tide all species were commonly seen on vertical surfaces, though usually not near where vertical and horizontal surfaces met. He suggested that this was due to predation on these limpets by the Black oystercatcher (*Haematopus bachmani*), which can only feed effectively on horizontal surfaces and low ledges. Mercurio et al . (1985) found that selection by visual predators (fish and birds) can maintain the spatial separation of two limpet species, with one found on mussels and the other on barnacles.

Both intra- and interspecific competition have been shown to cause variation in spatial distribution of intertidal animals. Barnes and Powell (1950) reported that intense crowding of barnacles (*Balanus crenatus* and *Semibalanus balanoides*) on rocky shores of the Firth of Clyde, Scotland, lead to the formation of hummocks in the barnacle cover. These hummocks were torn loose by wave action within the first year of settlement. Menge (1976) and Grant (1977) found that bare patches in the *Semibalanus balanoides*-dominated high intertidal zone at a site in New England were usually due to similar intraspecific competition for space among barnacles. Fucoids were generally absent from exposed sites, possibly due to the competitive exclusion by mussels (Menge 1976). The mosaic of patches of S. *balanoides*, *M. edulis*, and *Fucus vesiculosis* which characterize the transitional region between mid and high intertidal zones on rocky headlands in Maine, are partially due to the patchy distribution of overgrowth leading to density-dependent mortality (Grant 1977). Haven (1971) found that on exposed granite shores of Pacific Grove, California, the limpet C. *scabra* occurs on horizontal surfaces and vertical surfaces, while *C. digitalis* is largely restricted to vertical surfaces and overhangs. Where both species co-occur on vertical surfaces, *C. digitalis* is higher than *C. scabra*, and individuals of *C. scabra* are smaller than their conspecifics on horizontal surfaces. He suggested that interspecific competition may partly explain these differences in microhabitat distribution.

Species that provide shelter for other species create small scale patchiness within intertidal zones. Glynn (1965) found that 93 different species were associated with clumps of the red alga *Endocladia muricata*, and Hill (1980) and Gunnill (1983) found a diverse and abundant fauna associated with the brown alga *Pelvetia fastigiata* in southern California. Mussel beds provide environments which trap sediment, detritus, and debris. These microhabitats provide food and shelter for a wide variety of species which form the 'mussel community' (Reish 1964; Suchanek 1979; Kanter 1980).

Spatial variation can also be due to the effect of biological characteristics of the substratum on patterns of larval recruitment. On rocky shores of southeast Australia, areas exposed to intermediate wave exposure have a mix of patches dominated either by barnacles or grazed bare by limpets. The particular configuration of the patchwork at any particular place or time depended upon the last period of intense recruitment and on the interactions between the adults and recruits (Underwood et al. 1983). Suchanek (1978) found that *Mytilus edulis* larvae could invade and dominate patches of bare space in beds of *M. californianus* on the exposed coast of Washington. Due to selective predation by gastropod, however, *M. edulis* is eventually replaced by *M. californianus*.

b. Wave Exposure

The extent to which rocky shores are exposed to the forces of breaking waves has an overriding influence on the spatial variation of intertidal animals. On Carnac Island in western Australia, Marsh and Hodgkin (1962) found that the richest and most diverse fauna was found in wave-exposed areas. Their transects crossed relatively flat benches, and they found that "transverse" zonation along these transects was related to wave action rather than vertical tidal height. Lewis (1968) reviewed European work related to patterns of spatial variation created by variations in wave exposure, and found that four types of mechanisms were important. 1) The morphology of species characteristic of protected areas cannot withstand the mechanical stress of strong wave exposure. 2) Species characteristic of protected areas out-compete species typically found in exposed habitats. 3) Sheltered sites are subject to levels of siltation which are not tolerable by species in exposed habitats. 4) Species characteristic of exposed sites are excluded from protected sites because their propagules do not reach protected areas in sufficient numbers. Denny et al. (1985) discuss the mechanical limits to the size of organisms on exposed shores, and notes that there are a variety of adaptations to high water motion.

Recent work has shown that one of the more profound ways that wave exposure exerts its influence on community structure is by modifying the degree to which predation versus competition exert their effects. In other words, variation in wave exposure can lead to variation in the relative importance of competition versus predation (Peterson 1979; Menge 1983), which in turn can produce spatial variation. In areas of high exposure to wave shock, the predatory activity of *Thais lapillus* in the mid-intertidal is restricted to crevices. Consequently its prey (mussels and barnacles) are widely distributed in these habitats but are absent from crevices (Menge 1978). In protected areas predation intensity is greater and prey abundance is kept below levels where competition can occur. These areas may have significant amounts of bare space (Menge 1976), or they may be dominated by predation-resistant species such as algae that are unpalatable to herbivores (Lubchenco and Menge 1978). At intermediate sites spatial variation is much greater because both competition and predation interact to form a patchwork of species assemblages (Menge 1976; Lubchenco and Menge 1978). Peterson (1979) also found that competition was the more important factor structuring intertidal animal communities at an exposed site in New Jersey, while predation (especially by crabs) was most important in a nearby, protected site. Rocky shores of southeast Australia exposed to wave shock are dominated by barnacles, apparently because wave-induced water motion inhibits barnacle predation by the whelk *Morula marginalba.* At protected sites adult barnacles are rare due to high predation pressure by whelks but grazing molluscs are abundant. Recruitment into populations of these grazers is apparently high enough to balance predatory mortality (Underwood et al. 1983).

Wave exposure can influence spatial variation in other ways as well. The species composition of mussel communities in southern California depends upon the degree of exposure to wave shock (Harger 1972). In protected areas the bay mussel, *Mytilus edulis* dominates mussel clumps because silt accumulated inside the clumps and smothers *M. californianus*. *M. edulis* avoids this stress by active movement toward the outside of the clumps. In exposed areas *M. californianus* dominates because its growth rate is higher than that of *M. edulis*, which are incorporated into the matrix of the clump and suffocate (Harger 1970a). In areas of intermediate exposure the two species co-occur in varying relative abundances (Harger 1972). In this case, spatial variation in the species composition of mussel communities is primarily a function of wave shock through its influence on siltation and the competitive abilities of the two species involved.

c* Disturbance

Natural disturbance, or any natural event that creates space for colonization, is reviewed in detail in Section IV. Here we will restrict our discussion to a few examples of localized mass mortality that are particularly important to variation within zones. Many of the factors that we have just discussed can be considered disturbances since they cause local removal of organisms. For example, predation caused local extinction in populations of *Patelloida latistrigata* in southeast Australia (Creese 1982), and competition for space caused hummocks to form in the barnacle zone which were then torn loose by wave action (Menge 1976).

According to Dayton (1971), the high degree of spatial variation in the barnacle/mussel assemblage on the coast of Washington state is due to continuous physical and biological disturbance preventing complete monopolization of space by any one species. The disturbances he identified were grazing by limpets, predation by carnivorous gastropod and sea stars, and battering by wave-propelled logs. Paine and Levin (1981) propose a model which describes the composition of mussel communities of the outer coast of Washington as a mosaic of patches of various ages and sizes in various stages of recovery. These patches are created by various forms of disturbance, including battering by logs, mortality due to freezing, and the shearing stress of waves themselves. Other factors, such as the timing and magnitude of disturbances, also contribute to spatial variation within the mussel community. The structure of the mid-intertidal zone of Mehuin, Chile, has also been explained in terms of disturbance regimes (Jara and Moreno 1984).

Disturbances, in the form of limpet grazing, waves, wave-born rocks, and heat stress resulted in highly variable species composition among tidepools within a given tidal height on the outer coast of Washington (Dethier 1984). In protected areas of the Santa Barbara coast, *Mytilus edulis* could potentially dominate all mussel communities. It does not because it suffers high mortality from storm-generated waves. Its congener, *M. californianus*, is more resistant to wave disturbance and enjoys a temporary dominance after storms. During subsequent periods of calm weather cleared areas will here-colonizedbybarnacl es and ultimately *M. edulis* (Harger 1970a,b, 1972). Spatial variation in the species composition of mussel communities in this region is thus the result of storm-mediated mortality of *M. edulis* and subsequent recovery. Other disturbance agents that result in spatial variation in rocky intertidal animal distribution include sand scour (Marsh and Hodgkin 1962), grazing and territorial behavior of limpets (Stimpson 1970), grazing bylittorines (Petraitis 1983), and mechanical stress by harbor seals (Boal 1980).

d. Microhabitat Variation

Substratum heterogeniety (Grant 1977; Petraiti s1983), degree ofinsol ation (Denley and Underwood 1979), water flow (Lewis 1968), and desiccation stress (Kensler 1967; Haven 1971) have all been shown to contribute to microhabitat variation of rocky intertidal invertebrates. Tidepool s contribute to small-scale spatial variation by providing discrete patches in which environmental factors are different from surrounding areas. Dethier (1984) found that tidepools at a given vertical height on the exposed coast of Washington could be dominated by any one of six species, and at no time was more than 20 to 50% of the pools dominated by the same species. As mentioned above, this spatial heterogeniety was due to high frequency of disturbance and slow rates of recovery which prevented any one species from dominating all tidepools at a given level, Animals themselves can modify microenvironmental conditions and thus contribute to small scale spatial variation. By creating a moist microenvironment in the desiccated and thermally stressed upper intertidal levels, the anemone *Anthopleura elegantissima* allows the development of coralline algae and populations of small sand tube worms (*Phragmatopoma californica*) at higher levels than they would normally occur (Taylor and Littler 1982). The positive correlation between densities of the limpet *Patelloida latistrioata* and the barnacle *Tesseropora roses* is at least partially due to protection from desiccation afforded by the barnacles (Creese 1982).

From this discussion it is clear the spatial variation within zones on rocky intertidal shores is an integral part of these communities that cannot be ignored. The underlying mechanisms leading to spatial variation are related to a myriad of both physical and biological factors and their interrelationships. Modification of biological interactions by disturbance has been found to have a profound influence on the distribution and abundance of intertidal organisms. Also important are temporal patterns of recovery from disturbance events.

Because all of these phenomena will directly influence the recovery of rocky intertidal systems from disturbance, we should recognize that recovery will indeed be complex, and that generalizations about it should be made with extreme caution.

B. Temporal Variation

1. Within Years

Daily, tidal, and seasonal changes in climate influence intertidal animals in a variety of ways. Winter storms normally remove old or unstable sessile animals (e.g. , mussels, barnacles, and honeycomb tubeworms; Harger and Landenberger 1971; Grant 1977; Mayer et al. 1981) and many plants with animal associates (e.g., blades of algae and surfgrass with limpets and snails; Black 1976; Gunnill 1983). Such seasonal removal of intertidal organisms provides cleared areas for new recruits and is important in maintaining mosaics of different species in the rocky intertidal (Paine and Levin 1981). However, as pointed out by earlier workers (e.g., Hewatt 1937; MacGinitie 1938; Gislen 1943, 1944; Glynn 1965), seasonal fluctuations are moderate along the west coast of the U.S. and overall winter-summer differences in rocky intertidal communities are not marked. There was little seasonal change in abundances of animals, for example, in a two-year quantitative study along the coast of Santa Cruz and San Mateo counties (Doyle and Pearse 1972; Pearse 1980, Figure 4). In a more detailed quantitative study of a mussel bed community at Santa Cruz, Beauchamp and Gowing (1982) found virtually no difference in animal species diversity or abundance in summer and winter.

Nevertheless, there are marked temporal changes or rhythms in the activities of many or most intertidal animals of central and northern California, as elsewhere (see general reviews in DeCoursey 1976 and Naylor and Hartnoll 1979). In particular, feeding, growth, and reproductive activities of intertidal animals often display marked temporal patterns that are driven by daily, tidal and/or seasonal rhythms. These activity patterns can have major impacts on patterns of distribution and abundance of intertidal animals.

a. Feeding and Growth

Intertidal animal s maybe divided into two general categories with respect to their mode of feeding: (1) sessile or sedentary forms that capture or filter food particles from the water (suspension feeders) and (2) motile forms that move about in search of plant or animal prey. Suspension feeders only feed when they are covered with water so their feeding activity is largely regulated by tidal patterns. Most sessile suspension feeders are stationary as adults, and their feeding activities might seem to have little or no impact on patterns of their distribution. However, because of the tidal rhythm, suspension feeding animals living low in the intertidal can spend more time feeding than those living higher in the intertidal, and differences in feeding times can cause differences in animal sizes. For example, Kopp (1979) found that the different amount of time, available for feeding had a substantial effect on the growth and shape of mussels; those in lower areas had thinner and flatter shells because they were open and feeding for longer periods of time and grew outward more than those that were higher in the intertidal and remained closed most of the time (they grow whether they are open or closed). Similarly, feeding activity and growth form of some species of sea anemones are determined by the tidal rhythm; those living lower in the intertidal feed more and grow to larger

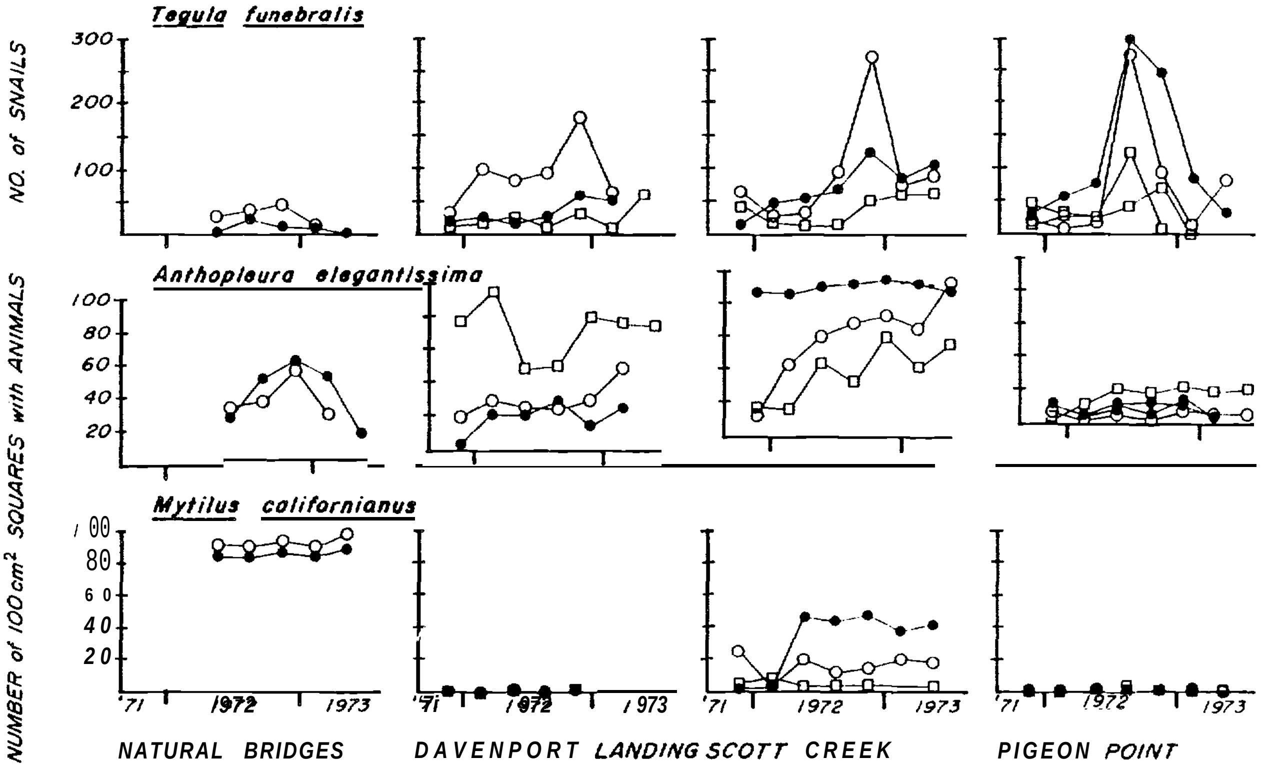

Figure 4. Changes over a 20-month period in abundance of turban snails (*Tegula funebralis*), cloning sea anemones (*Anthopleura elegantissima*), and mussels (*Mytilus californianus*) found in 1-m square quadrats placed in permanently marked positions in the mid zone of rocky intertidal benches at four sites on the Santa Cruz and San Mateo County coast. Abundance of snails estimated by counting total number of individuals in each quadrat; abundance of anemones and mussels estimated by scoring number of 100 cm^2 squares containing one or more animals (total number of squares = 100); each line represents changes in one quadrat. (Unpublished data, J.S. Pearse; collected with assistance from students at the University of California, Santa Cruz, and financial support from California Sea Grant and the Association of Monterey Bay Area Governments.)

individual sizes before dividing than those living higher in the intertidal (Bucklin 1981; Sebens 1983). Even feeding activity and growth of motile forms such as limpets are influenced by tidal rhythms, resulting in distinct distributional patterns of animal sizes (e.g., Sutherland 1970; Phillips 1981).

The activities of most animals that graze microalgae from rocks display a mixed daily/tidal rhythm and actively graze mainly at night during low tides (e.g., crabs: Hiatt 1948; gastropod: Stimpson 1970; Breen 1971, 1972; Abbott et al. 1964, 1968; chitons: Burnett et al. 1975). Presumably this behavior is a response to solar heating and drying, as well as bird predation (Frank 1982), during low tides by day, and perhaps fish predation or the threat of being swept away during high tides (night or day). Such behavior results in a short-term rhythm in the distribution of these animals, as they often rest in cryptic sites some distance from their feeding areas.

The semimonthly, monthly, to semiannual tidal rhythms also modify the foraging areas of motile animals, particularly those that occur in the lower zones. During periods of neap tides, the lower tidal levels are exposed for only short periods, or not at all. This is particularly true in early fall (September) and early spring (March) when few tides extend below the mean lower water level. Grazing snails (especially *Tegula brunnea*), predacious. snails (especially *Nucella emarginata*), and sea stars (*Pisaster ochraceus*) all tend to move higher into the intertidal during neap tide periods (P.K. Dayton, pers. comm.; J.S. Pearse, pers. ohs.). As low spring tides become more extreme in the late fall (December) and late spring (June), these animals are exposed for progressively longer periods of time, and they move down. This sort of movement even occurs during a single spring tide series, and more individuals of mobile animals are seen on the first days of a spring tide series than on later days.

Along the coast of Greenland (Petersen 1962), New England (Menge 1976; Grant 1977), Britain (Lewis 1964), the Antarctic Peninsula (Stockton 1973) and other places where there are freezing water temperatures, activities of many- or most animals are severely curtailed in the winter. Such severe winters do not occur along most of the coast of western North America, but major storms, often with heavy rains, usually occur in the winter months and influence animal activities. For example, Frank (1965) found that the limpet *Collisella digitalis* tends to ascend in the intertidal of Oregon during fall and winter and descend in the spring. Similarly, Phillips (1981) found that the limpet *Notoacmea scutum* moved much more in central California during the summer and fall than in the winter and spring, and the mean vertical position of the animals was 33 cm higher in January, as the winter storms began, than in May. At least part of this activity was related to feeding and algal abundance; growth rate was highest in spring-summer when algal abundance was highest, and movement peaked in late summer as algal abundance decreased. Also on the coast of central California, turban snails (*Tegula funebralis*) *were* much more abundant on flat rock surfaces during the summer and fall than winter and spring (Figure 4); presumably the snails, known to be long-lived (Frank 1975), nestled among cracks and boulders during the winter then emerged to graze rocks after the winter storms subsided. Changes in turban snail densities in the open, however, were the only marked seasonal pattern of animal distribution and abundance noted during the two-year study. This and other studies (e.g., Nybakken 1978; North et al. 1983) suggest that there is little seasonal change in the distributional patterns of most intertidal animals of central California. Even species that do undergo seasonal changes in activity farther north show little or no seasonal change in activity in central California. For example, while Mauzey

(1966) found that individuals of the sea star *Pisaster ochraceus* stop feeding, clump together, and virtually hibernate in midwinter in Puget Sound, Feder (1970) could find no evidence of seasonal differences in feeding or distributional patterns by individuals of this species on the Monterey Peninsula.

b. Reproduction

As in most shallow-water marine communities at temperate latitudes (Giese and Pearse 1974), most species in the rocky intertidal of the west coast of the U.S. have distinct reproductive periods (Hewatt 1938; Houk 1973). In central California, over 50% of the species are full of gametes and inbreeding condition in the spring and summer (Figure 5). A group of species with feeding (planktotrophic) larvae are in breeding condition slightly earlier than most of those without feeding larvae (lecithotropic); presumably feeding larvae of these species need to spend a month or so in the plankton before settling, and the time most suitable for settling and recruitment is about the same for most species, regardless of their mode of development.

The period when the lowest proportion of intertidal animals in central California are in breeding conditions is in the fall (October-November; Figure 5); in contrast to intertidal algae that are commonly reproductive in the fall (Section II). This is the time of lowest productivity and highest sea temperatures (Bolin and Abbott 1962), and it immediately precedes the winter storms, presumably all factors selecting against many kinds of animal recruits, and selecting for algal recruits. Nevertheless, even at this time of year between 30 and 40% of the animal species are in breeding condition, emphasizing the lack of overall seasonality along the coast of central California.

Most species of intertidal invertebrates in central and northern California have pelagic larvae that drift and feed in the plankton for days to months before settling. Because most spawn in the spring and summer (April-August; Figure 5), their larvae would be expected to be present at about the same time. Few studies are available, however, to document the presence of larvae of intertidal species in the plankton. One such study is that of Grossberg (1982) who found 1 arvae of acorn barnacles in the plankton in May. Moreover, these were stratified in the water; those of *Chthamalus* spp. were very near the surface while those of *B. glandula* were slightly deeper, corresponding to" the adult's stratification on the shore.

Although a considerable body of descriptive information has accumulated over the past 25 years on gonadal growth and spawning cycles of intertidal invertebrates of central California, beginning in particular with the work of Giese and his students (Giese 1959), experimental work on factors regulating these cycles remains sparse. Most such work has been done on species of the north Atlantic and has indicated that changes in sea temperature are of prime importance for timing reproductive cycles (Giese and Pearse 1974). However, seasonal temperature changes are not marked on the west coast of the U.S., and there is little evidence that such changes directly influence seasonal reproductive activities of west coast intertidal species. There is evidence that seasonal changes in food supply influence temporal patterns of reproduction. For example, Sutherland (1970) found that individuals of the limpet *Collisella scabra* produce gametes throughout the year when they occur in the low zone at Bodega Bay, but other individuals living only a few meters higher, where algal production is restricted mainly to the spring, produce gametes only in the spring. In addition, recent work has shown that the reproductive cycles of

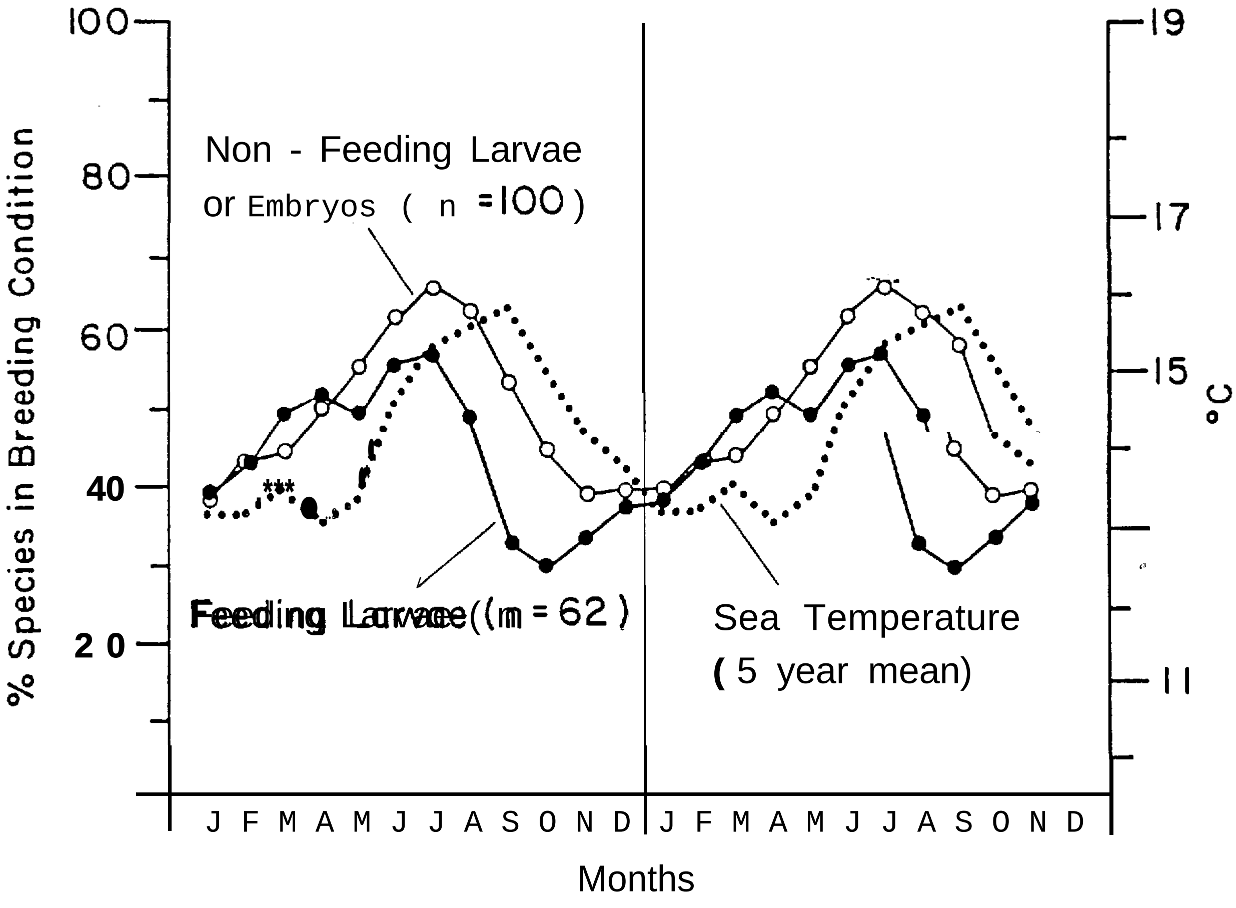

Figure 5. Changes in monthly mean sea water temperature (dotted line) and percentage of intertidal animals on the coast of central California in breeding condition (solid lines) and divided into species with and without planktotropic (feeding) larvae; plotted over a two-year period for clarity; sea temperature records are 5-year means (1979-1982, 1984) taken at Long Marine Laboratory, Santa Cruz; breeding data compiled by J.S. Pearse and S. Finch from Morris, Abbott, and Haderlie (1980).

common west coast intertidal sea stars and sea urchins are under photoperiodic control (Pearse and Eernisse 1982; Pearse et al. in press-a,b).

The environmental factors selecting for discrete reproductive periods, as opposed to environmental cues such as photoperiod that synchronize reproduction, remain particularly elusive, and because they act over long periods of evolutionary time, they cannot be investigated directly or experimentally. The predominance of reproductive activity among north Atlantic species in the summer is assumed to be a response to favorable summer temperature and food conditions for the developing larvae. The predominance of spring and summer reproduction by central California species, however, corresponds to the time of low to rising temperatures rather than the time of supposedly more favorable (higher) temperatures in the fall (Figure 5). Moreover, al though the spring upwelling provides anutrient pulse that initiates the main seasonal phytoplankton bloom, animals that produce non-feeding larvae or only juveniles tend to spawn at the same time as those with planktotrophic larvae. Himmelman (1975) found that substances associated with the spring phytoplankton bloom stimulated several species of chitons to spawn, even though chiton larvae do not feed on phytoplankton. Perhaps the most plausible evolutionary/ecological explanation for the predominance of spring-summer reproduction among intertidal animals of central California is that more space is open and available for settlement after the winter storms, and the generally benign conditions of the summer favor the establishment and growth of juveniles. Paine and Levin (1981) similarly suggest that many common species spawn in the winter because more space is available then for recruitment. In addition, the variable and generally weak current patterns in the summer (Griggs 1974) may tend to maintain larvae near the region of the adult populations that spawned them.

Because there is such variability among the spawning times of different species, the natural history of particular species must be well understood before much can be said about its particular temporal pattern of reproduction. For example, Hines (1978", 1979) found very different spawning times for the three common acorn barnacles of central California, and these corresponded to very different life history patterns suited for different portions of the intertidal. Small gregarious individuals of *Chthamalus fissus* occur in the highest regions of the intertidal where they grow rapidly, reach sexual maturity within three months, and produce a brood of eggs approximately monthly until they are killed by adverse climatic conditions - usually within a few months. In contrast, large, mainly solitary individuals of *Tetraclita squamosa* occur in the lowest regions of the intertidal; they grow slowly, reach sexual maturity in about three years, then produce a few broods of eggs each summer for many years, perhaps decades. Intermediate between these two species is *Balanus glandula* which is physiologically unable to survive in the higher portions of the intertidal where C. *fissus* predominates. However, *B. glandula* is quickly discovered and eaten by predators in the lower intertidal where the thick-shelled individuals of *T. squamosa* survive for so long. Juveniles of *B. glandula* recruit mainly in the spring, grow over the following year then produce several broods; few survive for more than a year.

Even species that seasonally produce large numbers of gametes each year may not show any sort of predictable pattern of recruitment and population turnover. For example, although the purple sea urchin *Strongylocentrotus purpuratus* produces enormous numbers of gametes each winter and early spring (Pearse 1981), the appearance of juveniles in central and northern California, and farther north, is an unusual event. Ebert (1982a) found only one episode of recruitment of *S. purpuratus* in an intertidal area in southern Oregon over a period of nearly 20 years. We also have noted only occasional recruitment of this species in central California. Farther south, in southern California and Baja California, recruitment is a much more predictable event, with numerous recruits being noted nearly every year (Pearse et al. 1970; Ebert 1982b). The reason for this difference in recruitment between the northern and southern portions of the range of *S. purpuratus* is unknown, as is the reason why some years are "good" and others "bad" for recruitment; the differences are perhaps due to regional and year-to-year differences in current patterns related to year-to-year variations in the California Currrent (Chelton et al. 1982). However, some of these trends may be an artifact of looking at only a few sites. Ebert (pers. comm.) recently looked at 25 sites between Baja California and Oregon, and suggests that differences in *S. purpuratus* recruitment between nearby sites may be greater than between latitudes. Other intertidal species also have been noted to recruit more regularly in the southern part of their range (southern and central California) than in more northerly regions (Oregon, Washington), for example, the turban snail *Tegula funebralis* (Frank 1975), and the file limpet *Notoacmea scutum* (Phillips 1981).

2. Between Years

Although tidal and seasonal patterns of change have been detected and studied in a variety of species and processes, as noted above, much less information is available about long-term patterns of change by animal populations in the rocky intertidal. The reason for this lack of information is not obscure: detection and documentation of long-term change usually demands the maintenance of well-designed, long-term monitoring programs. Such programs are rare (e.g., Coe 1956; Jones et al. 1979; North et al. 1983; Hartnoll and Hawkins 1985; Paine et al. 1985). Like those collecting weather data, monitoring programs can continue for years without showing dramatic or clearly delineated patterns of change. Thus, they instill little enthusiasm either from granting agencies or ambitious and creative investigators. Consequently, the literature contains reports of dramatic events, but little on background patterns that continue over most "normal" years. Reports of the impact of "El Nine" provide an example of this non-planned type of investigation. Mass strandings of pelagic crabs on the beaches of central California were reported for the first time in a century after the 1958-59 El Nino (Glynn 1961), but it is not clear whether this was really an unusual event or simply the result of a conscientious observer reporting it. Mass strandings of these crabs have been noted, for example, after the El Nino events of 1973 and 1983 (A. Baldridge, pers. comm.), but no reports have been published of them. Moreover, little or no change has been reported in the animal communities of the rocky intertidal during or following El Nino events, perhaps because careful monitoring programs have not been in place to detect such change (it is also possible that intertidal animals are insensitive to changes resulting from most El Nino conditions).

It is well recognized that winter storms vary in intensity, duration, and impact among different years, and such variation would be expected to cause considerable variation from year to year in the abundance and richness of intertidal life. When severe winter storms are phased with periods of extreme spring tides in December and January, the impact can be particularly dramatic. For example, the severe winter storms of January 1982 led to major rock slides and shore erosion along the Big Sur coast, decimating at least one intertidal community that had been visited repeatedly the previous four years (Pearse 1984). The same storms, however, had little noticeable impact on rocky intertidal communities on the Monterey Peninsula or along the coast of Santa Cruz and southern San Mateo counties (J.S. Pearse, pers. ohs.). Indeed, on-going studies by students of the University of California, Santa Cruz, indicate that the abundance of major species of animals in these communities remained remarkably constant for over a decade, although their abundance varied from area to area (Figure 6).

Long-term studies at Diablo Canyon have shown that sand scouring and boulder movement during winter storms produce barren patches of substrate that are subsequently recolonized by invertebrates and algae, and the extent of change is related to storm intensity (Mayer et al. 1981). Similar effects by irregular seasonal sand movement has been noted at San Nicholas Island (Littler et al. 1983), as well as in New England (Daly and Mathieson 1977). Conversely, North et al. (1983) qualitatively monitored the same area at Diablo Canyon between 1969 and 1982, and did not detect any obvious difference in distributional patterns of the major species present.

The above studies indicate that rocky intertidal communities can remain relatively unchanged for periods of over a decade, even when substantial storms occur. Similarly, distributional patterns of animals in other rocky intertidal areas that have been studied for moderate lengths of time appear to remain relatively unchanged (e.g., Washington State: Connell 1970; Paine 1974, 1976, 1984; Paine and Levin 1981; Isle of Man: Hartnoll and Hawkins 1985). Moreover, activities such as annual rhythms of reproduction, although showing some variation among different years, maintain considerable stability as shown by decade-long records for the chiton *Katharina tunicata* (Giese 1969) and the sea star *Pisaster ochraceus* (Halberg et al. 1969). In terms of recruitment, Caffey (1985) found that recruitment and early mortality of the barnacle *Tesserapora roses,* varied significantly at all spatial and temporal scales examined on Australian shores. Connell (in press) found that there is great variability in larval recruitment from year to year of barnacles, limpets, clams, and sea stars, but particular sites still maintained consistently higher recruitment levels than others, Thus, although still not unequivocally demonstrated, differences among sites may be related directly to differences in recruitment.

However, studies that span times greater than a decade or so indicate that abundances and distributional patterns of animals can change dramatically over time. For example, Hewatt (1935, 1937) and MacGinitie (1938) described extensive mussel beds at Hopkins Marine Station in the mid-1930's; these had nearly disappeared by the late 1960's (D.P. Abbott, pers. comm.; J.S. Pearse, C. Harrold, M.S. Foster, pers. ohs.). Although mussel beds are known to undergo small fluctuations in some other areas, due to storms (Paine and Levin 1981) or perhaps in relation to changes in water temperature (Coe 1956), the dramatic reduction in the mussel bed cover at Hopkins Marine Station almost certainly was due to predation by sea otters. These animals returned to Monterey Bay in the 1960's after being nearly exterminated in the previous century. Changes in the abundance of mussels and other shellfish that are preyed upon by sea otters also have been noted elsewhere along the coast of western North America after sea otters return, as recently summarized by Estes and Van Blaricom (in press) . Dramatic changes in community organization over periods of hundreds to thousands of years related to human activities and sea otters also have been documented for the Aleutian Islands (Simenstad et al. 1978).

Other causes of long-term changes in community organization also are undoubtedly important, although their identification has been difficult. Sergin (1980), for example, suggested that the precession of the earth's orbit causes long-term oscillations of climate and seasonal timing of the tides; these could lead to long-term, cyclic changes in intertidal communities. Moreover, Gray and Christie (1983) showed that cycles of 3-4, 6-7, 10-11, 18-20, and

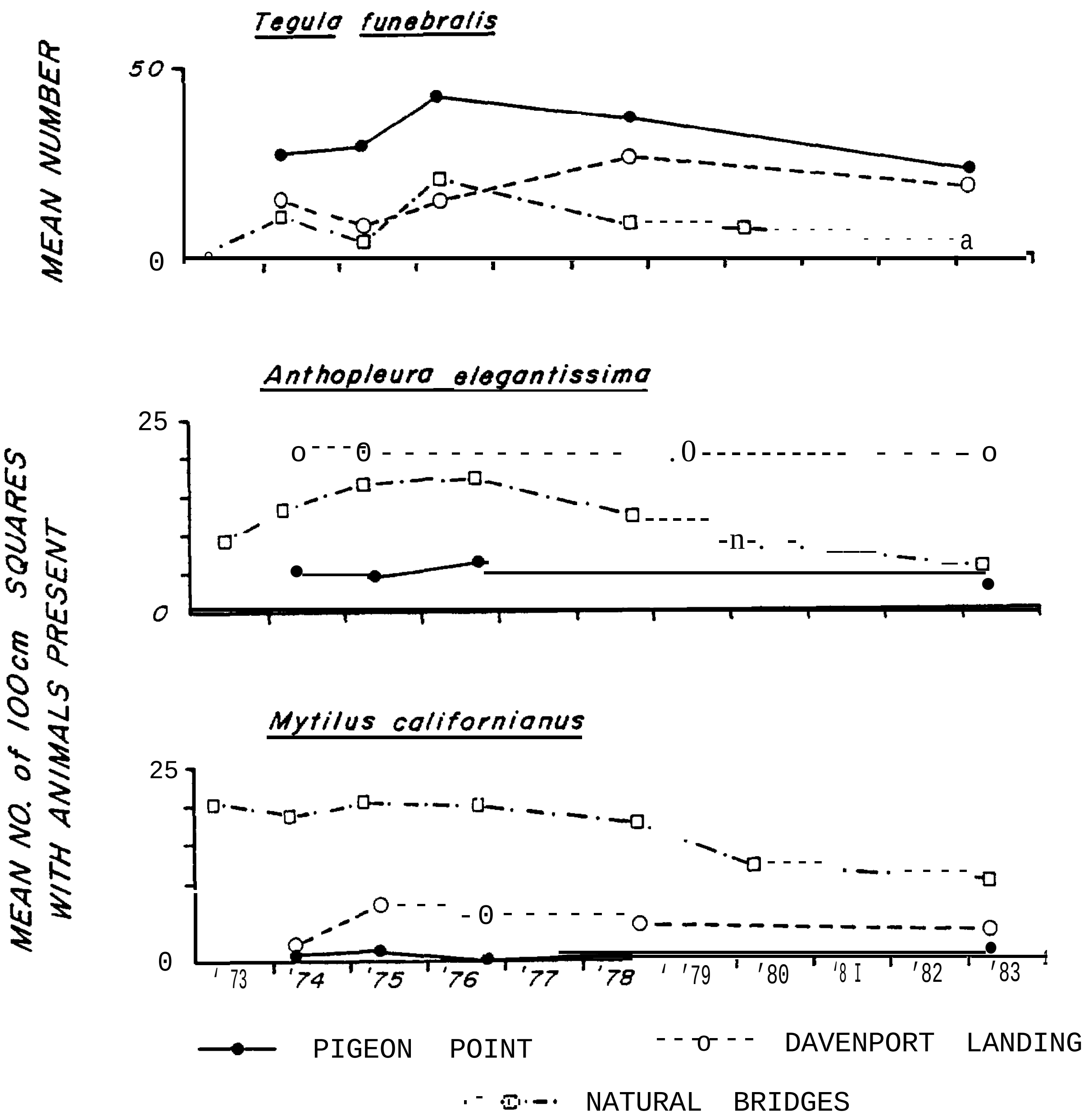

Figure 6. Changes in abundance of turban snails (*Tegula funebralis*), cloning sea anemones (*Anthopleura elegantissima*), and mussels (*Mytilus californianus*) over a ten-year period in the mid zone of three contrasting-intertidal rocky benches on the Santa Cruz and San Mateo County coast. The Natural Bridges site was visually dominated by mussels, that at Davenport Landing by cloning sea anemones, and that at Pigeon Point by the alga *Gigartina papillata*. At each site, permanent areas, 50 x 100 m were sampled with 12 to 30 randomly placed 0.25-m^2 quadrats. The quadrats were divided into twenty-five 100 cm^2 squares and the number of squares occupied by the anemones and mussels were scored; the total number of snails in each quadrat was counted. (Unpublished data, J.S. Pearse; collected with assistance from students at the University of California, Santa Cruz, and financial support from California Sea Grant.)

about 100 years can be detected in hydrographic data, and that many benthic species respond to the long-term cycles. Nevertheless, predicting long-term changes in communities by following these cycles may be an unattainable goal due to the long periods involved; Gray and Christie (1983) present evidence for cycles with periods of up to over 4,000 years.

Non-cyclic events, which by definition are unpredictable, also could lead to dramatic changes in community organization. Examples include: 1) Catastrophic disease that removes important members of intertidal communities, as occurred in the Gulf of California (Dungan et al. 1982). 2) Large-scale variations in the flow of the California Current that cause large-scale variations in the biomass of zooplankton along the coast of western North America (Chelton et al. 1982). 3) Earthquakes and other geological disturbances that dramatically modify the underlying topography, as occurred in Alaska (Haven 1972; Johansen 1972; Lebednik 1973). 4) Catastrophic oil spills that can alter intertidal areas for a decade, as occurred on the southwest coast of Britain after the Torrey Canyon spill (Southward 1979; Section V).

Long-term changes in animal distribution and abundance in the rocky intertidal can thus be expected to result from predictable (cyclic) and unpredictable biotic and abiotic changes. The resulting altered communities may eventually revert to the earlier state of "dynamic equilibrium," as found by Southward (1979) after the Torrey Canyon spill. Hartnoll and Hawkins (1985) present evidence that such an equilibrium exists on the rocky shores of the Isle of Mann, and the abundances and spatial pattern of the major species fluctuate with approximately a seven-year cycle. Simenstad et al. (1978) further proposed that there may be "several stable-state communities," and disturbances can shift communities from one stable-state to another. On the other hand, Connell and Sousa (1983) reviewed the evidence for community stability and persistence and found little support for the idea of natural equilibriums within stable limit cycles, and they found no unequivocal examples of multiple steady-states in unexploited natural populations or communities. Rather, they found that natural populations, including those of the rocky intertidal, show considerably temporal variability within stochastically defined bounds. Long-term monitoring studies, as established at Diablo Canyon in central California (Mayer et al. 1981; North et al. 1983) and on the coast of Britain (Lewis 1977; Jones et al. 1979), appear to be crucial for resolving whether natural equilibriums actually occur or, if not, what the range of temporal variation in intertidal communities is.

IV. EFFECTS OF NATURAL DISTURBANCE

In the previous sections we have reviewed patterns in rocky intertidal communities and the processes that cause these patterns at various spatial and temporal scales. In the few assemblages so far examined, and particularly at the scales of within assemblages and between years, much of the variation in patterns of distribution and abundance appears to result from disturbances that, by definition, remove parts of, or entire assemblages of sessile organisms. This produces space for potential colonists and thus initiates succession (Foster and Sousa, in press; Sousa 1985). Disturbances may not only account for much of the pattern in the rocky intertidal zone (Dayton 1971; Sousa 1979a, 1984, 1985; Paine and Levin 1981) but may also be in part responsible for local differences in diversity (Lubchenco 1978; Sousa 1979b; Section III) and for the presence of at least one annual species (Paine 1979) and various ephemeral species that require newly cleared space for colonization (fugitive species; Sousa 1984, 1985). A greater appreciation of the real and potential effects of disturbance on community structure, combined with a more thorough understanding of the mechanisms that create variability during succession, has, moreover, made questionable many of the traditional paradigms "explaining" community structure (Connell 1972, 1980; Connell and Slatyer 1977; Connell and Sousa 1983).

The relationship between disturbance and patterns in rocky intertidal communities has recently been reviewed by Sousa (1985), and biological disturbance (e. g., removal of algae by grazers) has been discussed in previous sections. We will confine our discussion below to physical disturbance, and to succession after both biological and physical disturbance. Finally, a note of caution about the evidence for successional processes, particularly the relationship of recovery from experimental disturbances vs. natural ones, is warranted. In the majority of successional studies on rocky intertidal shores, sessile organisms have been completely removed from experimental areas. However, as discussed by Foster and Sousa (in press), most natural disturbances result in less than complete removal, particularly of plants. Since what is left behind may regrow and/or affect colonization by other species, subsequent succession and recovery rates may be quite different from those found in total clearings. Moreover, the time of disturbance, its areal extent, position relative to sources of recruits, etc., all may affect succession (Foster and Sousa, in press). With the possible exception of mussel beds (Paine and Levin 1981; Sousa 1984), the importance of these parameters to intertidal succession remains unknown for most assemblages (for review of the relationship between these parameters and succession in other habitats, see Pickett and White 1985).

A. Experimental Disturbance

1. <u>Complete Clearing</u>

Complete removal of organisms from experimental areas has been done to describe succession in particular areas, to investigate factors that may affect succession, and to estimate recover rates. Most intertidal studies (see references in Table 5) have found a successional sequence that begins with ephemeral diatoms, green, and/or blue-green algae. These organisms are commonly replaced by longer-lived, perennial species more characteristic of the assemblage in which the clearings were originally made. This process was traditionally thought to be facilitative; early colonists created microhabitats necessary for the establishment of later species (e.g., Northcraft 1948). However, evidence from both intertidal (Lee 1966; Sousa 1979a, 1980; Foster 1982) and subtidal (Foster 1975; Connell and Slatyer 1977) studies indicates that early

Table 5. Results of Successional Studies in the Northeastern Pacific That Used Total Clearing.

Location	-Assemblage Cleared -Time of Clearing -Number of Clearings -Size of Clearings -Time Observed	Recovery Time	Reference -Notes
La Jolla, California	-Not defined -January 1923 -3 -30 x 60 cm and one 91 cm dia. pool -4 mos.	>> 4 mos.	Wilson 1925 -most of the common algae did not reappear in clearings.
Friday Harbor, Washington	-Barnacles/limpets -June 1925 -6 clean rocks placed along each of 2 transects -Rocks ~ 25 cm dia. -43 days	~1 mo.	Pierron and Huang 1926 -recovery based on rocky rocky transect only. -after 43 days, more barnacles and snails on clean rocks than undisturbed rocks.
Monterey, California	-*Mytilus californianus* -November 1931 -1 -91 x 91 cm -2.5 yrs.	> 2.5 yrs.	Hewatt 1935 -mussels recruited after 5 mos. but abundance still low at last observation. Richness of associated species also still low.
Monterey, California	-*Endocladia/Gigartina papillata* (1), *Rhodoglossum* (2), *Iridaea flaccida* (3), *Rhodymenia pacifica* (4) -2 seasons, 1944 -3 transects in Jan., 1 each in April, July, and Oct. -30 cm wide strips -9 to 27 mos.	(1)> 27 mos. /18 mos. (2) 6-9 mos. (3) ~6 mos. (4) 9-12 mos.	Northcraft 1948 -recovery estimated by similarity to pre-clearing abundance.
Yoakam Point, Oregon	-*Mytilus californianus* (1), *Iridaea flaccida* (2), *Odonthlia* (3) -2 transects one in 1958, one in 1960. -1 mwide strips -6 to 8 yrs.	(1)> 8 yrs. (2 and 3) 2 yrs.	Castenholz 1967

Table 5. (Continued)

Location	-Assemblage Cleared -Time of Clearing -Number of Clearings -Size of Clearings -Time Observed	Recovery Time	Reference -Notes
Olympic Peninsula, Washington	-*Fucus distichus* -November-December 1966 -3 large rocks -Size not given -2.5 yrs.	> 4 yrs.	Dayton 1971
Eureka, California	-*Collisella/Balanus* (I), *Mytilus califorianus* (2), *Chthamalus* (3) -October 1968 -2 transects through zones -10 cm wide -36 mos.	(1) 2 mos. / 36 mos. (2)> 36 mos. (3) 3 mos.	Cimberg 1975 -recovery based on index of redevelopment relative to controls. *M. califorianus* settled 2 mos. after clearing but eaten by *Pisaster*. 40% recovery of organisms in mussel zone in 36 mos. Recovery inversely proportional to size of largest invert. in zone.
San Diego, California	-*Lithothrix* -Seasonally, 1973-74 -3 quadrats/season -0.05 sq. m quadrats -1 yr. for each set of seasonal clearings.	*Lithothrix* cover> 1 yr. Species richness 1 to 4 mos.	Emerson and Zedler 1978 -colonization of some species varied with season. *Lithothrix* recruited quickly but grew slowly.
San Clemente Island, California	-*Gigartina canaliculata/Corallina officinalis* (1) Blue-greens/*Ulva*, *Pseudolithoderma* (2) -December 1974 -3 in each assemblage -0.15 sq. m plots -30 mos.	(1)>30 mos. (2) 1 mo.	Murray and Littler 1978 -blue-green assemblage in area polluted by sewage. Recovery based on similarity to controls, (1) almost recovered in 30 mos.
Twelve sites in southern California	-Varied depending on site -1975-77, various seasons -1 to 40 per tidal height -1 sq. m quadrats -12 to 24 mos.	> 24 mos.	Murray and Littler 1979 -scraping left some encrusting organisms. Plants recover faster than animals. High intertidal perennial algae and large sessile animals slow to recover.

Table 5. (Continued)

Location	**-Assemblage Cleared** -Time of Clearing -Number of Clearings -Size of Clearings -Time Observed	Recovery Time	Reference -Notes
Santa Barbara, California	*-Gigartina canaliculata* -February 1975 -12 blocks, "a number" of clearings -165 sq. cm blocks and 100 sq. cm clearings -30 to 36 mos.	2 to 3 yrs.	Sousa 1979a -recovery faster in clearings due to vegetative growth from edges.
Tatoosh Island, Washington	*-Mytilus californianus* -Various times -Various replications -Various sizes. -5.5 yrs.	5 to 7 yrs. if recover via recruitment	Paine and Levin 1981 -small (<10 sq. m) patches recover more quickly because of migration,
Monterey, California	*-Endocladia/Pseudolithophyllum* (1), *Iridaea flaccida/Tetraclita* (2), *Prionitis* spp. (3) - (1 and 2) October 1973, (3) October 1973 and May 1974 -6 per assemblage -20 x 20 cm quadrats -27 mos. plus misc. observations for ? yrs.	(1) ~ 4 yrs. (2) 24 mos. (3)> 7 yrs .	Foster 1982 and unpublished data -recovery based on cover of dominant plants relative to controls.
Bodega Head, California	*-Mytilus califorianus* -July 1979 -16 of each -25 x 25 and 50 x 50 cm quadrats -36 mos.	>>3 yrs.	Sousa 1984 -no *M. califorianus* recruitment in 3 yrs. but some recovery by migration. Some algal species on tops of mussels recruited into clearings within 12 mos. (*Gigartina, Pelvetiopsis*). *Endocladia* recruited but not back to precleaning abundance after 36 mos.

colonists may inhibit or have little effect on later species. The low intertidal *Phyllospadix* spp. assemblage is one exception; the seeds of surf grass are adapted for recruiting to the branches of other plants (Dawson 1966) and Turner (1983a) has shown that plants such as articulated coralines do facilitate surf grass recruitment.

If cleared areas suffer no further physical disturbance, the factors that affect subsequent succession include recruitment, growth, and survival of colonizing species (Northcraft 1948; Emerson and Zedler 1978; Sections II and III), grazing (Sousa 1979a, 1984; Foster 1982), predation (Cimberg 1975), and factors associated with clearing size (grazing, dispersal; Sousa 1984, 1985). These factors have all been shown to be important in one study or another, but there has not been enough replication of appropriate experiments in space and time to suggest some interactive model or even a ranking of factors important to rocky intertidal succession.

As might be expected given the diversity of organisms and processes that occur in the rocky intertidal zone, reported recovery rates, even within one assemblage, are highly variable. Table 5 summarizes recovery rates found or estimated in succession studies done between British Columbia and Baja California using complete clearings. Although the places, times, and sizes of clearing are often different, these studies support Murray and Littler's (1979) conclusion that assemblages dominated by plants generally recover faster than those dominated by animals. The exception appears to be high intertidal barnacle assemblages that may recover in less than one year. Among assemblages dominated by perennial plants, those in the high intertidal also appear to recover more slowly than those lower on the shore. Again, *Phyllospadix* spp. may be an exception since recruitment is facilitated by the presence of perennial algae that must first become established after clearing (Turner 1983b), and most recovery occurs by the slow vegetative ingrowth of surrounding rhizomes (Turner 1985).

As found by Sousa (1980, 1984), the above generalizations are consistent with what is known about dispersal, recruitment, and growth of the organisms involved (Sections II and III). Perennial algae appear to recruit from fairly local parental stocks and the planktonic life of the propagules is probably short (Sousa 1984). Growth conditions for plants are generally less favorable higher on the shore (Underwood 1980; Underwood and Jernkoff 1981; Foster 1982; Cubit 1984). Long-lived sessile animals appearto have highly variable recruitment and grow relatively slowly (Section III). The recruitment of some species, like *Mytilus californianus*, may be enhanced by perennial algae such as *Endocladia muricata* that are slow to recover (Table 5).

2. Partial Clearing

Partial clearings have generally been done to determine the effects of a particular organism, usually the cover or numerical dominant in a given assemblage, on associated species. This type of clearing is quite different from complete removal because the remnants of organisms left behind may regrow, increasing the recovery rate. Organisms left in partial clearings may inhibit (Lubchenco 1980; Foster 1982) or enhance (Barnes and Gonor 1973) later recruitment into cleared areas. Removal of canopy species such as *Hedophyllum sessile* or *Pelvetia fastigiata* can alter microclimates or topography such that understory organisms die or migrate from the clearings (Dayton 1975; Hill 1980) or increase in abundance if growth is inhibited by the canopy (Dayton 1971).

Partial clearings are more similar to most natural disturbances in rocky intertidal communities than are complete clearings (Foster and Sousa, in press; Sousa 1985). Natural disturbances such as moderate waves, exceptionally hot or cold weather during low tides, freshwater runoff, etc., commonly remove only the upright parts of many seaweeds. When this is done experimentally, recovery to predisturbance cover is usually faster than after complete removal (*Fucus distichus* - Dayton 1971; articulated corallines - Murray and Littler 1979; *Phyllospadix scouleri* - Dethier 1984). This is not always the case as Hill (1980) found that *Pelvetia fastigiata* recovered at almost the same rate (complete recovery in 38 months) from remnant holdfasts or via recruitment. Such variation might be expected in future studies because recovery is affected in part by proximity of propagule sources (Sousa 1984).

Removal of the dominant species can, however, also result in different species preempting space for long periods. DeWreede (1983) removed *Sargassum muticum* from quadrats in the *S. muticum* zone in British Columbia during the same month in three different years. In two cases, *S. muticum* returned to its generally high (approx. 80%) surrounding cover within a few months, while in the third case *Rhodomela larix* rapidly colonized and remained dominant during four years of observation. DeWreede (1983) suggests that the colonization of *R. larix* was favored by the coincidence of available space in a year when few *S. muticum* propagules were available.

Recovery after partial clearing may also vary in space, as Dayton (1975) found for *Hedophyllum sessile*. This kelp and its obligate understory recovered to precleaning abundance in two years at one site, while it had not recovered after four years at another, more sheltered site. Turner (1983b) also found that the recovery process after removal of *Phyllospadix scouleri* varied significantly within a site depending on season of removal and other unknown factors.

The above are examples in which late successional species, the generally common, large organisms that typify particular intertidal assemblages, were removed. To date, only Sousa (1979a) has examined the effects of removing early (e.g., diatoms, *Ulva* spp.) or mid- (various species depending on the site) successional species. By definition, these species do not necessarily "recover" when disturbed as they are not the late successional dominants. At Sousa's (1979a) site near Santa Barbara, *Ulva* spp. was the common early successional species, *Gigartina leptorhynchos* and *Gelidium coulteri* the middle species, and G. *canaliculata* the late successional species. Removal of *Ulva* resulted in an increase in the abundance of the middle and late successional species, and removal of the middle species resulted in an increase in the abundance of G. *canaliculata*. This indicates that these species inhibit rather than enhance recovery of the late successional dominants characteristic of this zone, and that natural disturbances to these species have significant impacts on subsequent patterns of recovery.

Sousa (1979a) also found that herbivores, particularly the crab, *Pachygrapsus crassipes*, increased the recovery rate of G. *canaliculata* by preferentially eating *Ulva* spp. Similar effects of herbivores on succession have been found by Lubchenco (1983) in the northeastern United States. In contrast, Foster (1982) found that limpets retarded the recovery of *Iridaea flaccida* in the *I. flaccida* assemblage. However, this alga was among the first, and was the most abundant macroalga, to colonize after clearing.

In the high intertidal and splash zone, limpets may completely eliminate the dominant but visually ephemeral macroalgae during times when conditions for algal growth are poor, producing a regular seasonal succession (Cubit

1984). In the low intertidal and tide pools, selective removal of patches of sea urchins (*Strongylocentrotus purpuratus*) within areas otherwise dominated by macroalgae generally results in colonization by macroalgae (Paine and Vadas 1969; Dayton 1975; Gaines 1985). There are no published accounts concerning the recovery rates of sea urchins in these former sea urchin patches.

B. Natural Disturbance

A number of natural biological and physical disturbances have been identified in rocky intertidal communities. Biological disturbances such as predation by starfish on mussels (Harger and Landenberger 1971), by gastropod on mussels and barnacles (Connell 1970; Lubchenco and Menge 1978), and by sea otters on a variety of intertidal animals (Palmisano 1983) have been shown to significantly affect intertidal community structure. Harbor seals also disturb the intertidal zone by hauling out and perhaps by nutrient enrichment (Boal 1980). Grazers such as sea urchins can completely alter local community structure (see Partial Clearing above, and Lawrence 1975), urchins, and crabs may affect recovery rates from other disturbances (Sousa 1979a, 1980), and limpets can cause a seasonal succession in the high intertidal (Castenholz 1961; Cubit 1984). However, such biological disturbances are often diffuse and continuous. Thus, these types of disturbances have been studied primarily with experiments involving removals or exclusions that document only the effects of natural densities versus complete absence. We know little about disturbance effects of these species relative to natural variation in their densities and activities. Lubchenco (1978) and Lubchenco and Gaines (1981) point out that grazers may have variable effects depending on their densities, food preferences, and food availability, and studies such as that of Underwood and Jernakoff (1981) using a variety of grazer densities would lend further insight into the natural effects of these animals.

Physical disturbances have received much recent attention, especially along the exposed coast of the northeastern Pacific, and we are beginning to gain a better appreciation of the importance of these phenomena to community structure. Dayton (1971) was the first to try to quantify physical disturbance by logs in Washington, and found that a point in the intertidal zone had a 5-30% probability of being struck by a log in three years. Paine and Levin (1981) estimated that between 0.4 and 5.4% of the mussels on an exposed island in Washington, are removed during each winter month by wave action. Dethier (1984) estimated that tide pools in her Washington study areas were disturbed once every 18-20 months. These estimates suggest that rocky intertidal assemblages are dynamic, and that much of the patchiness within an assemblage reflects variation in recovery from prior disturbances (Sousa 1985).

Perhaps the best documented effects of physical disturbance are in mussel beds where waves remove patches of various sizes (Paine and Levin 1981), and where much of the patchiness at any one time in the community does reflect differences in recovery (Sousa 1984). Dethier (1984) studied the effects of various physical and biological disturbances on the species composition and recovery of tide pool assemblages. As suggested by the information from experimental clearings discussed above, she found that the more common partial clearings recover much faster than total clearings. She concluded that disturbance is the major stochastic process generating variability in tide pools.

Earlier species in a particular successional sequence may affect later succession (Sousa 1979a), and these species may also have variable responses to disturbance. Sousa (1980) mimicked natural disturbance from waves on various successional stages in an intertidal boulder field by overturning boulders with varying species composition for different lengths of time. He found that early successional species suffered more damage from any particular length of disturbance, but that these species also recovered more quickly. The responses of different species were related to their life history characteristics, especially spore production, dispersal, and ability to grow from remnant holdfasts. This is in agreement with information from experimental clearings, and further indicates the importance of knowing both the disturbance regime and the biology of the species involved to understand the recovery process.

Sand movement is also a disturbing process in rocky intertidal communities (Daly and Mathieson 1977; Mathieson 1982; Taylor and Littler 1982; Littler et al. 1983; Turner 1983b) and can set the lower boundaries of distribution of certain species (Frank 1965; Daly and Mathieson 1977; Littler et al. 1983; Section III). In areas where sand movements are seasonal, burial often kills ephemeral species (e.g., *Chaetomorpha linum*, *Ulva lobata*, *Chthamalus dalli*) that later resettle when sand moves offshore (Daly and Mathieson 1977; Littler et al. 1983). The resulting seasonal succession is thus similar to that caused by limpets in the high intertidal. Rocky habitats regularly disturbed by sand are also usually inhabited by a few perennial species, such as *Anthopleura elegantissima*, *Phyllospadix scouleri* (Littler et al. 1983), *Gymnogongrus linearis* (Markum and Newroth 1972), *Laminaria sinclarii* (Markum 1973), and algal turfs (Stewart 1983) that can tolerate abrasion and burial.

Perhaps the most pervasive physical disturbance other than wave shock is that produced when extremely hot weather coincides with low tides. Most investigators making regular visits to the shore have observed the general “bleaching” of seaweeds resulting from such conditions. To our knowledge, neither such disturbance nor later recovery has ever been quantitatively examined, but most of the algae appear to rapidly produce new blades from undamaged basal and holdfast tissue (Foster, pers. ohs.). A similar bleaching may result from freshwater runoff. Extreme cold may cause loss of limpets by exfoliation of rock (Frank 1965), and damage to various organisms in tide pools (Dethier 1984).

Changes in weather conditions may also indirectly affect intertidal organisms by encouraging disease outbreaks. Dungan et al. (1982) describe a “catastrophic” decline of a predatory sea star in the Gulf of Mexico, a decline caused by a disease associated with a prolonged period of elevated temperatures. The consequences of this decline were not documented.

Landslides, and elevation changes resulting from earthquakes and nuclear testing are examples of extreme physical disturbances. There are no published observations of recovery after landslides in the rocky intertidal of the northeastern Pacific, but such observations would be a valuable contribution to our knowledge of succession because subsequent “recovery” would have to be solely from new settlement. Uplifting from the 1964 Alaska earthquake and the 1969 "Milrow" nuclear test caused a die-off of most species whose elevation was raised. These species were replaced by others that generally occur higher in the intertidal zone than those originally present (Haven 1972; Johansen 1972; Lebednik 1973).

These studies all suggest that a variety of disturbances affect rocky intertidal communities. The types, severity, and frequency of disturbance on mussel beds, boulder fields, and tide pools at selected sites have been documented and related to within-zone patterns of distribution and abundance. However, similar studies in the same habitats at different sites are needed to determine the general importance of these events. This is especially necessary because we know that changes resulting from storms vary with site (discussed in Sections II and III). Moreover, with the exception of Dayton (1975) and Sousa (1979a), there are no studies of the importance of the disturbance process in assemblages dominated by perennial macroalgae (e.g., *Endocladia muricata*, *Iridaea flaccida*) in the northeastern Pacific. In Chile, Jara and Moreno (1984) studied the structure of a mid-intertidal assemblage composed of a mosaic of areas dominated by either *Iridea boryana* or barnacles and crustose algae. The structure of the assemblages depended upon the occurrence of various disturbance agents that create free space within the community. Depending upon the time of year and local herbivore abundance, two different ensuing successional sequences occurred. Thus, at any given time the spatial variation in this community is due to three interrelated factors: bare space created by disturbance, different successional sequences initiated by the disturbance, and the phase of succession at the time of observation. Similar studies of ubiquitous perennial macroalgal assemblages in other temperate areas would aid in determining the degree to which we can generalize about the importance of disturbance, particularly physical disturbance, in structuring rocky intertidal communities.

V. EFFECTS OF DISTURBANCE CAUSED BY HUMANS

Pollutants discharged by humans, which may cause alterations in distribution, abundance, and composition of rocky intertidal communities, differ in important ways from natural factors which may cause similar changes (Auerbach 1981). Man's wastes discharged to the ocean typically emanate from point sources, and may result in gradients of change that decrease with distance from the source (e.g., municipal wastes). These wastes are often composed of complex variable mixtures of toxic substances, and are discharged almost continuously. Non-point sources of wastes also enter coastal waters (e.g., storm runoff). Pollutants that are transported by rivers and streams, form a third type of input.

The present level of understanding of the effects of each of these different modes of discharge differ greatly with ability to sample the input adequately, and to detect and interpret ecological effects. The types of wastes or disturbances considered in this review include: petroleum hydrocarbons, chemical dispersants, municipal wastes, pulp mill effluent, and recreational uses. These types were selected because: 1) there was demonstrated evidence of direct impacts on rocky intertidal communities, 2) insight could be gained even if evidence of effects was obsered in other habitats, 3) potential for impacts along the California coast was likelyto continue or increase, 4) evidence of community degradation or recovery was clearly linked to presence of a waste discharge,

This review should not be considered exhaustive, particularly in the case of petroleum hydrocarbons. Although the literature on ecological effects of pollution is voluminous, the-literature on these types of wastes is represented very unevenly, and this is reflected in our level of treatment. Nevertheless, much has been learned about the structure, behavior and composition of marine communities as a result of studies of changes in communities due to pollution, particularly from point source effluents. Unfortunately, there has been a strong tendency to focus attention on catastrophic acute effects, like oil spills, rather than to examine the low-level impacts from chronic input. Therefore, the quantity of information does not necessarily reflect the seriousness of potential ecological effects for a particular waste type.

A. Petroleum Hydrocarbons

Although the scientific literature associated with oil spills is exceptionally large, it is generally anecdotal, and based on short-term studies and syntheses ofpost-accident observations. Consequently, results from different oil spills are not readily comparable, certain habitats are emphasized (e.g., rocky intertidal) while others are often omitted (e.g., subtidal), only catastrophic effects are usually studied and, other than conjecture about habitat sensitivity, few predictions are possible.

This situation is largely attributable to the fact that no two spills are alike and because numerous variables affect spill impact, including: type of spill, duration of exposure, volume and type of oil, oil state and age (degree of weathering), hydrographic conditions, weather, season, biological environment, use of dispersants, etc. (Straughan 1972; BNCOR 1980). It is also partly due to our limited understanding of the structure and functioning of marine littoral and sublittoral communities and to our ability to sample these habitats quantitatively and interpret changes. Nonetheless, Boesch and Hershner (1974) concluded that it is clear that oil pollution may cause mortality directly through: coating and asphyxiation, contact or ingestion, exposure to toxic fractions, impacts on sensitive early life stages, and through disruption of insulation properties of birds and mammals. Mortality may also be caused by more subtle means through: disruption of feeding, lowered resistance to stress, uptake of carcinogenic or mutagenic constituents, impaired reproduction, and altered behavior.

The study of accidental oil spills can yield important qualitative information about cause and effect relationships (Moore and McLaughlin 1978). However, long-term effects are poorly understood and the few studies that have been done have focused on single habitats and selected species. Consequently, generalized statements regarding community recovery are not possible. The status of knowledge in these matters has been critically reviewed by Boesch and Hershner (1974), Baker (1976), BNCOR (1980), and more recently by Baker (1983), Teal and Howarth (1984) and Johnston (1984).

Although several oil spills on the west coast received considerable scientific attention (e.g., the Santa Barbara blowout in 1969, and the collision of the Arizona Standard and the Oregon Standard in San Francisco Bay in 1971), much of our understanding of oil spill impacts is derived from studies of spills on other coasts. Of the hundreds of spills reported over the last 25 years throughout the world, about 50 are discussed in the literature, and only a dozen or so of these have been studied in depth. These include the spills listed in Table 6, which are discussed by NAS (1975), Teal and Howarth (1984), and by Johnston (1984).

1. Sources

Although a catastrophic oil spill is one of the most conspicuous forms of marine pollution it is not the major contributor of hydrocarbons to the ocean. Chronic low-level input from terrestrial runoff, discharge of municipal wastes, aerial fallout, natural seeps, tanker operations. and refineries contribute significantly greater quantities of petroleum hydrocarbons to the ocean, yet these inputs are inconspicuous, poorly monitored, and inadequately quantified. General estimates of worldwide input from these diverse sources have been made by numerous authors (i.e., NAS 1975; Hardy et al. 1977; Mileykovskiy 1979; Wardley-Smith 1979; Johnston 1984). Detailed discussions of global inputs have been published by Clark and Macleod (1977) and Grossling (1976) and U.S. inputs are reviewed by the NAS (1975, 1985) and by Boyd et al. (1976). In 1975 the NAS estimated that acute tanker spills (1,373,832 barrels) account for only 3.3% of the total annual hydrocarbon input of 42,057,440 barrels, while tanker operations, such as bilges bunkering, dry docking, load-on-top and non-load-on-top tankers, etc., (13,278,084 barrels) accounted for 31.6%. In 1985 these estimates were revised. The NAS (1985) estimated that the total annual input of petroleum hydrocarbons to the marine environment ranged from 11,696,000 barrels to 60,544,000 barrels, and that the input from tanker operations (4,128,000 to 14,448,000 barrels) continued to exceed the input attributable to acute tanker spills (2,064,000-2,752,000 barrels).

The nearshore waters of the northeastern Pacific receive petroleum hydrocarbons from each of these sources. Data on input to this region, however, are incomplete and estimates have been made for only a few categories. Even though their overall input is relatively small, worldwide acknowledgement of the ecological effects that can result from catastrophic oil spills, principally from tankers, has generated concern for similar potential disasters along the California coast. For example, tanker traffic to the Ports of Los Angeles/Long Beach is expected to double. Since the number of tanker accidents is correlated

Table 6. Examples of Well Documented Major Oil Spills. Date is day spill began.

Date Day/Mo/Yr	Oil Source	Impact Location	Volume Spilled (barrels)	References
29/03/57	Tampico *Maru*	Baja California	60,000	North et al. (1965)
13/01/67	Chryssi P. Goulandris	Milford Haven, England	860,000	Nelson-Smith (1968)
18/03/67	Torrey Canyon	Cornwall, England	804,960	Smith (1968)
16/09/69	Florida	West Falmouth, Mass.	4,500	Blumer & Sass(1972)
28/01/69	Platform A	Santa Barbara	75,561 - 769,346	Foster et al. (1971 a,b)
04/02/70	Arrow	Chedabucto Bay	108,000	Thomas (1973)
18/01/71	Arizona Standard & Oregon Standard	San Francisco Bay, Cd.	20,000	Chan (1973)
09/08/74	Metula	Strait of Magellan, Chile	357,760	Baker et al. (1976)
15/12/7'6	Argo Merchant	Nantucket	192,640	Pollack & Stolzenbach (1978)
22/04/77	Platform Bravo	Ekofisk Field, North Sea	137,600	Teal & Howarth (1984)
26/10/'77	Tsesis	Baltic	7,568	Kineman et al. (1980)
16/03/78	Amoco Cadiz	Portsall, France	1,720,000	Hess (1978)
03/06/79	IXTOC 1	Bahia de Campeche, Mexico (M in millions of bbls)	3M - 10M	Teal & Howarth (1984)

1 barrel (bbl) =42 gallons (U.S. Liquid) = 321 pounds

with the volume of oil produced and the amount of tanker traffic (Beyer and Painter 1977; Goldberg et al. 1981; Meade et al. 1983), the increased tanker traffic would increase the probability of a catastrophic oil spill. Beyer and Painter (1977) analysed data on world-wide tanker spills recorded during 1962-1972 and found that the average frequency of tanker accidents was positively correlated with proximity to harbors, number of port calls (0.92 spills/10^3 port calls), volume transported (12 spills/10^9 barrels transported), and vessel age (20 spills/10^3 vessel years) and negatively correlated with vessel size. Although the average spill was about 7,100 barrels, use of this statistic can be misleading for spills that result in ecological damage. For example, the NAS (1975) reported that while 98% (3,468 spills) of the spills in the U.S. (totaling 17,200 barrels) were each less than 220 barrels, 4 spills accounted for 65% (221,536 barrels) of the volume lost during 1970. Such analyses of world wide data are useful because they basically corroborate trends observed in the northeastern Pacific. Although California offshore production is expected to increase over six times from 80,000 barrels to 500,000 barrels per day (J. Boyd, pers. comm.) by 1991, most of this oil will be transported by subsea pipelines.

According to the U.S. Coast Guard's Pollution Incidents Reporting System (PIRS) data base from 1973 to 1984 a total of 335 spills were reported between San Diego and the Strait of Juan de Fuca, representing a volume of 43,883 gallons. Eighty-eight percent of this volume (38,518 gal.) was reported lost from vessels and 12.1% (5,267 gal.) from coastal marine facilities. Most of the vessel oil spilled was either distillates (20,687 gal.) or crude oil (11,406 gal.), resulting from 150 distillate spills and 28 crude oil spills. Unfortunately, the PIRS data base only includes spills related to vessel accidents attributable to collision, grounding, ramming, fire or explosion and to operational spills associated with refueling, and loading or unloading cargo. Reliable estimates of the large quantities of input from intentional, routine, operational discharges from deballasting, bilge pumping, and tank cleaning are not readily available.

Of the total number of vessel related spills, the majority occurred along the Olympic Peninsula (37.4%), San Francisco Bay (30.3%), and the Los Angeles/Long Beach (17.5%) harbor area. These spills were attributed to numerous small accidents. A total of 12,333 gal. from 58 individual spills were lost from vessels between Point Conception and Crescent City.” The majority of marine facility related spills occurred along the Olympic Peninsula (15.4%), Point Arena (32.4%) and the Los Angeles/Long Beach harbor area (45.1%). A total of 1,765 gal. from eight individual spills were lost from marine facilities within the Point Conception-Crescent City area. Over this period (excluding 1984) there has been an average of 30 spills per year throughout the region examined, totaling approximately 3,900 gal. each year.

Quantitative spill records were not carefully kept prior to 1973, so the picture presented above excludes a number of major oil spills including the collision of the Arizona Standard and the Oregon Standard in San Francisco Bay in which 35,700-45,200 barrels (1 barrel = 42 gal.) were lost in 1971, the blow-out of Platform “A” off Santa Barbara in 1969 in which over 70,000 barrels were lost, the Yukon in Cook Inlet (5,000 barrels), a barge near Anacortes, Washington (5,000 barrels), the Manatee off San Clemente, California (29 barrels), the Private Joseph Merrell off Monterey, California (381 barrels), as well as a pipeline break in Bellingham, Washington (11,905 barrels) and a tank valve failure in Oakland, California (4,167 barrels).

2. Biological Effects

Much is known about the acute affects of large catastrophic oil spills on rocky intertidal communities (see reviews by Hardy et al. 1977; Clark 1982a,b; Baker 1983; Johnston 1984; Teal and Howarth 1984). However, little is known about long-term effects or recovery processes (Clark 1982b), and even less is known about the effects of low level inputs (Hardyet al. 1977). Field analyses are hampered by the lack of controls and inherent population variability (Michael 1976; Mann and Clark 1978; Teal and Howarth 1984); further documentation of immediate impacts in the field is not likely to produce information pertaining to these questions.

Clark (1982a) urged that even though effects at the population and community level are more difficult to detect than those at lower levels of organization, more attention should be given to study of population dynamics. However, natural background variability in populations makes the detectionof effects of low levels of pollution very difficult. Furthermore, the significance of local changes in population density should be interpreted for a particular species on a broader coastal scale and in terms of its role in the community. Fortunately, it appears that since community response to stress are often similar, regardless of the type of stress, information from work on natural disturbances may be relevant to determining responses to disturbance from pollution (Clark 1982b; Kinne 1984).

Van Gelder-Ottway (1976), the NAS (1975), and Johnson and Pastorok (1982) compiled lists of the major world oil spills for which rocky intertidal impacts have been documented. Of these 30 or so spills, relatively few occurred on the West Coast of the United States. These include the Tampico Maru (1957) wreck off Baja California, Mexico, the Santa Barbara blowout at Platform A (1969), the collision of the Arizona Standard and the Oregon Standard (1971) at the entrance to San Francisco Bay, the wreck of General M.C. Meigs (1972) in Washington, the wreck of the Irish Stardust in British Columbia (1973), the wreckof a barge in Anacortes, Washington (1971), and more recently, the explosion of the Puerto Rican (1984) off San Francisco Bay. Each of these spills proved to be unique, and impacts differed markedly. Nevertheless, it is useful to identify from these accidents species that were affected in both the short term and long term, and what was learned concerning recovery.

Clark et al. (1973, 1978) investigated the effects of the wreck of the General M.C. Meigs on the rock intertidal community near Cape Flattery, Washington, and compared disturbed areas to an unoiled control site 6.4 km to the north. Initial oil-related loss was relatively small. Blade loss in *Laminaria setchellii* and *Phyllospadix scouleri* was evident, as was bleaching of *Corallina vancouveriensis*, *Prionitis lanceolata*, and *Ceramium* sp. There were no gross impacts on sessile animals (e.g., barnacles, mussels and anemones). Dead and abnormal (i.e., spine loss) *Strongylocentrotus purpuratus* were encountered. Tissue analyses suggested that bioaccumulation of petroleum hydrocarbons occurred in *Fucus gardneri, Pollicipes polymerus*, and *Hemigrapsus nudus.* Long-term monitoring after the accident indicated continued spill related impacts on urchins, barnacles, mussels, and anemones as well as bioaccumulation. *Hedophyllum sessile* became the dominant alga after 1 1/2 years. After 2 1/2 years "normal" cover of the algae *Halosaccion glandiforme*, *Egregia menziesii*, *Desmarestia* sp., *Gigartina papillata*, *Rhodoglossum affine*, *Iridaea* sp., *Codium fragile*, and *Ulva lactuca* was evident.

Cretney et al. (1978) did successive qualitative studies of the impact of 200 tons of spilled fuel oil on an isolated and sheltered rocky cove on

Vancouver Island, British Columbia, following the wreck of the *Irish Stardust* in 1973. Initial biological effects, extending over nine months, included loss of heavily oiled *Fucus distichus* and mortality of limpets,' amphipods (*Orchestia* sp.), and periwinkles (*Littorina* spp) . Presence and degradation of various oil fractions from stranded oil patches were documented over a four-year period, even though most biota had "recovered" within a year.

Chan (1973) reported a significant decrease in marine life at Sausalito and Duxbury Reef near San Francisco as a result of the collision of the *Arizona Standard* and the *Oregon Standard* in 1971. Disturbances attributed to smothering were patchy as the oil stranded unevenly throughout the upper rocky intertidal zone. Chan was able to resample specific pre-spill study sites, and found significant mortality in *Balanus glandula*, *Chthamalus* sp., *Mytilus californianus*, *Collide? la digitalis*, *Collisella scabra*, *Littorina scutulata*, *Tegula funebralis*, *Pollicipes polymerus*, and *Pachygrapsus crassipes*. Oil residue was still visible ten months after the spill. Species for which changes in abundance could not be attributed to oil included *Pisaster ochraceus*, *Lottia gigantea*, *Aplysiopsis smithi*, rock boring piddocks, *Cancer antennarius*, sea anemones, chitons, *Haliotis rufescens*, *Endocladia muricata*, and *Gigartina papillata*. Higher than normal abundances were found after the spill for *Urospora pencilliformis*, *Porphyra perforata*, *Enteromorpha intestinalis*, and *Phyllospadix scouleri*. Normalgrowth was found for *Halosaccion glandiforme* and *Iridaea flaccida*.

Chan (1975) subsequently reported on long-term recruitment to the impact sites. After 39 months, less than 5% of the original oil residue remained on rock surfaces. Significant recruitment was observed for barnacles, mussels, periwinkles, limpets, and algae. Species that had not recovered were *Pachygrapsus crassipes* and *Littorina keenae*. The algae had generally recovered to pre-spill densities, while *Urospora pencilliformis* was reduced significantly. Densities of *Tegula funebralis* returned to pre-spill values within six months while limpet densities nearly doubled within 18 months, and then returned to normal at 30 months. Numbers of *Mytilus californianus* doubled within 18 months.

One of the earliest and, perhaps, most interesting biological studies of oil spill effects on intertidal and subtidal rocky shores was done by North et al. (1965). The effects of the wreck of the *Tampico Maru*, which occurred on the Pacific coast of Baja California in 1957, were studied qualitatively over a period of six years. The purpose of this study was to examine the time required for recovery and to observe the recovery process. Since no pre-spill data were available, thereby making all conclusions tentative, comparisons were made to adjacent unoiled sites for reference. Although initial observations were made about a month after the accident, oil spillage was still apparent and continued periodically over a period of eight months. The authors distinguished several phases of disturbance and recovery, including complete disappearance, immigration and colonization, and maturation. Widespread mortalitywas obvious in many species (e.g., *Haliotis fulgens*, *H. rufescens*, *H. cracherodii*, *Panulirus interruptus*, *Tivela stultorum*, *Mytilus* spp., *Strongylocentrotus franciscanus*, *S. purpuratus*, *Pisaster giganteus*, and *P. ochraceus*). Survivors included *Littorina keenae*, *Anthopleura xanthogrammica*, *A. elegantissima*, and *Corynactis californica*. Within four months immigration of mobile species was evident (e.g., fish, *P. interruptus*, *Aplysia californica*, *Pisaster* spp. , *Pachygrapsus crassipes*) as well as some colonization (e.g., *Mytilus* spp., *Chthamalus* spp., *Patiria miniata*). At 31 months extensive recovery had occurred. The authors assumed that severe damage to macrophytes had occurred since there were few attached algae on the shore. Within three months, rapid algal colonization had occurred both intertidally and subtidally, and included *Macrocystis pyrifera*, *Cystoseira osmundacea*, *Halidrys dioica*, *Porphyra perforata*, *Egregia menziesii*, *Iridaea* sp., and *Ulva lactuca*. Rapid algal colonization was attributed to differences in toxic thresholds, reduction of grazer and filter feeder density, and wave protection afforded by the sunken vessel. Subsequent development of a *M. pyrifera* forest may also have altered conditions and fostered algal colonization. Long-term changes included development of the kelp bed and continued slow recovery of urchins, mussels, and abalone.

Because of their potential for release of significant quantities of oil, offshore oil platforms are of major concern. The blowout of Platform A, well No. 21, 9.7 km offshore in the Santa Barbara Channel was one of the first platform spills of major size. Its effect proved difficult to evaluate, and caused considerable controversy (Neushul 1972). Much of the heavy crude oil remained below the water surface and also underwent considerable weathering prior to stranding on shores (Straughan 1971). The oil was unevenly distributed along the coast over a distance of 100 miles and persisted as asphaltic patches on upper intertidal rocky surfaces in some locations for at least seven months (Nicholson 1972). The spill also coincided with severe winter storms, freshwater coastal runoff, and turbidity (Straughan 1971). In fact, Cimberg et al. (1973) concluded that at some sites sand movement and substrate stability were more important in affecting presence of intertidal organisms than was presence of oil. Observed impacts were difficult to interpret in the absence of measures of pre-spill conditions and meaningful reference sites (Neushul 1972; Foster and Holmes 1977). Moreover, estimates of input along the shore ranging from 2.7 to 118.1 metric tons/km, indicated extreme variability in shore exposure (Foster et al. 1971a). The presence of kelp forests may have protected some rocky shores (Neushul 1972). Evidence of damage was reported by numerous authors, including: Battelle Northwest (1969), Foster et al. (1971 b), and Nicholson and Cimberg (1971). However, Foster and Holmes (1977) concluded that it was impossible to make any more than very gross quantitative estimates of overall mortality, and inferences about recovery could only be qualitative for a few species. Significant, widespread impact was only reported for *Phyllospadix torreyi* and *Chthamalus fissus* (Foster et al. 1971b). Although numerous other algal species (16) were clearly damaged by oil, it was not possible to interpret the overall level of impact. Mortality was also reported for *Notoacmaea paleacea*, *Mytilus* spp., *Pugettia products*, *Pagurus* spp., *Idotea* spp., *Pollicipes polymerus*, *Enteromorpha* spp., *Ulva* spp., *Porphyra* spp., *Gigartina* spp., and *Hesperophycus harveyanus* (Straughan 1971; Foster and Holmes 1977).

Other than the common loss of grazers followed by algal blooms, it is difficult to generalize about these spills, or to make specific statements about effects that might be anticipated should a new major oil spill occur in the region. Even a cause-effect relationship between grazer loss and algal blooms is questionable as blooms could also result from mortality of competitors. Analyses of oil spills that were studied in depth at a few sites yield evidence about the local nature of oil spill effects, but provide little comprehensive information about possible widespread significance of these affects. These studies may or may not be able to detect sublethal or long term effects. Conversely, impact assessment studies designed to yield information about extent of the overall impacts, e.g., total number of acres of kelp lost or birds killed, have not yielded information concerning altered community structure and perhaps function, or provided a basis upon which to make statements concerning recovery. These studies may only enable detection of catastrophic impacts, even though not all spills cause catastrophic impacts. To complicate the situation further, Nicholson (1972) pointed out that rocky intertidal populations in southern California may have already been stressed by years of chronic pollution, particularly those in the upper intertidal, causing an increase in ephemeral plants (e.g., *Ulva* spp., *Enteromorpha* spp., diatom films, and small green algal turfs), and a decrease in slow growing perennials such as *Endocladia muricata*, *Pelvetia fastigiata*, and *Hesperophycus harveyanus*.

3. Oil Spill Experiments

Despite a convincing argument by Moore and McLaughlin (1978) in favor of intertidal oiling experiments, there have been very few such experiments in rocky intertidal communities. Moreover, dosing protocols have varied considerably to suit different study objectives. Dosing has been done by spraying oil at sites during low tide followed by additional oil applications during successive tides and/or use of dispersants, or by application of oil to the water overlying the intertidal zone during high tide. In fact, Moore and McLaughlin (1978) were not optimistic about obtaining realistic information from such experiments because of the practical difficulties of using oil as a dose treatment adjacent to a control, and because of the compromises in experimental design that must be made due to the inherent heterogeneity of the habitat.

Crapp (1971) observed reductions in densities of pure stands of *Semibalanus balanoides* and *Chthamalus stellatus* at Stackpole Quay following a six-hour dose of Kuwait crude oil (100%) applied directly during low tide. No impact was noted in a second experiment at Greenala Point using an undiluted crude oil dose of 2 l/m^2. In a third experiment, an "atmospheric residue" of the same Kuwait crude oil caused physical dislodgement of littorines and topshells, producing a greater impact than did Kuwait crude oil applied directly. The latter was apparently readily removed by tidal action.

Nelson (1982) conducted a series of comprehensive quantitative oil experiments in a Norwegian fjord using weathered Ekofisk crude to examine the effects of dose level and duration, and test site exposure and seasonality, on the cover of intertidal organisms. Random point sampling was used to estimate changes in area occupied by each species and the area covered by algal canopy before and from 4-51 days after oiling at low tide. The major species of interest were *Semibalanus balanoides*, *Mytilus edulis*, *Patella vulgata*, *Fucus vesiculosus*, *Cladophora rupestris*, *Ascophyllum nodusum*, *Gigartina stellata*, as well as isopods (*Jaera albifrons*, *Idotea pelagica*), an amphipod (*Hyale nilssoni*), gastropod (*Nucella lapillus*, *Littorina* spp.) and *Spirorbis corallinae*. No changes were found at doses of 0.2 and 2.0 l/m^2. An increase in cover of *Mytilus edulis* (by redistribution? immigration?) at the multiple dose site eight days after oiling was the only significant change observed with change in dose frequency. Decreases in cover of *Gigartina stellata* and *Fucus vesiculosus*, and abundance of *Littorina* spp. were noted at protected sites, but not at exposed sites. Nelson (1982) concluded that few gross negative impacts of oiling were observed on adult organisms. Increases were attributed to seasonal changes in biological activity. *Semibalanus balanoides*, *M. edulis*, and *F. vesiculosus* adults appeared to be highly resistant to oiling, while juveniles were sensitive. In the future it would be beneficial to study the effects of oiling on reproduction and recruitment, in addition to changes in existing community structure.

Bonsdorff (1983) studied effects of Ekofisk crude oil on tide pools near Bergen, Norway. Significant mortality of the invertebrate community inhabiting *Corallina officinalis* (ostracods, harpacticoids, and amphipods) occurred, followed by recovery in less than a month. *Patella vulgata* accumulated aromatic hydrocarbons tenfold and then depurated to normal with 38 days.

Other workers have used artificial substrata or done transplant studies to examine recovery of intertidal communities from oil spills. As part of a larger experimental oiling study in the Strait of Juan de Fuca, Vanderhorst et al. (1980) studied epifaunal recruitment and the survival of limpets on experimentally oiled bricks. Oil significantly reduced recruitment density and species richness. Detritivores were insensitive to oil treatment while limpets and suspension-feeders were very sensitive. Although most of the oil (84%) was leached from the bricks within five days, the residual oil was sufficient to significantly inhibit recovery. After observing barnacle settlement on weathered, oiled surfaces in the field, Straughan (1971) studied barnacle recruitment to oiled and unoiled settling plates. Recruitment to oiled plates increased with oil weathering and also varied with tidal level due to thermal effects.

Few predictions have emerged from studies of post oil-spill effects. Field experiments have greater predictive potential as various treatment effects can be rigorously evaluated. We conclude that greater emphasis should be given to experimental field studies, even though “dosing’’m ethodologyr epresents a significant design obstacle.

B. Oil Dispersants

Chemical oil treatment agents (e.g., dispersants, emulsifiers, detergents) have been included in this review because of their high potential for use in “control” of oil spills at sea or as a “clean-up” method for removing stranded oil on the shore.

Despite a large, well reviewed literature (e.g., Nelson-Smith 1980; McAuliffe 1984; IPIECA 1980), our understanding of ecological impacts of dispersants is still very limited, variable in quality, and controversial (NAS 1975; Johnson and Pastorok 1982; Sprague et al. 1982). In effect, obvious acute oil spill impacts are traded for less obvious perhaps sublethal impacts, as dispersed oil penetrates a greater range of habitats and organisms (Sprague et al. 1982). The ecological consequences of dispersing oil at sea have been almost impossible to document, and predicting field effects from laboratory studies intended for ranking dispersant effectiveness has not been fruitful. Information obtained from studies of actual oil spills where dispersants were used has provided the most insight into ecological effects. Unfortunately, much of this information is based upon qualitative estimates of changes in abundance of species, presence/absence of species, or observations about “biological condition.” It has also been difficult to compare impacts from different spills because of confounding differences in oil composition, spill conditions, and variation in habitat attributes. Perhaps the most insight has come from actual field experiments in intertidal environments, even though these are difficult to do because of problems associated with handling or containing specific dose treatments and in defining and locating treatment and control replicates.

1. Impact of Dispersants Applied to Spills

The ecological impacts of use of chemical oil spill cleanup agents to remove stranded oil from rocky shores have been well summarized by Nelson-Smith (1968, 1978), Crapp (1971b), Cowell (1978), and by Johnston (1984). Impacts vary with dispersant type, frequency and quantity used, type of shore and exposure, season, species sensitivity, sampling ability, and from acute to more subtle delayed effects, e.g., changes in growth. Use of dispersants in the field enhances the potential toxicity of crude oil (BNCOR 1980), especially in sheltered habitats on shore (Sprague et al. 1982). In cases where densities of algal grazers or sedentary filter feeders (e.g., mussels, barnacles) were reduced, dramatic changes in assemblage structure, dominants, and distribution have been reported. Crapp (1971b) found that emulsifiers reduced or eliminated many dominant animal species which permitted invasion and dominance by green and brown algae, resettlement of grazers, and potential recovery over an extended period of time. This apparent settlement and unchecked growth of algae has been documented several times as a result of shore cleaning, but also has been reported as a consequence of natural perturbations (Southward and Southward 1978; Section IV). However, Crapp (1971b) pointed out that little information was available for evaluating impacts on species other than conspicuous dominant forms. Cowell (1978) reports that use of dispersants near shore does not have a measurable effect on commercial fisheries offshore.

2. Dispersant Experiments

a. Laboratory

There is an extensive literature on the acute toxicity response of numerous marine species to various oil dispersant chemicals tested in the laboratory. More recently, sublethal effects on growth, respiration and biochemistry have been reported. Much of this literature has been reviewed by Beynon and Cowell (1974), McCarthy et al. (1978), Swedmark et al. (1971) and Swedmark et al. (1973). There has also been interest in standardizing test procedures to facilitate comparisons of toxicity and effectiveness among dispersants (Hazel et al. 1970; LaRoche et al. 1970; Tarzwell 1971; Wilson et al. 1973; Baker and Crapp 1974; Bellan 1974; Cowell 1974; Gunkel 1974; Swedmark 1974; Wilson 1974; Wilson et al. 1974; Doe and Wells 1978; Norton et al. 1978; Lewis and Suprenant 1983). This has enabled development of less toxic dispersants which are now being actively reconsidered as a preemptive control method offshore (NAS 1975; Wardley-Smith 1983). However, by formalizing test procedures and selecting standardized test species, simulation of actual field conditions is often ignored and ecological predictions of effects have become difficult if not impossible (Baker and Crapp 1974; Cowell 1974; Wilson et al. 1974; Grassle et al. 1981).

b. Field

The general lack of data on pre-spill conditions has compromised the usefulness of much of the information gathered from studying effects of actual oil spills in which dispersants have been used (Cross and Thomson 1982). Such studies have also been generally deficient in supportive oceanographic, atmospheric, and water column hydrocarbon concentration data.

Bryan (1969) reported on the range of impacts of various detergent treatments on populations of the dogwhelk, *Nucella lapillus*, following oiling of the rocky shores of Porthlevon, Cornwall from the wreck of the Torrey Canyon. Dogwhelk populations clearly declined with increased use of detergent. At "sublethal" levels, growth was affected as evidenced by shell markings. Based on counts, Crapp(1971b) found greater mortality of mid-littoral barnacles (*Semibalanus balanoides* and *Chthamalus stellatus*) exposed during low tide to sequentially applied oil and dispersant than to barnacles exposed to only oil. *Littorina neritoides*, *L. saxatilis*, *Mytilus edulis*, *Patella vulgata*, and

IV. lapillus were also more sensitive to oil and dispersant treatments than to oil alone. Battershill and Berquist (1982) reported that both dispersed fresh and weathered oil were more toxic to caged intertidal gastropod (*Nerita atramentosa*), dosed at low tide, than the same oils untreated with dispersants.

In an attempt to compare differences in effects of oil alone and when treated with modern dispersants Crothers (1983) compared oil only, dispersant only, and combined oil-dispersant treatments on fixed quadrats in winter and summer on a mid-littoral rocky shore in West Somerset, England. There were no changes in densities of lichens or mussels (*Mytilus edulis*) and no changes or only slight reductions in barnacle (*Chthamalus spp., Semibalanus balanoides, Eliminius modestus*) densities in oil or oil plus dispersant treatments. Neither *Littorina littorea* nor *L. saxatilis* were affected. Density of limpets (*Patella vulgata*) was significantly reduced by both oil and oil plus dispersant treatments, but not by the dispersant alone. Subsequent cover by *Fucus* sp. seemed to vary with the number of limpets and with the amount of initial cover prior to treatment. Impacts were greater during winter, and recovery was slower.

Preliminary results reportedly Blackall and Sergy (1983) on an experimental oil spill on Baffin Island indicate that while dispersants appear to enhance immediate littoral and sublittoral effects, the organisms may be able to survive and recover from such short term, high level exposures. Marked mortality of benthic organisms was observed subtidally at depths of 3 and 7 m at dispersed oil test sites. Oil alone has some impact on littoral amphipods and some larval fish, on the density of sublittoral sea urchins, and growth of *Macoma calcarea*. The authors felt that they may have underestimated impacts by conducting the first post-spill survey too soon. In a subsequent study, Boehm et al. (1984) indicate that both treated and untreated oil that had been incorporated into the beaches continued to be a chronic source of oil, as evidenced by bioaccumulation in *M. calcarea* and *Strongylocentrotus droebachiensis*.

In a series of field and laboratory experiments, Rowland et al. (1981) showed that dispersants increase penetration of oil into and movement within intertidal sediments. Consequently, sand beaches may be assumed to function as a potential reservoir of accumulated petrol cum, thereby prolonging oil exposure to any adjacent rocky intertidal habitats.

3. Recolonization After Application of Dispersants

Straughan (1971) did a simple field colonization experiment to determine the differential effects of oil, oil plus detergent, or no oil on settlement of *Chthamalus fissus* on treated asbestos plates. She concluded that larvae settled in greater numbers on plates treated with oil and oil plus detergent due to the absence of competing algae and darker color of the plates, suggesting that oiled substrata in the upper intertidal favored settlement of barnacles, while oil cleaning would favor algal colonization.

Documentation and interpretation of recolonization processes of rocky intertidal communities following actual oil spills that were subsequently "cleaned" by use ofdispersants, has proven to be extremely difficult. Recolonization events following use ofdispersants, such as those described by Southward and Southward (1978) for a limpet dominated shore at Cornwall, are still only predictable in a very general way. Recolonization events described by Southward and Southward (1978) include: 1) development of a diatom film, 2) *Enteromorpha* maximum, 3) maximum *Fucus* cover, replacement of *Enteromorpha*, 4) minimum settlement of barnacles, 5) maximum densities of *Patella* and reduction of *Fucus* settlement by grazing, 6) increase in barnacle settlement and reduction in *Patella*, and 7) stability of the *Patella*-barnacle dominated assemblage. Other events reported, which varied with exposure, oiling and dispersant use, habitat composition, types of trophic structures, etc., included: 1) changes in vertical ranges of algae in the absence of grazers, 2) changes in vertical ranges of invertebrates benefiting from increased cover of algae, 3) alterations in species interactions, 4) differing time scales of resettlement, 5) changes in recruitment, 6) reduction in number of species, and -7) increase in biomass. Southward and Southward (1978) surmised that in other areas where limpets were less dominant and grazing and predatory systems more complex (such as the Pacific Coast of North America), induced disturbance from oiling and use of dispersants could be even more severe.

In the absence of clear definition of terms, "recolonization" (i.e., settlement and growth of recruited organisms) has sometimes been used synonymously with "recovery," i.e., recolonization and succession leading to reestablishment of a community similar in composition to that prior to a pollution event. In the oil literature, this prior community is also aften assumed to be "balanced," "normal, " "stable," and/or "healthy." Such terms are usually not defined. In attempting to dispel the misconception of rapid and complete recovery that has become established in the literature, Southward and Southward (1978) reiterated the earlier observations of Cowell et al. (1972), who suggested that recovery would be very protracted. In summary, use of dispersants to clean up stranded oil on shore has been found to be inadvisable. Their use to control oil spills offshore enhances biodegradation, minimizes bird mortality and fire hazard, "protects" shore habitats, and reduces formation of tar-like residues. However, enhanced toxicity and uptake of oil by pelagic food chains, long-term ecological consequences, degree of spreading, organism uptake, and accelerated deposition are still of concern in offshore applications.

C. Municipal Wastes

There is little doubt today that "excessive" discharge of complex municipal wastes into coastal marine environments has resulted in ecological change. Impacts on communities associated with hard substrata may be more transitory than those associated with unconsolidated substrata, where accumulation of sewage derived organic particulate alters the interstitial sedimentary environment (Gerlach 1981; Reish 1984). Several studies, however, have reported conspicuous sewage impacts on marine littoral and shallow sublittoral macrophytes. For example, Littler and Murray (1975) studied the impacts of a small, untreated sewage effluent in Wilson Cove, San Clemente Island, California. Intertidal algal assemblages adjacent to the discharge were characterized by reduced community diversity, stratification (spatial heterogeneity) and complexity, and possibly lowered "stability." The macrophytes *Egregia laevigata*, *Halidrys dioica*, *Sargassum agardhianum,* and *Phyllospadix torreyi,* were replaced by *Ulva californica*, *Gelidium pusillum*, *Pterocladia capillacea*, and blue-green algae in the mid-intertidal zone, and by the mollusc *Serpulorbis squamigerus* and *Corallina officinalis* var. *chilensis* in the lower intertidal in the area disturbed by sewage. Results of a clearance experiment designed to measure rates of recolonization indicated that the wastewater plume was selective for rapidly growing, opportunistic colonizers, such as *U. lactuca*, *G. pusillum*, *P. capillacea*, and blue green algae, as well as for suspension feeders. The unpolluted control stations were characterized by less productive, morphologically complex macrophytes, high species diversity and abundance, predominance of Perennial forms with complex life histories, and greater spatial heterogeneity (i. e., layering). Impacted stations were characterized by opportunistic species with simple life histories, turf-like form, low spatial heterogeneity, high production and more macro-invertebrates and in general an earlier successional stage. The outfall stations exhibited significantly less algal cover and more macro-invertebrates in the lower intertidal, but greater algal cover and fewer macro-invertebrates in the upper intertidal.

Borowitzka (1972) found reduced macrophyte species diversity and biomass associated with shallow sewage discharge in New South Wales. Brown and red algae were totally absent from stations adjacent to the outfall. No animals were present at the outfall, and *Enteromorpha* spp. and *Chaetomorpha* sp. formed a dense algal mat throughout the intertidal. Recovery of these green algae in 1-m^2 sterilized areas of substrate at the outfall occurred within two months, while more complex algal assemblages at stations away from the outfall recovered within twelve months.

Munda (1974) studied the effects of sewage discharge on littoral algae in a land-locked fjord in western Norway (Bergen) and on the coast of the northern Adriatic at Rovinj and reported large changes in benthic algal associations. At the coastal site, fucoids were eliminated from polluted shores (i.e., *Pelvetia canaliculata, Fucus spiralis, Fucus serratus, Ascophyllum nodusum, Fucus vesiculosus*) and replaced by *Enteromorpha* spp. associations. Immediately adjacent to the outfall, algal biomass was very much reduced and represented by *Blindingia minima* and blue-greens. Similarly, with increased sewage input to the fjord, the *Fucus vesiculosus* association was replaced by *Ascophyllum nodosum* or *Chondrus crispus*. An *Enteromorpha intestinalis* - *E. compressa* association dominated moderately polluted shores, while only a *Blindingia minima* - blue-green association was present at heavily polluted sites adjacent to the discharge.

Thorn (1983) found that cover of *Fucus distichus* var. *edentatus* in Puget Sound decreased with increasing sewage pollution as well as with increasing wave exposure and depth. Bellan-Santini (1968) reported on the disappearance of *Cystoseira stricta* in the presence of sewage in Marseille, France. Dawson's 1959 and 1965 surveys in southern California indicated that sewage had greatly altered intertidal communities, particularly at Whites Point. Recovery has followed changes in treatment and outfall location (Thom and Widdowson 1978; Harris 1983). Both the intertidal flora and fauna adjacent to a Carmel Bay, California discharge were less diverse than at a control site (Abbott 1973). Only 50% of the algal species typical of the area were represented at the discharge site, while 85% were present at the control station.

D. Pulp Mill Wastes

It is generally recognized that ecological impacts of organic pollution such as pulp mill wastes on soft-bottom benthic communities is attributable to the long-term sedimentation and accumulation of organic matter and associated materials. While accumulated organic wastes have also been reported to impact hard bottom subtidal communities (e.g., Christie and Green 1982), there is little information on effects of organic wastes on rocky intertidal habitats. This may be because these wastes do not accumulate on rocky shores.

Pearson (1980) noted that the effects of pulp mill effluent have been related to 1) deposition of suspended solids, 2) toxicity of constituents, 3) biochemical oxygen demand (BOD) of dissolved organics, and 4) to effluent turbidity. Although changes in these parameters are more likely to affect soft bottom subtidal communities, effects have been documented in rocky intertidal habitats. For example, Hellenbrand (1979) found some evidence for reduced productivity of *Fucus vesiculosus* exposed in the laboratory to treated Kraft mill effluent. Respiration was also reduced in *Chondrus crispus* and *Ascophyllum nodosum*, but no changes in photosynthesis were detected. Results of transplant experiments in the field indicated that algae maintained in close proximity to the outfall (600-2100 m) showed increased rates of photosynthesis.

Cross and Ellis (1981) studied changes in the distribution and abundance of oligochaetes, *Fucus*-epifauna, and rocky intertidal assemblages in a British Columbian "fjord" resulting from reductions in discharge of sulphite pulp mill wastes. Their data suggest that tolerance of littoral algae to pulp mill effluent varied with species and distance from the discharge. The order of tolerance of algal species was *Enteromorpha* > *Fucus* > *Ulva*.

E. Recreational Use

The ecological effects of recreational use of rocky intertidal shores represent impacts that differ greatly from those normally associated with pollution. We have little understanding of the biological responses to such disturbances as trampling (Liddle 1975). Human use effects, e.g., trampling, "souvenir" collection, handling, bait collection, also vary in time and space. Consequently recreational impacts on rocky shores are not easily studied and data are difficult to interpret. Most of the published information is based upon qualitative observations made at high public use sites and inferences made from ecological surveys (e.g., Dawson 1965). Documentation relating recreational use to specific impacts is still very tenuous. Beauchamp and Gowing (1982) and Ghazanshahi et al. (1983) summarize the limited information on this subject.

Beauchamp and Gowing (1982) studied three rocky intertidal sites that varied in degree of public accessibility. Based upon destructive quadrat sampling and counts of people, species richness and density decreased with increased accessibility, a trend that was more pronounced in the mussel bed assemblage than in other hard substrate assemblages. Presence of *Pelvetiopsis limitata* and the bivalve *Lasaea* sp. varied directly with accessibility, while no differences in densities of mussels or barnacles, or in algal diversity were detected. Seasonal differences in invertebrate and algal densities were evident at all sites.

In a study of visitor impact on Anacapa Island, California, Littler (1978) surmised that algae with a high surface to volume ratio (e.g., filamentous and sheet forms) were indicative of stressful environments, i.e., increased human use.

In their review of the literature, Ghazanshahi et al. (1983) note that Chan (1970) and Chan and Molina (1969) reported lower abundances of mussels, anemones, gastropod, and seastars with greater human use. Similarly, Zedler (1976, 1978) found lower abundances of corralling algae, *Phragmatopoma californica*, *Collisella digitalis*, and large *Lottia gigantea* in areas of greater human use at Cabrillo National Monument, Pt. Loma, California. In their own study of 13 littoral sites around the Pales Verdes Peninsula, Ghazanshahi et al. (1983) list species likely to be affected by public use (Table 7). Although sampling error, spatial and temporal heterogeneity, and other differences between sites contributed to substantial variation in the data, changes in abundances could be related to public use for some species, including: *Mytilus californianus*, *L. gigantea*, *Pisaster ochraceus*, *Collisella digitalis*, *Balanus glandula*, and *Phragmatopoma californica*. No differences between sites were evident based upon total species numbers or diversity, even though changes in abundance were detectable. Abundant algae were more likely to be damaged by trampling while less abundant algae were less likely to be so damaged. Reduction in competitively dominant algae enabled increase in some less abundant invertebrates. Mobile invertebrates were less impacted by trampling than sessile species. The authors concluded that recreational use can alter rocky intertidal ecosystems, and some types of recreation uses may have long-lasting effects (e.g., collection of long-lived limpets might alter grazing patterns for several years.).

Table 7. Rocky Intertidal Species Likely to be Affected by Public Use (trampling, overturning rocks, collections; from Ghazanshahi et al. 1983).

Algae	Invertebrates
Chosen from general survey results	
Egregia menziesii	*Tegula funebralis*
Corallina vancouveriensis	*Collisella conus*
Rhodoglossum affine	*Notoacmaea fenestrata*
Gigartina spinosa	*Nuttalina fluxa*
Gigartina papillata	*Chthamalus* sp.
Gigartina leptorynchos	*Balanus glandula*
Gigartina canaliculata	*Serpulorbis squamigerus*
Gelidum pusillum	
Chondria californica	
Colpomenia perigrina	
Ulva sp.	
Enteromorpha sp.	
Chosen from literature reports	
	Strongylocentrotus purpuratus
	Collisella scabra
	Collisella digitalis
	Anthopleura sp.
	Tetraclita squamosa
	Pollicipes polymerus
	Lottia gigantea
	Phragmatopoma californica
	Mytilus californianus
	Pisaster ochraceus

VI. CONCLUSIONS

The studies we have reviewed indicate that there are complex spatial and temporal patterns on rocky shores in central and northern California. At the large spatial scale of latitude, gradual and, in a few cases (e.g., Point Conception), fairly abrupt changes occur in intertidal species composition. Some of these changes undoubtedly have secondary effects on associated species, but few of these effects have been examined (Sections II.A.1 and III.B.1). There is evidence that recruitment of some invertebrates may be more sporadic north of Point Conception (Section III.B.1.b), perhaps leading to more variable succession on more northerly shores. Studies needed to answer this question remain to be done.

Temperate rocky shores are renowned for their spatial variability between tide marks. There have been numerous descriptions of this zonation (Section I), and experimental studies have found a variety of causes (Sections II.A.2 and III.A.2). Spatial variability or patchiness within particular intertidal zones or assemblages also has been long recognized, but quantitative descriptions of these patterns are few, and experimental investigations of their causes are just beginning (Sections II.A.3 and III.A.4).

With the exceptions of seasonal changes in the high intertidal and splash zones, and changes associated with occasional severe storms and toxic chemical spills, temporal variability in this community is not as obvious as spatial variability. As discussed in Sections II.B and III.B, however, and emphasized by Connell and Sousa (1983), this apparent temporal stability may be an illusion resulting from lack of information on the demography of those species that are the visual dominants of intertidal assemblages.

It is apparent that numerous factors are responsible for spatial and temporal patterns on any particular rocky shore, with disturbances caused by wave action, grazing, and predation being of special significance. Succession following such disturbances is a complex phenomenon that changes with the degree of disturbance, the life history characteristics of the organisms disturbed, dispersal, recruitment, and a variety of possible interactions among species. The importance of dispersal and recruitment to recovery from disturbance still remains largely unknown in this and other geographic regions; studies of these processes are essential if succession isto be better understood.

Discrete disturbances resulting from oil spills and other pollution events are often most extensive in the high intertidal and commonly result in a particular recovery sequence of ephemeral algae followed by perennial species (Section V). This sequence is perhaps a result of the removal of grazers that often selectively consume ephemeral species, and the removal of other organisms that would otherwise inhibit ephemeral algal recruitment. Ephemeral species persist when human disturbances become chronic. Studies of natural disturbance suggest that this may be because these species produce more propagules that disperse relatively far and readily colonize and grow rapidly on bare rock, They may also persist because biological disturbance is reduced in the continued absence of large grazers and predators, because recruits of sessile perennials are continuously killed, or as a result of some combination of these processes and life history characteristics.

Prior reviews of rocky intertidal communities in the northeastern Pacific have concluded that variation and instability are the norm rather than the exception (e.g., introductory quote; Castenholz 1967; Connell 1972), and this review substantiates that conclusion. In this context, it is refreshing to note that since the reviews by Castenholz and Connell, a major shift has occurred in intertidal research from descriptive-correlative studies and searches for single factors to explain pattern (e.g., tidal factors, all important predators or grazers, competition) to investigations that describe and examine a variety of processes over a range of temporal and spatial scales. We now know much more about the causes of variation. Additional research on community and demographic patterns, combined with descriptive work at more sites, should provide the larger context needed to evaluate the generalizations that emerge.

The following generalizations were abstracted from the text and provide a formatted synopsis of conclusions:

A. Objective: To review the spatial and temporal variation, and its causes, in rocky intertidal communities of central and northern California.

1. <u>Limitations to generalizations</u>

   a. Non-random distribution of research sites

      o most studies are done in vicinity of marine labs where habitats may not be typical

      0 most studies are done on relatively low relief, gentle inclines while most common habitat may be irregular rocky outcrops and boulder fields

      0 some processes are poorly investigated (e.g., recruitment)

      0 studies are rarely repeated at different sites

B. Spatial Variation

1. <u>Description</u> - spatial variation has been described at various spatial scales, especially geographic (with latitude), local (site), within site (zonation), and within zones (patches).

   a. Geographic

      o major emphasis is on changes in species composition

      o three zoogeographic provinces are generally accepted to occur along the coast between Alaska and Baja California (Aleutian, Oregonian, and San Diego)

      o changes in species are generally gradual with exception of area around Point Conception

      o rapid changes in species composition around Monterey may be an artifact of collection intensity and habitat diversity

      o recruitment of certain intertidal animals may be more sporadic at higher latitudes

b. Local (site)

- most commonly noted pattern is change in species composition and distribution along gradient of wave exposure
- descriptions at this scale are mostly qualitative
- "wave tolerant" species are more common, and intertidal zones are elevated and widened as exposure increases

c. Within Site (zonation)

- most well studied spatial pattern
- plants and animals, especially sessile species, generally have discrete vertical limits of distribution on the shore, producing horizontal bands or zones.
- species composition and extent of zones varies, but there is a general pattern of ephemeral algae and herbivorous gastropod in the splash zone, barnacles, herbivorous gastropod and perennial red and brown algae in the high intertidal zone, mussels, goose barnacles, turban snails and various algae in the mid-intertidal or mussel zone, and various red and brown algae and surf grass in the low intertidal zone

d. Within Zone (patches)

- organisms commonly occur in patches within a zone
- with few exceptions, patchiness has not been quantitatively described

2. <u>Causes</u> - most studies have examined processes affecting adults, and many described "causes" are based on correlations.

a. Geographic

- temperature: gradually increases tothe south with discrete increase at Point Conception. This is the primary factor correlated with changes in species composition but there are few experimental tests
- disturbance: waves and associated disturbance such as log battering may decrease to the south
- species interaction: latitudinal changes in one species (e. g., grazer, competitor, canopy-forming alga) may affect the distribution of associated species

b. Local

- wave action: varying tolerance to physical removal by water motion directly affects distribution. Secondary effects on oxygen concentration, desiccation, sedimentation, scour, etc.

- topography: variations in slope and relief are associated with changes in species abundance and distribution (via changes in submergence time, small scale water motion, etc.)

- substratum type and stability: affects water holding capacity, ability of organisms to attach, scour, and burrow

- species interactions: differences in species distribution caused by any of the above physical factors may have secondary effects on associated species (e.g., predators on mussels)

c. **Zonation** - the results of field experiments have led to the rejection of the critical tide level hypothesis as a general explanation of intertidal **zonation.** The current working hypothesis is that upper limits are determined directly by physical/chemical factors associated with tidal changes, while low limits are determined by biological factors.

- tidal fluctuation: appears to generally determine the upper limits of distribution via changes in desiccation, food availability, etc., however, there are few experimental tests of this. There is some evidence for grazer control of upper limits

- predation: can determine the lower limits of prey distribution

- competition: can determine the lower limits of competitors

- grazing: can affect lower and upper limits of algae

- **mutualism:** may determine the distribution of associated obligate species (e.g., fauna in mussel beds)

- sand burial and abrasion: may alter or eliminate zones, especially the lowest

d. Patchiness - evidence for causes derived primarily from correlations

- substratum topography and stability: primary effects are on microclimate (e.g., presence/absence of tide pools) and creation of bare- space 'when rock breaks away. Effects on grazer/predator foraging has secondary effects on prey distribution

- physical disturbance: water motion, extreme climatic events, sand burial, battering by cobbles, etc., produces clearings at various time intervals of varying severity and size

- predators and grazers: may remove patches of prey

- successional processes: affect composition of a particular patch after disturbance (see Disturbance below)

c. Temporal Variation

1. <u>Description</u> - has been poorly described (few long-term studies). Overall qualitative impression is that, with few exceptions, temporal variation in the abundance of adults is low both seasonally and from year to year.

   a. Year to Year

      - low natural variability in abundance with exception of mussel beds within the range of the sea otter
      - reduction in number of species and increase in abundance of ephemeral species in areas chronically affected by pollution
      - episodic, site specific variability in species composition and abundance associated with discrete environmental changes

   b. Seasonal and Smaller Scale Patterns

      - perennial algae may vary in cover by up to 50%, with highest cover in summer. Variability in long-lived animals appears low
      - most algae reproduce throughout the year, with peaks in fall and, to a lesser extent, in summer and winter
      - intertidal animals in central California often reproduce throughout the year, with peaks in the spring and summer, and lows in the fall
      - animals with feeding larvae reproduce slightly earlier than those with non-feeding larvae
      - animals such as some sea stars may become less active in winter at high latitudes
      - mobile predators and grazers commonly move up in the intertidal during neap tides of early fall and spring
      - many grazing animals are more active at night during low tides

2. <u>Causes</u>

   a. Year to Year

      - Sea otter foraging: decline in extent of mussel beds
      - chronic pollution, especially from sewage: local effects on species composition and abundance
      - earthquakes, rockslides, extreme hot weather, discrete pollution events: variable changes in communities depending on severity of disturbance and subsequent recovery processes

b. Seasonal and Smaller Scale

- o winter storms and associated sand movement: mortality
- 0 changes in temperature, day length, food supply: influence reproduction
- 0 neap tides: allow some animals to spend more time foraging higher in the intertidal zone
- 0 low tides at night: more activity due perhaps to reduced desiccation and-predation

D. Disturbance and Succession

1. Natural Disturbance

a. Numerous factors (discussed in B.2.d above) cause the removal or organisms from rocky intertidal habitats. These disturbances vary in time and frequency of occurrence, severity of removal of organisms, and extent of removal.

b. The resources (especially space) made avail able by disturbance become available to other organisms, initiating succession.

- o all factors that affect the demography of a particular species (including availability and dispersal of spores and larvae, recruitment, growth rates, competition, grazing and predation) can affect the composition of a patch after a disturbance

c. The variability in disturbance and succession thus appears to produce much of the patchiness noted within intertidal zones.

d. Total disturbance or complete clearing probably rarely occur in nature, so the use of data from complete, experimental clearings to understand natural disturbance should be done with caution.

- o in addition to the processes in D.1.b above, succession in the edges of large, completely cleared plots is more affected by grazing than in the centers

2. Man-caused Disturbance

a. Disturbance (pollution) from petroleum hydrocarbons, oil dispersants, municipal wastes, pulp mill wastes, and recreational use in the intertidal zone is reviewed.

b. Tanker spills and operations account for about 35% of hydrocarbon input to the oceans. Most catastrophic (large, concentrated) oil pollution occurs near shore and often impacts the intertidal.

- o effects vary with kind, amount and duration of spill

- o in general, grazers are killed leading to blooms of ephemeral algae that are replaced by perennial species in varying lengths of time if pollution is not chronic

c. Oil dispersants vary in toxicity. Their effects vary depending on kinds and amounts used, and duration of use. Dispersants may cause more disturbance than oil itself.

- o recovery processes are similar to those following oil pollution

- 0 studies of accidental oil spills and associated clean-up procedures suffer from lack" of uniform methods, lack of controls, and lack of assessment of all but gross mortality of abundant, large organisms. Experimental studies vary in design, making generalization difficult.

d. Pollution by municipal wastes is usually chronic, and generally leads to a reduction in numbers of species and an increase in ephemeral ("tolerant") opportunistic species.

- o recovery occurs as treatment improves or if outfall is removed

e. Effects of pulp mill wastes are poorly known. Available data suggest they are similar to sewage.

f. Disturbance from recreational use comes mainly from trampling and collecting.

- o as use increases, species richness decreases and ephemeral species often increase

- o collection of long-lived species can have long lasting effects of their abundance

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VIII. PERSONAL COMMUNICATIONS

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Mr. A. De Vogelaere. 1985. Moss Landing Marine Laboratories, Moss Landing, California.

Mr. B. Anderson. 1985. Moss Landing Marine Laboratories, Moss Landing, California.

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Mr. J. Boyd. 1984. California Air Resources Board.