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CHAPTER 17

The Importance of Scale in Community Ecology: A Kelp Forest Example with Terrestrial Analogs

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CONTENTS

1 INTRODUCTION

The scale of resolution chosen by ecologists is perhaps the most important decision in their research program, because it largely predetermines the questions, the procedures, the observations, and the results. This chapter summarizes aspects of our long-term studies in southern California kelp forests which have focused on (1) community structure as modulated by patch dynamics and (2) the population dynamics of a few important species. Here we discuss our results and argue that larger scales would improve our understanding and that this is generally true in ecological research, a position we document with literature from the American Southwest.

There seems to be a tendency for ecologists to reduce the scale of their research both to make it more tractable and to ensure prompt and clean results. Marine examples and good summary papers include boundary layer hydrodynamics of algae and their role in nutrient transfer and irradiance (Wheeler and Neushul, 1981) and soft substrata (Eckman, 1979), larval behavior (Thorson, 1946; Wilson, 1952), adult polychaete behavior (L. A. Levin, 1981, 1982), adult–larval interactions (Woodin, 1976), resistance of fouling communities to invasion (Sutherland, 1981), and so on. Research continues on such popular questions as competition (Connell, 1983) and predation/disturbance (Paine and Levin, 1981). Here we argue that populations of coastal marine species, especially those contributing the "strong interactions" (*sensu* Paine, 1980), are characterized by episodic recruitment patterns unpredictable in time and/or space (see summary in Dayton, 1983). Because most such species have long-lived individuals and slowly declining populations, recruitment pulses result in long-lasting spatial and temporal patterns. The importance of year-class phenomena is well known in pelagic fishery literature (Cushing, 1975), where much research focuses on large (1000s of km) and mesoscale (100s of km) oceanic patterns (Cushing and Dickson, 1976; Parrish et al., 1981, for summaries) and climatology (Lasker, 1978). Many ecologists, on the other hand, focus on their small scale questions amenable to experimental tests and remain oblivious to the larger scale processes which may largely account for the patterns they study.

2 PATCH DYNAMICS OF KELP FORESTS

Like most communities kelp forests are distinctly patchy. The patch types are characterized by vegetation layers which are defined by distinct morphological adaptations including (1) a floating morphological structure in which the canopy is at or near the surface, (2) a stipitate morphology that supports the canopy above the substratum, (3) a prostrate structure in which the fronds lie on the substratum attached by a short stipe, (4) a turf composed of many species of coralline, foliose, and siphonious red algae, and (5) a pavement of encrusting coralline algae. There is a convergence into these morphological types as most kelp communities have similar canopy guilds, but the actual species differ. In California kelp forests the above categories often include more than one species within a given patch.

The persistence, resistance, and resilience stabilities of these patches have been evaluated in three California habitats: Pt. Loma, San Diego County; Bird Rock, Santa Catalina Island in Los Angeles County; and Pt. Piedras Blancas, San Luis Obispo County (Dayton et al., 1984, in press). The three habitats represent different types of physical stress. The persistence of individual patches was evaluated when possible by observing their edges over time and by evaluating survivorship curves which document that the patches have persisted more than one generation. Indeed, some patches in the Pt. Loma forest are thought to have persisted since 1946 (Ron McPeak, personal communication). Resistance to invasion can be evaluated by canopy removal and transplantation experiments, whereas resistance to disturbance must be evaluated by observation and, when appropriate, by manipulation of disturbance agents. Resilience refers to the recoverability rate following a perturbation sufficient to allow colonization by different species.

The taller perennial canopy guilds dominate the competition for light but are more susceptible to wave stress, and the dominance hierarchies appear reversed in areas exposed to increasing wave stress from storms. There is a threshold (at which the plant is ripped free) beyond which the intensity of the storm is irrelevant to the plant. More important, however, is the frequency of storms sufficient to rip plants free. The main source of mortality at Pt. Loma is from entanglement with storm-dislodged *Macrocystis pyrifera* plants. But normally the disturbed area is sufficiently small that the previous patch type recovers. At Pt. Piedras Blancas, where storms are much more frequent and intense, there are different patterns: in some areas *Macrocystis* fronds are ripped free but the plants (and the patch) persist, but in other areas (successful transplantations notwithstanding) this species simply does not persist. In more wave-stressed situations, the long-lived stipitate species (*Pterygophora californica*, *Eisenia arborea*, and *Laminaria digitata*) seem more tolerant. Finally, the prostrate *Dictyoneurum californica* and turf-forming articulated coralline algae seem extremely tolerant to wave stress. In these more exposed situations the lower canopy guilds become the respective dominants. In other areas, often with unstable substrata or patchy but intense sea urchin grazing, annual species such as *Nereocystis luetkeana* or *Desmarestia* spp. are most abundant.

Sea urchin grazing is another well-known form of disturbance in kelp forests (Lawrence, 1975); and Vadas (1968), working in Puget Sound, Washington, has documented the tradeoffs between unpalatability (*Agarum* spp.), ephemeral tactics with high palatability and low competitive ability (*Nereocystis*), and high palatability and competitive ability (*Laminaria* spp.). In southern California sea urchins are occasionally responsible for denuding large areas of algae, but predators such as spiny lobsters and fishes (Tegner, 1980; Tegner and Dayton, 1981; Cowen, 1983; Tegner and Levin, 1983) or, north of Pt. Conception, sea otters (Lowry and Pearse, 1973; Woodhouse *et al.*, 1977) usually prevent sea urchin populations from devastating entire kelp forests as they do in Nova Scotia (Mann, 1977) or sea otter-free areas of the northeast Pacific (Estes and Palmisano, 1974; Simenstad et al., 1978). The scale of urchin disturbance varies from the small <1 m ambit from a refuge to a few square meter area in a boulder area patch to a few hectares to an entire coastline. Obviously it is extremely important to understand the processes determining the actual scale; and probably in most cases the processes involve dispersal, which immediately implies a large scale oceanographic study.

Resistance to invasion is another important asset of each patch type in southern California (Dayton et al., 1984, in press). In most cases distinct patches resisted invasion for over 10 years. The mechanisms of resistance involve competition for light and limits to spore dispersal as demonstrated by clearance experiments and seeding with fertile sporophylls. The area of the disturbance is an integral component of patch stability: small disturbances killing only a few plants usually do not alter the patch composition because the disturbed area is almost certain to be recolonized by members of the existing species, both from preceding sporulations and from swamping by spores from nearby plants. Larger disturbances involve the relative dispersal abilities of the different species. The mechanisms of kelp dispersal involve very limited spore dispersal or most commonly, drifting plants leaving a trail of recruits or fragments of fertile material which need to be snagged and held against the substratum long enough to inoculate an area with a high density of spores. Furthermore, the different species (especially their gametophytes) have very different physiological thresholds (Lüning and Neushul, 1978). Finally, the reproduction of most kelps is distinctly seasonal, with the spores being released in the winter. For these reasons there are different thresholds affecting the probabilities of invasion into different-sized disturbances. The actual observed spatial scales range from that of the attachment site of single plants to very large areas resulting from catastrophes such as overgrazing, unusual storms, or severe climatic fluxes such as the northern "El Niño" of the late 1950s, which devastated the kelp forests (IMR, 1963; Chelton et al., 1982).

3 ROLE OF SEA URCHINS

As mentioned above, sea urchins are particularly important grazers; in southern California *Strongylocentrotus purpuratus* and especially the large, motile *S. franciscanus* are the most important. For reasons not completely understood but probably relating to hunger, they occasionally move out of their crevices and forage in large aggregations; when this happens large areas of a kelp forest can be denuded of macroalgae, leaving only a pavement of encrusting coralline algae (the "barren areas" of Lawrence, 1975). Enough urchins remain foraging in these "barren areas" to preclude recruitment of macroalgae so that these patches, too, are stable for months and sometimes years.

Even when restricted to its crevice habitat, *S. franciscanus* has important community roles. It has a nocturnal foraging pattern in which it grazes out about a meter from its crevice or boulder; this results in a "barren" zone free of macroalgae, and in some areas this barren zone offers a superior habitat to a cup coral, *Balanophylia elegans* (Gerrodette, 1981; Dayton et al., 1984, in press). Perhaps more important, the encrusting coralline algae offer important inducements for abalone larvae to settle (Morse et al., 1980); thus urchins maintain recruitment areas for abalone. In addition, the spine canopy of *S. franciscanus* is a refuge from predators to recently metamorphosed individuals of several species, including abalones and the *S. franciscanus* themselves (Tegner and Dayton, 1977). Another important role of sea urchins is that of snagging and holding drift kelp, much of which is fertile, long enough to allow a local inoculation of spores, especially along the ridges and ledges above the urchins. This is a critical factor in the dispersal of kelp.

4 KELP FOREST EFFECTS ON CURRENTS: NUTRIENTS AND LARVAL TRANSPORT

Dominant current flows in southern California coastal areas are in the longshore directions (Winant and Bratkovich, 1981). The terrestrial boundary constrains cross-shore currents to be weaker and generally to have long-period motions. The main sources of cross-shore transport are internal tides, the strength of which vary with the seasonal stratification of the water column. These currents supply nutrients and planktonic larvae. Just as terrestrial forests affect the wind (Raupach and Thom, 1981), the drag of the kelp forest strongly alters the water flow (Jackson and Winant, 1983). Jackson and Winant's preliminary data show that the mean current inside the kelp forest at Pt. Loma is 0.1 cm/sec compared to 0.3 cm/sec outside the forest. The magnitude of the calculated drag implies that the most important transition from the outside to the inside of the forest in the longshore direction should occur within approximately 100 m of the upstream edge. While organisms on the outer edge get nutrient- and larval-rich water, those on the inside are exposed to water from which nutrients and plankton are filtered. The longshore within-kelp-forest water movement along the length of the 8 km kelp forest at Pt. Loma is sufficiently slow that the transit time is about 220 hr. The biological uptake of nitrate can occur at 23%/hr (Jackson, 1980), so nutrient stress may be rather common. Similarly, once presented with appropriate clues, at least some larvae begin settlement behavior very quickly (Hinegardner, 1975). It is clear that the kelp-induced drag is sufficient to much reduce or eliminate the transport of nutrients and many larvae from the interior of the kelp forest. Cross-shore currents provide an alternate mechanism to reach interior parts of the kelp bed. Such currents are weaker and more sporadic than the longshore, but the shorter distance may compensate. Because an important source of cross-shore transport is internal tide motion, this depends on the thermal stratification of the water column, which is much stronger in the summer.

The time that larvae spend in the water column is variable but obviously important to the scale of study. Larvae known to have long (weeks to months) planktonic lives (the cyphonautes larvae of the bryozoan *Membranipora membranacea* and the plutei larvae of the sea urchins) tend to have large (often order of magnitude) decreases in density from upstream to the middle to the downstream edge of the kelp (Bernstein and Jung, 1979; personal observation). Recruitment of *S. franciscanus* over a 3-year period was consistently about two times higher on the outside than the inside edge of the Point Loma kelp forest (Tegner and Dayton, 1981). Animals with somewhat shorter larval life-spans such as green abalone, *Haliotis fulgens*, which have larval spans of 4–9 days (Leighton et al., 1981), are strongly influenced by current flow rates and distances between appropriate habitats. The depression of the current by the kelp forest can act to "trap" the larvae within a large kelp forest such as Pt. Loma. Finally, many of the invertebrate species within the kelp forests—such as sponges, bryozoans, and tunicates—have larvae with very short larval life spans (minutes to a few hours). These larvae are likely to be retained within the kelp forest. Thus, physical events on the scale of a kelp forest have important consequences regarding gene flow and population dynamics.

5 EDGE EFFECTS AND THE CRITICAL SIZE OF A KELP FOREST

Edge effects, such as the apparent aggregation of organisms at the periphery of the patches, are another general ecological feature; all naturalists are aware of the importance of this environmental heterogeneity (Elton, 1966). The mechanisms contributing to edge effects are varied. They include the simple physical effect described above and the aggregation of animals that use the shelter as a refuge from predation such as seen for sparrows (Pulliam, personal communication), rodents (Bartholomew, 1970), and herbivorous fish (Randall, 1965). The edge facilitates the filtration of food (perhaps by species including web spiders or insectivorous birds). These mechanisms contribute to a pronounced edge effect in larger kelp forests. This has been described by Hobson and Chess (1976), and Bray (1981) experimentally documented the filtering of plankton by planktivorous fishes. Hobson (1976) and Bernstein and Jung (1979) found this edge effect for a picker fish, which cleans other fish and forages on the bottom and on kelp fronds. The kelp forest may offer shelter from predation by sharks (Tricas, 1979) or seals or simply provide structure for fish to orient to; we suggest also that the plankton accumulates at the upper edge of the kelp forest as the kelps slow and divert the currents and that those larvae competent to settle do so, either on the bottom or on the fronds directly.

Another scale-related complication of an edge effect is that it can determine size thresholds of kelp forests. Kelp fronds are grazed by fishes such as the half moon, *Medialuna californiensis*; the opaleye, *Girella nigricans*; and the señorita, *Oxyjulis californica*, which may consume the frond directly or, more commonly, incidentally as they pick encrusting organisms (North, 1971; Bernstein and Jung, 1979). Isolated or small patches of *Macrocystis* plants too small to have an edge effect often attract unusually high densities of encrusting organisms throughout the patch and are thus especially attractive to the fishes that graze the fronds at a rate much higher than the frond growth rate. This sets a size threshold for the establishment of a stable kelp forest (North, 1971). At the other extreme, it is conceivable that the absorption of nutrients by the outer plants can decrease nutrients sufficiently that plants in the inner areas cannot survive. Although this has not been observed, inner kelp plants often are much less healthy (Bernstein and Jung, 1979; Dayton et al., 1984, in press), and this could, at least in theory, establish the maximum dimensions of a kelp forest.

6 THE IMPORTANCE OF LARGER SCALES IN SPACE

Kelp forests are not isolated systems driven entirely by local processes; they are also driven by much larger mesoscale physical forces which may involve all of the Southern California Bight and the very much larger California Current System (Fig. 1). Large but poorly understood oceanic processes in the Pacific cause large scale, low frequency changes in the California Current leading to highly significant interannual variability in physical and biological parameters throughout the system (Bernal, 1981; Chelton et al., 1982; Fig. 2). These and other more local (mesoscale of 100s of km) oceanographic anomalies are probably responsible for the episodic recruitment events which seem to characterize most of the world's coastal fisheries. These patterns are also true for many coastal benthic populations (summarized in Dayton and Oliver, 1980).

An example of a large scale event was the "El Niño" of 1957–1959 when the California Current system was marked by abnormally high water temperatures (Fig. 2), an increase in salinity, decreased southward flow, raised sea level, decreased abundance of zooplankton, and a virtual collapse of all the kelp forests, even those of the offshore islands (IMR, 1963; Chelton et al., 1982). In addition, many southern species were observed far north of their usual range and some successfully spawned off southern California (Radovitch, 1961). It is clear that a large amount of tropical warm water intruded into the California system in the same manner as the more famous southern "El Niño" off Peru. There was little documentation of effects on kelp communities; however, it is clear that most of the kelp forests virtually

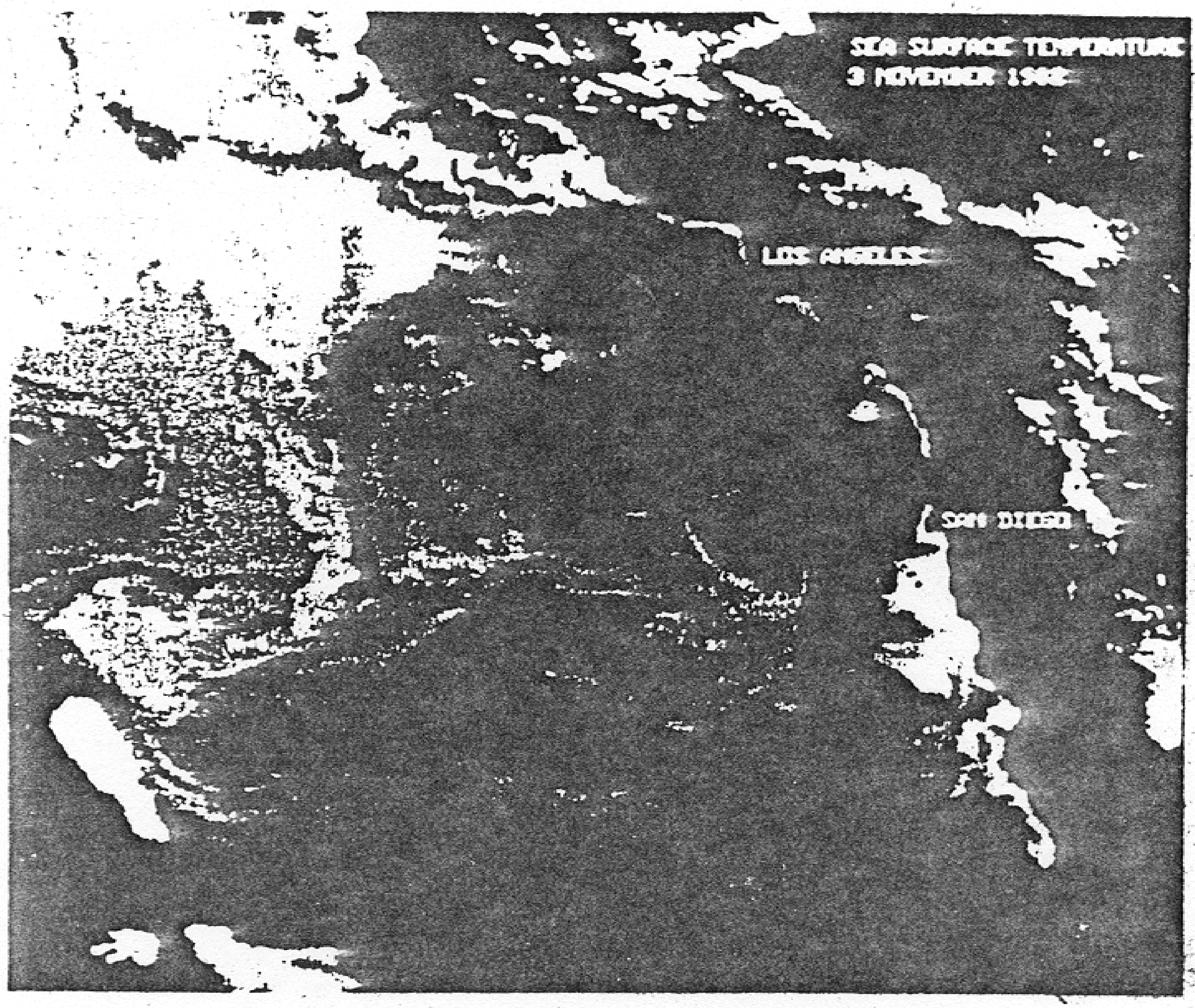

Figure 1. Thermal image of the Southern California Bight on 3 November 1982. The warmest surface temperatures, black, grade to the coldest, white; however, the white masses over the mainland and in the lower left are clouds. Conspicuous processes include the cold California Current moving south from Point Conception. There is strong upwelling along the coast from San Diego south. Tongues of warm water are visible in black. The one closest to the coast, called the southern California eddy, brings warmer water from the south and mixes with the California Current south of the northern Channel Islands. Courtesy of Mark Abbott, Scripps Institution of Oceanography.

disappeared and sea urchin densities vastly increased (IMR, 1963). In some areas such as Palos Verdes, Los Angeles County, the kelp only started returning in the late 1970s; on the other hand, kelp forests returned within a few years in other areas such as the southern Channel Islands. Unfortunately, the patterns are confused by improvements in coastal sewage disposal systems and heavy increases in fisheries, especially of lobsters and abalones, both of which affect sea urchins (Tegner, 1980) and active kelp restoration.

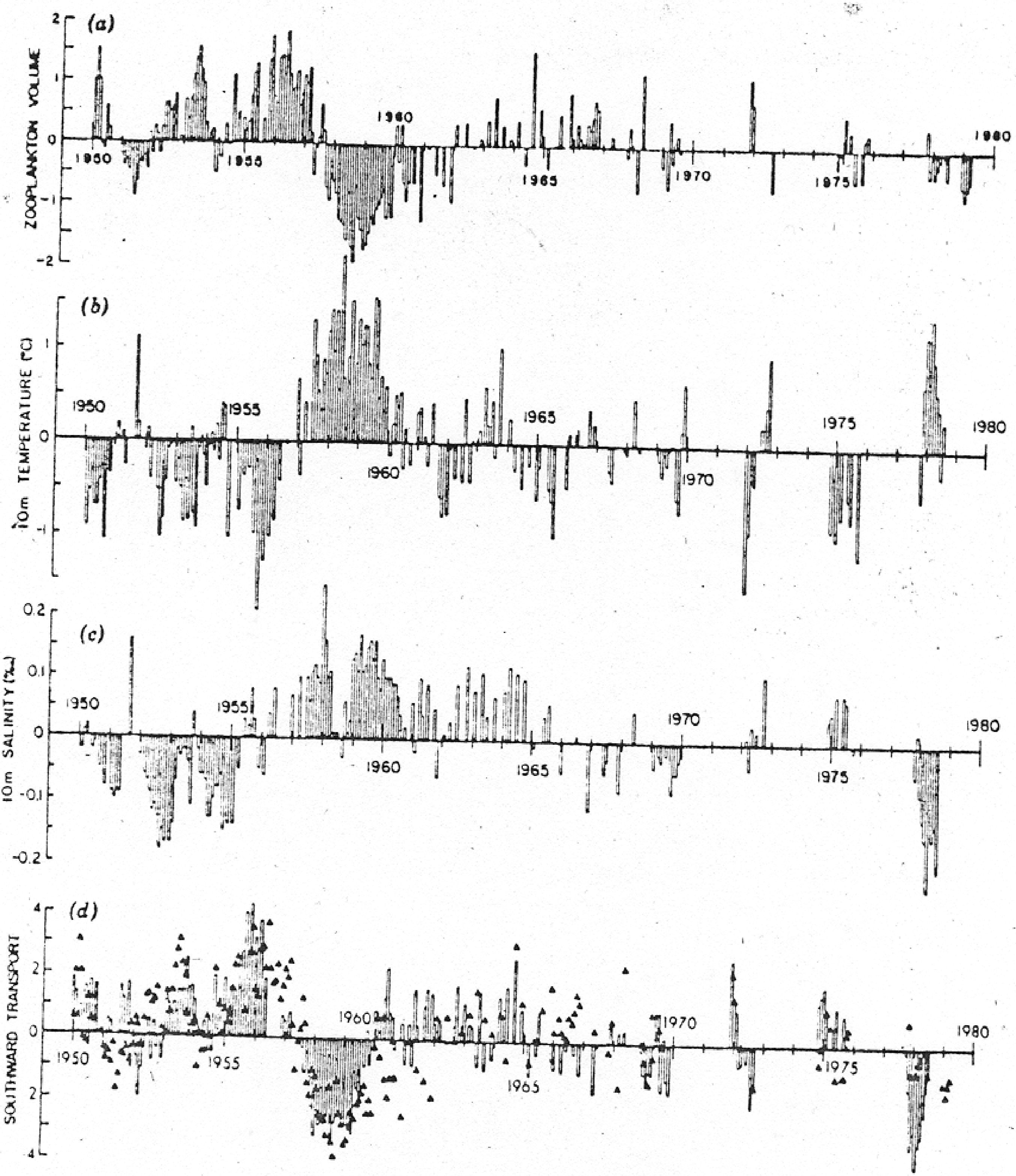

Figure 2. Time series of nonseasonal values of four parameters in the California Current: (*a*) the average zooplankton volume (10^{-3} ml m^{-3}) time series for CalCOFI lines 60-136; (*b*) the average 10 m temperature over 150 hydrographic stations in the same area; (*c*) the average 10 m salinity over 150 hydrographic stations in the same area; (*d*) southward transport as determined by principal component analyses of 0/500 steric height. The triangles in (*d*) represent the zooplankton time series shown in (*a*). From Chelton et al. (1982).

Populations with long-term planktonic larvae have been troublesome to naturalists and theoreticians alike (Thorson, 1950; Scheltema, 1974; Strathmann, 1974; S. Levin, 1976; Jackson and Strathmann, 1981). We argue that larval dispersal is a key to understanding the response of communities to such disturbances, but despite the obvious importance to most nearshore communities, larval ecology and dispersal remain mysteries that are rarely acknowledged. This is surprising because important species in even such well-known systems as the rocky intertidal commonly exhibit rare or episodic recruitment events that probably relate to larval parameters but have important community consequences. For example, *Mytilus californianus* is the dominant species in the Pacific Northwest, yet its recruitment is highly episodic (Dayton, 1971; Paine, 1974, 1980). Similarly, the lower intertidal is strongly influenced by *Strongylocentrotus purpuratus* (Paine and Vadas, 1969; Dayton, 1975), the recruitment of which is also episodic and unpredictable (Ebert, 1968; Dayton, 1975a; Paine, 1980). Clearly larval dispersal is a major element of episodic recruitment and is critical to the structure of most benthic communities.

We have observed large scale spatial variation in recruitment of the giant red sea urchin, *Strongylocentrotus franciscanus*. *S. franciscanus* has a relatively long-lived pelagic larval stage (from 50 to 130 days; Strathmann, 1978; Cameron and Schroeter, 1980), and these patterns are relatively consistent over time, suggesting that large scale oceanic processes may be mediating recruitment success. Recruitment of sea urchins has been evaluated in many locations, including the Channel Islands and other parts of the Southern California Bight (Tegner, personal observation). The northwestern San Miguel and Santa Rosa Islands had recruitment rates averaging 16% and 9%, respectively, of the total populations per year from 1976 to 1980. In contrast, Santa Barbara and San Clemente Island which are further south and east in the bight, had average recruitment rates of 55% and 33% per year. The pattern observed on the northwestern islands appears to be similar to that observed along the coast of central California north of Point Conception, where recruitment rates are very low; and the southeastern islands compare with the coastline from San Diego south (Tegner, personal observation).

A number of parameters such as temperature, larval food and current patterns might be expected to affect recruitment on large spatial scales. Temperature probably has little effect as *S. franciscanus* is a northern species and southern California is near the southern limit of its range, yet the colder areas of our study (the Pt. Conception area and the northern Channel Islands) have lower recruitment. Larval food availability is undoubtedly higher in the upwelling, plankton-rich region around the northwestern Channel Islands and along the coast of central California (e.g., Smith, 1978; Parrish et al., 1981), where recruitment is lower, suggesting that larval food is not limiting recruitment success. Parrish et al. (1981) have recently proposed a relationship between large scale seasonal patterns of ocean surface drift along the California coast and reproductive strategies of successful coastal fishery species. They describe a region of maximum upwelling from Cape Blanco to Point Conception along the coast, which includes San Miguel and Santa Rosa Islands. *S. franciscanus* spawns in April–May in central California (Bennett and Giese, 1955), during the height of the offshore Ekman transport when prevailing winds cause seaward drift of surface waters (Parrish et al., 1981); thus, the larvae are spawned into a nutrient-rich environment but dispersed offshore into the south-flowing California Current. In contrast, the Southern California Bight is characterized by minimal offshore Ekman transport and a geostrophic flow pattern that features a closed gyral circulation near the coast (the Southern California Eddy; Owen, 1980) and an onshore component of flow further offshore (Parrish et al., 1981). This circulation pattern would tend to maintain the larvae in the areas of high recruitment rates.

The length of the pelagic period of larval development (a temporal scale) is a factor in limiting distributions. Over long time periods, these effects may not be evident; however, recolonization of an isolated area that has undergone a severe disturbance suggests that the interaction between time and space scales is important. Green abalones, *Haliotis fulgens*, which inhabit the shallow inner margins of kelp forests, are an example of a species with a relatively short larval life [ranging from 4 to 9 days as a function of temperature (Leighton et al., 1981)]. Our study of the recovery of green abalone populations on the once badly disturbed Palos Verdes Peninsula and a drift bottle experiment (Tegner and Butler, personal observation) suggest that the combination of the interaction of this species' location in a low current region of the forest with the currents during its spawning season and its short larval life make *H. fulgens* poor long-distance dispersers. The results from drift bottles released into green abalone habitat indicate that transport between isolated kelp forests within appropriate time periods is probably rare. They underscore the importance of endemic brood stock for the maintenance of local populations of animals with limited dispersal capabilities (Tegner and Butler, personal observation).

7 SCALES IN TIME

Developing a proper temporal perspective may be one of the most important unresolved problems in ecology, because none of us has more than one lifespan to study patterns that often have longer duration. More realistically, funding, constraints on duration of study, and academic promotional procedures force ecologists into 2- to 3-year projects; few natural patterns are of such short duration. Eventually it is only the old, often tired voices that call for better perspective; these pleas seem easily ignored. Nevertheless, the many examples of episodic natural disasters and/or recruitment and usually long-term population decline demonstrate that the natural patterns we see are "footprints" of previous events (see also Colwell, Chapter 14). This emphasizes the importance of perceiving and appreciating temporal patterns even if only by inference.

The San Diego kelp forests have been reasonably stable since 1911 when the first records were made (North, 1971). They were, however, declining in the early 1950s for various reasons including pollution, overfishing, and so on (Tegner, 1980), and they were reduced to 1% of their former cover (IMR, 1963; North, 1974; Dayton et al., 1984, in press) by the El Niño. Since their recovery from the El Niño, the percent cover has varied considerably with major storms, but the canopy has usually recovered rapidly. The data and observations in Dayton et al. suggest that 10 years is a minimal time to study patch dynamics at Pt. Loma, but cursory study of mosaics of air photos of the Pt. Loma forest taken by Wheeler North and Kelco Company suggest that 20 years is needed to see major changes in *Macrocystis* cover. The mean generation time of *Macrocystis* which survive to adulthood is less than 6 years, but stipitate kelps have much longer life-spans. Other long-term patterns observed or inferred for shellfish (Coe, 1956) and echinoderms (Merrill and Hobson, 1970; Warner, 1971) suggest that several decades are necessary for an appreciation of the temporal scale important to large invertebrates, and these scales are likely to be representative of many such populations. Some pelagic fish species have decade- to century-long fluctuations (Soutar and Isaacs, 1974; Cushing and Dickson, 1976).

Historical records in southern California show that within the last 200 years there have been several periods of very important climatological changes (Kuhn and Shepard, 1981). For example, extremely violent hurricanes from the southeast (described by mariners as being worse than the storms of Cape Horn) were relatively common in the early 1800s. The Pacific Railway Survey of 1853–1857 collected a suite of fish species off San Diego that was more tropical than any seen in subsequent decades (Hubbs, 1948). At the same time, much of the fish fauna of Monterey was made up of species now characteristic of the warmer waters south of Point Conception. Hubbs (1948), demonstrating a close correlation between average air and sea temperatures along the Pacific coast, used records of coastal air temperatures to argue that 1850 and 1860 decades were a prolonged warm period. In the early 1860s the state of California went bankrupt when the San Joaquin Valley became a lake of 30 × 300 miles while coastal areas were ravaged by floods. Another warm, wet period in 1884–1891 (including a measured ppt. of 11.5 inches in 80 min) resulted in devastating floods in southern California. These rains certainly included the Colorado Plateau, as the Colorado River at Yuma was reported to be 20 miles wide! (See Kuhn and Shepard, 1981, for more details and references.) While the El Niño of 1957–1959 was not associated with heavy rainfall, there is abundant evidence that these wet periods in the 1800s were associated with El Niños (Hubbs, 1948; Kuhn and Shepard, 1981). Thus, the massive marine shifts documented by the 1963 IMR report, Radovitch (1961), and Chelton et al. (1982) may be relatively common. Douglas (1976) correlated tree ring patterns and seawater

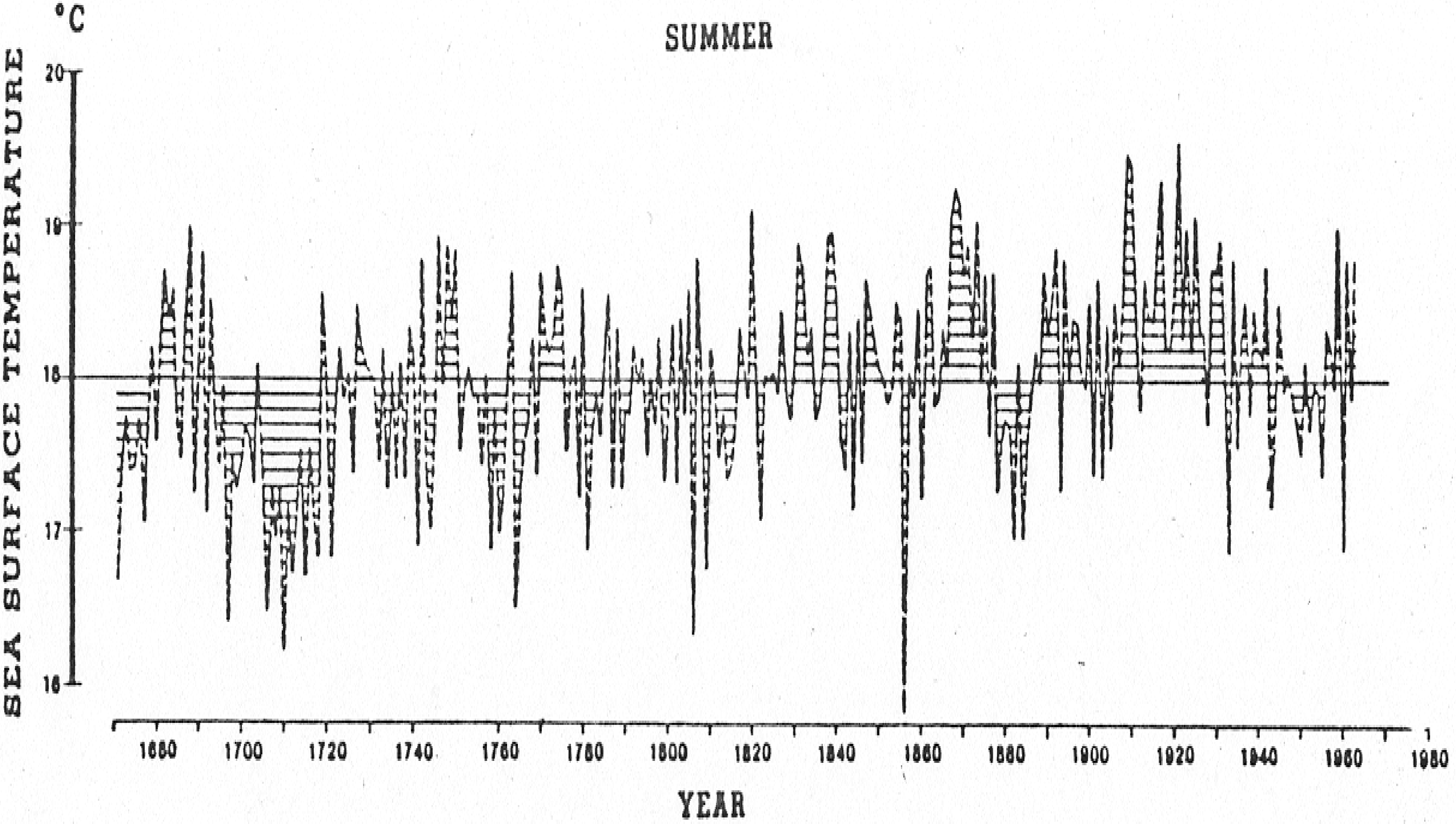

Figure 3. Summer sea temperatures 5 m below sea level at La Jolla, California, reconstructed from standardized tree ring indices for *Pseudotsuga macrocarpa* from 1214 m on the Santa Ana Mountains, California. Data from Douglas (1976, p. 188) were put in graphic form by Gerry Kuhn.

temperature. Then, using these correlations, he recalculated the sea temperature back to 1680 (Fig. 3). Although these calculations lack the precision of the anomalies evaluated by Chelton et al. (1982), they do show that major oceanic changes occur regularly in southern California.

Vermeij (1982) and Wethey (1983, in press) have compiled very convincing historical, archaeological, and paleontological data buttressing their argument that climatic shifts (over centuries) have resulted in major biogeographic shifts and even local extinctions. Several types of biogeographical shifts, each sensitive to different types of climatological change such as rainfall, temperature highs, duration of freezes, and so on, are well known in terrestrial systems; in addition, these climate changes often had catastrophic effects on human populations (see summary in Ford, 1982). Finally, at a much larger scale, there were major sea level lowerings during the Pleistocene, including a drop of several hundred meters below the present level. This would reduce the rocky habitat area of kelps because most of the shelf would be above sea level; the remaining habitat would be mostly sand and mud. Furthermore, the northern Channel Islands merged into a very large island (Johnson, 1978). What was left of the Southern California Bight would have been a very different habitat, as it would have lost its shelf and would be in the lee of the island and thus protected from most sea conditions (Johnson, 1978). The narrow channel may, however, have had large tidal bores such as is today seen between Tiburon Island and mainland Sonora, Mexico.

Which time scale is appropriate to community ecologists? Many regularly occurring processes (competition, predation, etc.) can be understood in short term (<10 years) studies. The mean generation times of kelps range from 1 to 15 years; hence, these would be minimal time spans to observe their population dynamics. But because the patches of particular kelps can persist for several generations, evaluation of the distribution and abundance of kelps necessitates decades, at a minimum. The same seems to be true of most large invertebrates, which have episodic recruitment and potentially are very long-lived. The historical records of southern California (Hubbs, 1948, 1960; Kuhn and Shepard, 1981) show that climatological events which happen at even 100-year intervals may involve habitat alterations that could cloud the understanding of present-day patterns. It is impossible to know the climatological and sea level effects of the Pleistocene on present day kelp and other coastal communities, but they may have had important evolutionary consequences, and it is important at least to be cognizant of these dramatic changes of thousand-year time scales.

8 THE ROLE OF MAN IN COMMUNITY PATTERNS

We all agree that it is important to preserve as much habitat as possible in as "natural" a state as is practical. However, it is difficult to objectively define "natural." There is a tendency to describe it as pre-white man, but this ignores what may have been substantial effects by native man. It is important to realize that we live in a considerable ecological shadow of primitive man. We make this case for the California kelp system as dominated by the sea otter, but the role of early man as a major influence in natural systems is probably general.

By eating sea urchins, the herbivore from which most kelps have no defense, the sea otter is known to have a keystone role in all the kelp communities where it occurs. This is especially true in Alaska, where sea urchins have no other important predators (for the Aleutian Islands: Estes and Palmisano, 1974; Dayton, 1975b; for southeastern Alaska: Duggins, 1980); it is probably also true in central California (McLean, 1962) but much less clear-cut as physical disturbances, substrate instability, and other environmental factors cloud the sea otter–sea urchin–kelp relationships (Miller and Giebel, 1973; Cowen et al., 1982). In southern California the sea otter is not the key predator that it is north of Pt. Conception because there are effective alternate predators. For example, sea otters have been functionally absent for at least 150 years, during which time there have remained luxuriant kelp forests while urchins have largely been controlled by the predation from spiny lobsters and sheephead (Tegner, 1980; Tegner and Dayton, 1981; Cowen, 1983; Tegner and Levin, 1983).

But have sea otters always had such a prominent role? We know that the presence of sea otters at their carrying capacity excludes commercial or sport shell fisheries (Miller and Giebel, 1973) and that remaining sea urchins and abalones are forced to live in deep crevices and cracks (Lowry and Pearse, 1973). Yet Indian middens in central California and the Channel Islands are ubiquitous, and dominated by the shells of large abalone, and large Aristotle's lanterns of sea urchins are common (Woodhouse et al., 1977; personal observations); this runs counter to the recent evidence that sea otter predation is important. There are also large sheephead in the middens, again indicating that otters were not functionally dominating the system. Because we have no estimates of the rate of deposition of the shell material in the middens, we cannot exclude the hypothesis that the large shellfish were the very rare collection from deep crevices. However most of the big shells we have seen do not have the degree of shell erosion usually seen on abalones from deep crevices. We know that the Indians harvested sea otters, and we feel that the situation in California paralleled that of Amchitka Island, Alaska, where the otters were apparently eliminated for a period by early Aleuts, thereby releasing shellfish (Simenstad et al., 1978). Unanswered is the question of what is a "natural" sea otter–sea urchin–kelp relationship in California. If early man has been in California >50,000 years (Bada et al., 1974; but c.f. Taylor, et al., 1983), it is possible that he has strongly impacted otter populations for much of that time and this impact could have been especially important during the lowered sea level periods at which time the kelp–otter habitat may have been much diminished. Furthermore, we can only guess what relationship existed between the huge, herbivorous, Steller's sea cow and the kelp community (Dayton, 1975b; Domning, 1978), but Steller found it in what must have been an island refuge from Aleuts. It seems clear that primitive man could have rendered such a large, defenseless animal locally extinct as readily as the Russian fur hunters, who rapidly hunted it to total extinction.

9 DISCUSSION

The proper integration of spatial and temporal scales is perhaps the most important challenge in ecology today. Certainly it is evident that organisms have patchy and aggregated distributions on a wide variety of both scales, and their integration must involve the more complex larger scales as well as the relatively well-studied smaller scales. Still lacking but perhaps obtainable in the kelp system is an understanding of the relationship between the small scale spatial patterns (centimeters to 10s of meters and <10 years) and the larger, coarse scales of 100 m to 100 km and 10–100 years. On the larger mesoscale level (100s of km) there has been recent progress from preliminary attempts to wed oceanography and climatology, especially with regard to plankton and fishery questions (Cushing and Dickson, 1976; Lasker, 1978; Parrish et al., 1981; Colebrook, 1982). Some of the approaches can be utilized in nearshore ecosystems such as kelp communities, but this has yet to be done. Time series analyses are available for canopy area and relative harvest of *Macrocystis* from 1911. Again, the fishery literature has time series data of catch records. But for marine species of no commercial interest, time series data of >10 years are extremely rare.

Although details differ, the same problems of scale exist for all systems. Marine systems are especially difficult because of their serious sampling problems, but terrestrial systems also integrate all levels of scales, and terrestrial parallels abound. Spatial scales integrate dispersal patterns which range from slow lateral growth to low dispersing seeds to widely dispersing wind and animal-borne seeds to animals with long migrations. Temporal scales involve everything from insects with very short (weeks) turnover times to annual grasses to the rare mast years of many trees to the same long-period climatological shifts discussed above. Terrestrial examples of long-term patch persistence are common in the American southwest. For example, Vasek (1980) speculates that clones of the creosote bush (*Larrea tridentata*) are over 11,000 years old. The photographs in Hastings and Turner (1965) and Gehlbach (1981) document numerous patches of plants persisting many decades (in most cases simply reflecting plant longevity), and Gehlbach also mentions examples of plant and animal changes and persistence over one to two decades. In the absence of fire, sage and chaparral patches remain distinct for many decades; a 1931 photograph in Mooney (1977) of Banner Grade, San Diego Co, shows patches which are still unchanged in 1983 (personal observation). Fire disturbance is an integral component of most plant associations in the Southwest (for reviews see Humphrey, 1958; Wright and Heinselman, 1973; Keeley et al., 1981; Minnich, 1983). This disturbance parallels that of major storms in kelp systems, as the affected area is relatively large and the impact varies for particular species. More local but still selective disturbances in terrestrial systems paralleling sea urchin grazing and smaller storms in kelp systems include the foraging of gophers, badgers, peccaries, rodents, rabbits, cervids, and so on.

It is difficult to think of many terrestrial parallels for the long-distance (100s of km) dispersal characteristic of some marine invertebrates. However, smaller scale dispersal mechanisms such as wind and sheet flooding (Reichman, 1979) are common, as is bird, rodent, cervid, ant, and even coyote seed dispersal in feces. Parallels to kelp edge effects are also probably common, as rodents and birds forage from shelter (Bartholemew, 1970; Halligan, 1974; Pulliam, personal communication). Other interactions roughly paralleling those of sea urchin–coralline algae–abalone interactions in kelp habitats can be found in such habitat modifications as nurse trees (Niering et al., 1963) and bacterial–fungal relationships (Kaminsky, 1981).

There are numerous examples of short-term temporal fluxes in the Southwest including many studies of the variation in seed predation (summarized in Brown et al., 1979) and of the duration of freezes (Niering et al., 1963). Longer-term and relatively important ecological changes over the last 100 years have been attributed to climate changes (Hastings and Turner, 1965), but for some reason southwestern ecologists have not considered the importance of relatively rare but catastrophic climatological events which are becoming appreciated in marine systems. For example the focus on overgrazing, predator control, and fire to explain the heavy erosion and gully formation of the 1880s (Hastings and Turner, 1965; Humphrey, 1958), may not sufficiently appreciate the extremely heavy rains of the 1860s, late 1880s and early 1890s (Brewer, 1974; Kuhn and Shepard, 1981). Finally, on a still longer time scale, the remarkable records of tree rings and especially packrat middens offer surprisingly precise records of climate and vegetation shifts through the Holocene (Phillips, 1977; Betancourt and Van Devender, 1981; Cole, 1982). These records are sufficiently precise to identify periods of early and late summer rains and slight species elevational shifts in some components of the life zones (A. Phillips, personal communication). Certainly the biological consequences of changing climates are much appreciated (Ford, 1982), but the issue of the integration of space and time scales is rarely explicitly addressed.

Another very difficult problem is that of integrating the ecological consequences of early man's activities with our concept of "natural." We try to minimize the effects of modern man in our studies by identifying old fields or logged areas, land subject to livestock grazing, introduced species, and so on. Yet it is rare to find ecologists cognizant of the effects of early man, the hunter and the farmer. There are probably many southwestern parallels of our scenario concerning the interwoven effects of early man on sea cows and sea otters and the consequences for kelps, abalones, sea urchins, and probably lobsters. One gazes with wonder at the list of some 200 genera of animals that became extinct during the Pleistocene (Martin and Guilday, 1967), many of which almost certainly went extinct directly or indirectly at the hands of early man (Deevey, 1967; Martin, 1967). In most cases the animals apparently lost to primitive hunters were "big game" mammalian and avian herbivores; collapses of dependent carnivores, scavengers, and commensals apparently followed. The ecological consequences of foraging by several species of mastodons and mammoths will never be known (but have been inferred; Johnson, 1980), but judging from the role of African elephants they must have had important effects on plant communities; mesquite thickets and other riparian habitats in particular must have been very different than they are now. Similarly, foraging by giant sloths, peccaries, bears, tapirs, and armadillos must have created patchy disturbances important to many species of weedy plants and birds. Horses, camels, pronghorns, cervids, bovids, and beavers also must have had important community roles in addition to seed dispersal (see Janzen and Martin, 1982). These roles have not been replaced; the "niches" are empty and in a real sense our perception of "natural" is illusory.

The activities of early man, the farmer, are perhaps less dramatic but still important. The importance of "wildfire" is becoming known, but early man's agricultural use of fire was extensive (Pyne, 1982) and its importance must also be recognized. In a similar vein, it seems likely that by stripping their environment of firewood, the Anasazi may have contributed importantly to erosion (see Betancourt and Van Deventer, 1981). Certainly, early farmers had intimate relationships with the earth, the effects of which persist today (see references in Nabhan, 1982, for desert people). Nabhan describes a large variety of desert native plants which were at least partially domesticated and can now be found growing with their wild forms. The desert people had many ingenious means of domesticating the land as well; Nabhan describes subtle but effective soil and drainage improvements. In some cases irrigation was practiced on a much grander scale; for example, the Hohokam constructed over 2000 km of canals in the Salt River Valley of Arizona; some of the canals were 11 m wide (26 m between crests) and 3 m deep (Masse, 1981). Many of these canals can still be seen in aerial photographs of modern farms. Undoubtedly, "primitive" irrigation systems significantly altered many additional terrestrial habitats we consider "natural."

Attempting to summarize the message of this essay brings to mind the parable of the blind men and the elephant. In their initial encounter with the proboscidian, each "sampled" a different location and came to vastly different conclusions about the nature of the beast. Our experience with the kelp forest has illustrated how easy it is to study an isolated component of the system without appreciation of larger temporal and spatial scales that are critical to an integrated understanding of the system. Events that seem random on one scale compose patterns on another. Certainly these conclusions are generally true in terrestrial ecology, where large spatial scales and especially long-term temporal scales are particularly important to a general evolutionary understanding of nature. It is especially important for evolutionary ecologists studying terrestrial systems to explicitly consider the important roles of early hunters and farmers, because even our most "pristine" sites are haunted by the empty niches of recently extinct species, by the genes of domesticated and partially domesticated crops, by the vestiges of fire, and centuries of agriculture. Clearly, it is not possible for each ecologist to work among all these scales; indeed, proper scientific methods demand more restricted scales amenable to challenging specific hypotheses. Nevertheless, it is very realistic and important to plead for an enlarged perspective in interpreting and generalizing the results of more specific research.

10 SUMMARY

Our research in California kelp communities has utilized classical approaches to the study of community structure and the demography of important kelp and invertebrate species. We have discussed the stability of small patches (square meters to hectares) in the kelp forest with regard to invasion, competition, grazing, and different types of disturbance. Sea urchins are important grazers, and we have studied their community roles and patterns of recruitment and mortality. These approaches are, however, inadequate to obtain a complete understanding of the system because many important patterns depend on processes that work on much larger scales in space and time. For example, the drag of the kelp forest itself slows the currents and substantially reduces the transport of nutrients and long-lived larvae into the forest. In addition, the reduction in current velocity can act to "trap" short-lived larvae that originate within the forest. Certainly the kelp forest has many important, usually nonlinear, intermediate scale effects on its environment.

Much larger scale oceanographic processes such as eddies spinning off the California current bring nutrients and larvae to kelp forests. Alternatively, warm water intrusions from the south can devastate kelp forests. Finally, man too has impacted kelp habitats in a myriad of ways. In recent years fishing and waste disposal have had many effects on kelp forests. But the effects of humans are not necessarily only recent. For example, sea otters are known to be important predators in some kelp communities and there is indirect evidence that their populations may have been limited by effective hunting by native human populations. Early man may also have much reduced the range of Steller's sea cow, a large herbivore that probably had a substantial impact on the nearshore environment.

Focusing only on the southwestern United States, we find that there are numerous parallels to our kelp story. There are many examples of patch stability and various dispersal patterns dependent upon physical and biological processes. There is abundant evidence that shifts in climate have had significant and long-lasting consequences. Finally, the role of early man structuring our "natural" ecosystems is even more dramatic in the terrestrial system; examples are the efficacy of his hunting with regard to the direct and indirect extinction of many important species, the far-ranging ecological effects of man-caused fire used for agricultural and hunting purposes, and long-lasting genetic and habitat effects of many agricultural procedures.

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