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Source: *Annual Review of Ecology and Systematics*, Vol. 16 (1985), pp. 215-245

Published by: Annual Reviews

Stable URL: <http://www.jstor.org/stable/2097048>

Accessed: 29-09-2016 19:23 UTC

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ECOLOGY OF KELP COMMUNITIES*

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INTRODUCTION

The shallow subtidal rocky habitats in most temperate coastal areas are conspicuously dominated by large brown algae in the orders Laminariales and Fucales. These algae are commonly referred to as kelps, although the term technically refers to Laminariales only. Their high productivity and complicated biological structure make kelps especially important members of their communities. For this reason, these communities have received a great deal of research, including one of the first scientific applications of diving (128). This review summarizes the status of research programs operating within very different scales and emphasizes the point that a real understanding of the processes under study must come from the proper perspective and integration of the other levels.

A taxonomic account of the world's kelps is far too complex for the scope of this review, but Mann (146) has characterized the world's kelp forests by their dominant genera. *Laminaria* species are found in many parts of the world but dominate both sides of the Atlantic and the coasts of China and Japan. *Ecklonia* dominates some kelp forests in Australia, New Zealand, South Africa, and a few other southern hemisphere localities. The giant kelp, *Macrocystis pyrifera*, forms dense forests in many parts of the world including areas of the northeast Pacific, the southern shores of South America, many Southern Ocean islands, and isolated areas of South Africa, Australia, and New Zealand. *Macrocystis pyrifera* does not occur in the eastern Pacific area north of San Francisco, California; however, this northern region has the highest species diversity of kelps in the world (63), with *Macrocystis integrifolia* and *Nereocystis*, *Alaria*, *Pterygophora*, and *Laminaria*, among other conspicuous genera.

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The life cycle of all kelps consists of an alternation of generations between microscopic haploid gametophytes and large diploid sporophytes which produce reproductive sori, often on specialized sporophylls. Reduction division occurs in the sporangium, producing microscopic zoospores which are released to settle on the bottom and develop into male and female gametophytes. Gametophytes produce antheridia and oogonia; fertilization results in zygote formation and the growth of sporophytes. Most ecological studies have focused on the large sporophyte stage; however, recent work emphasizes the different threshold factors important to the separate life-history stages, especially the gametophytes and juvenile stages (50, 205).

This review is possible because the huge and often rather diffuse literature has received excellent reviews (21, 80, 119, 146, 158, 183, 205). I will emphasize the kelp community models being developed in the northeastern Pacific because of my own familiarity with the system.

THE PHYSICAL ENVIRONMENT

Important environmental factors influencing kelp communities include light, substrata, sedimentation, nutrients, water motion, salinity, and temperature. The roles of these factors are difficult to evaluate because they may never be entirely independent of each other (for example, the thresholds of almost all such environmental factors are to some extent temperature dependent) and because they often have highly variable distributions in nature (for example, most parameters vary across depth gradients). It is relatively simple to evaluate one factor in the laboratory, but very difficult to differentiate key factors in natural situations. Environmental factors may also strongly influence juvenile stages, and therefore, the physical thresholds of juveniles.

Light

In many senses light is the most complex physical factor; fortunately it has been comprehensively reviewed by Drew (60). The spectral distribution of light in kelp forests is highly variable (86), and marine plants have pigments that absorb light of different wave lengths (usually but not always between 350 and 700 nm). Ramus & co-workers (175–178) showed that with proper acclimatization, algae can vary the total and relative amounts of the pigments. Nevertheless, the quality and quantity of irradiance are critical to all algal life-history stages, and many important physical and biological processes are ultimately light-related. Factors affecting irradiance may include turbidity (a physical factor) and/or between-canopy competition (a biological factor). The most extensive studies of irradiance were performed in the North Atlantic by Kain (117, 119), Lüning (138), Lüning & Dring (140). In the north Pacific juvenile *Macrocystis* sporophytes require about $0.7 \text{ E m}^{-2}\text{d}^{-1}$ for growth (50, 51). Dean (48) has

estimated that the San Onofre kelp forest receives only about $0.27 \text{ E m}^{-2} \text{ d}^{-1}$ at the lower depth limit of *Macrocystis*, which he points out is similar to values recorded at the lower limit of *Laminaria* in the North Sea (140). In almost all cases not involving canopy competition, the irradiance is most severely reduced by suspended particles in the water column. Phytoplankton differentially absorb the wave lengths needed by the kelp (48), but beneath a kelp canopy the productivity of the phytoplankton is in turn reduced (13).

Substrata and Sedimentation

Almost all kelp forests occur on hard substrata (158). The major exceptions are *Laminaria sinclarii* (147), *L. saccharina*, and the large and productive *Macrocystis angustifolia* forests lying between Point Conception and Santa Monica in southern California. Here very large and apparently old plants grow on sandy bottoms. Recruitment appears to be on the *Macrocystis* haptera or worm tubes (153). These plant complexes seem to be large biotic "islands" perpetuated by their massive nature. Unfortunately the violent storms of 1982–1983 destroyed many of these stands, and the kelp forests are very much smaller than in previous years. Populations of *Macrocystis pyrifera* in some protected fjords in Chile (43) and New Zealand (88, 151; P. K. Dayton, personal observation) constitute other exceptions to the hard-substratum generalization. While mature kelp populations are usually restricted to hard substrata, germination and recruitment are not, and juvenile *Macrocystis*, *Pterygophora*, *Laminaria*, *Eisenia*, *Egregia*, and others are often first observed on worm tubes or other plants; but for such kelps to survive, their haptera usually must become attached to primary substrata (44). Obviously not all hard substrata are identical; many such as mudstone or sandstone are friable and unstable, and in some cases are responsible for water turbidity (105). *Laminaria saccharina* often grows in sedimented and even soft-bottom habitats, and some kelps such as *Laminaria sinclarii* are well adapted to sand habitats where they tolerate burial, but even here the haptera are attached to hard substrata (147).

Sedimentation and scour are highly detrimental to kelp plants (44, 49, 54, 57). In most cases their effects are most severe on spores, gametophytes, and young plants, although some species such as *Laminaria farlowii* and *Eisenia arborea* seem more resistant than others such as *Macrocystis pyrifera* and *Pterygophora californica* (44). While difficult to quantify, the substrata and sediment effects can be pronounced. For example, the kelp forests at Point Loma and La Jolla (158), Del Mar (182), Encinitas (P. K. Dayton, personal observation), and San Onofre (49) all lie within San Diego County in southern California, and all differ in habitat. The same is also true of kelp communities in central California at Santa Barbara (68), Piedras Blancas (44), Pacific Grove (104), and the Santa Cruz area (34, 171) where differences are easily explained by wave action and the site-specific nature of the substratum.

Nutrients

The importance of nutrients to kelps is well known (53, 83–85, 119, 209–211). The evidence emphasizes the importance of dissolved nitrogen, especially nitrate, but phosphate (142) and other trace compounds may be important for algae just as for higher plants (53). Experimental fertilization of kelp forests with nitrate have dramatically enhanced growth (23, 51, 155, 159, 202), but these increases are confounded by other factors, especially temperature. The seasonality of nutrient stress is well known, and apparent storage of nutrients has been observed for *Laminaria* (39, 81, 88, 99) and *Macrocystis* (85, 188, 209). The stratification of nitrate concentrations in the water column is important to kelps with floating canopies; kelp canopies in southern California often deteriorate in the summer when surface nitrates are below 1 μM (109, 110), presumably because low levels will not support canopy maintenance. Because the factors are so tightly interdependent, field nutrient studies should observe simultaneously light, water motion, and temperature (110, 135, 159, 210). Finally, nutrient assimilation is much enhanced by water turbulence, and frond adaptations affecting boundary-layer processes are very important (26, 27, 211).

Water Motion

Many other physical factors important to kelp communities are related to water motion, be it currents, internal waves, surge, or surface waves. Unfortunately, proper measurements of such forms of water motion are expensive and difficult, and the kelp literature is limited in this regard. However, progress is being made (26, 27, 109, 110, 113, 131, 153, 162, 211), and researchers are coming to understand the roles of various types of water motion and the responses of the plants to each type. Wave-induced sweeping of *Laminaria pallida* maintains bare space and excludes herbivores in South Africa (207). A similar whiplash effect has been observed for *Lessoniopsis* (41). Water motion is an important cause of plant mortality (44, 161, 182) and growth adaptations (20, 27, 62, 87, 90, 119, 143, 151, 154, 162, 164, 198). In California, such growth adaptations may confer different community structures in different wave-stress regimes (44). In addition to stress, water motion affects light by moving canopies and influences the impact of sedimentation and scour. Probably most importantly, water motion determines the availability of nutrients. The most fruitful approaches will come from continued clever small-scale work (e.g. 23, 27, 99, 154, 211), and larger-scale studies (e.g. 109, 110, 129). The former approach addresses the algal adaptations for the acquisition and allocation of nutrients, whereas the latter describes the long-shore and cross-shore transport of nutrients within kelp forests and the interactions between kelp forests and these oceanic processes.

Salinity

Kelps are not often found in estuaries, but the role of salinity per se has received little study. Norton & South (163) studied the effects of reduced salinity on *Saccorhiza* and *Chorda* and found adverse effects, yet there was no simple relationship. Gessner (89) and Blinn & Markham (11) discuss the abilities of kelps to acclimatize to low and high salinities. I have seen apparently healthy kelps growing through freshwater lenses in Alaska, the San Juan Islands, and Washington and Chilean fjords.

Temperature

The fundamental importance of temperature to living systems is widely appreciated, yet surprisingly little is known about the relationship between temperature and the growth processes of kelps. Bolton & Lüning (12) offer the most comprehensive laboratory study and review of optimal growth and survival temperatures of *Laminaria*. Species-specific patterns for four species were remarkably consistent despite wide temperature variations between original collecting sites. Thus the wide temperature tolerances result from individual plasticity. Unfortunately it is almost impossible to isolate temperature effects from many other environmental factors in field conditions. For example, light thresholds are closely dependent upon ambient temperature (49, 50, 60, 119, 138, 141), as are nutrient absorption and growth (143, 210, 211). Indeed, the "warm water die-offs" of southern California kelps were long thought to be caused by higher temperature but now appear to result from nutrient depletion; NO_3^- concentrations in coastal waters are inversely related to temperature. Kelps can survive such high temperatures in the presence of adequate nutrients (109, 110, 216). On the other hand, North (159) describes an experiment in which nutrients were increased but kelp fronds became diseased at higher temperatures.

Physical Thresholds and the Biology of Gametophytes

Because gametophytes are small, their growth and survivorship are difficult to study in the field. However, the environmental thresholds important to gametophyte growth are amenable to laboratory research, which has demonstrated that a complex set of variables is important, especially temperature and the quality and quantity of light (60, 108, 141). Specifically, gametophytes grow vegetatively in red light, and they survive and grow at relatively low irradiance levels because vegetative growth is saturated at only $2 \mu\text{E cm}^{-2}\text{s}^{-1}$ (141).

The survival of the small gametophyte is almost impossible to measure in the field (156). Most workers assume relatively low survivorship, an hypothesis supported by studies done with settling plates, ropes, or other artificial substrata placed in the field (57, 108). It also received strong support from the response to "seeding" experiments (44). However, in laboratory experiments (54) or even

when cultured on artificial substrata and placed in the field gametophytes may be more susceptible to grazing and scour than when growing naturally in refuges such as tiny cracks and crevices where sedimentation may cover but not scour them. Their low light and nutrient requirements suggest an adaptation for such a quiescent or dormant tactic. Indeed, Klinger's (130) discussion of *Laminaria ephemera* shows that at least these gametophytes must persist in a semidormant stage because the sporophyte grows, releases spores, and dies in a matter of weeks, whereas the gametophyte presumably survives for the remainder of the year. Certainly other annual kelps such as *Nereocystis*, *Postelsia*, *Costaria*, *Cymathere*, and some *Alaria fistulosa* populations (66) spend at least several months in an inconspicuous stage, presumably as gametophytes. If the gametophyte stage can persist more than 1 year, it may provide a stabilizing storage tactic (208) similar to that of the seed banks of some higher plants. Some indirect evidence suggests that this may occur: Neushul (155) has maintained laboratory cultures of gametophytes over 7 years. Also suggestive evidence is the immediate massive kelp recruitment that occurred after the devastating southern California storms of 1982–1983 (47, 68); the uniform pattern of this recruitment differed from earlier observations of recruits clumped around adult plants (44), but the latter clumped pattern prevailed at Point Loma the following year (P. K. Dayton, personal observation). Perhaps a large number of persistent gametophytes underwent gametogenesis and grew to sporophytes. The following year's recruitment did not have such a "bank" of gametophytes and therefore depended on the remaining adult plants with their limited spore dispersal (1, 40, 44, 197). In summary, the questions about gametophyte survivorship are important because of the seed bank issue, yet they are unexplored. Annual plants depend on gametophyte longevity, yet long lived gametophytes appear rare for perennial species.

Two lines of evidence suggest an environmental trigger of gametogenesis. First, annual kelps tend to recruit at predictable times (P. K. Dayton, personal observation), suggesting a photoperiodic response, and the recruitment of kelps in southern California is highly episodic. For example, *Macrocystis* recruited two to three times in ten years (44, 49, 57). A growing literature demonstrates the importance of light quantity and quality in controlling Laminarian gametogenesis. Lüning & Dring (140) found that a critical dose of $200 \mu\text{E cm}^{-2}$ of blue light (360–500 nm) is necessary for gametogenesis of *Laminaria saccharina*. For California *Macrocystis* there was a linear relationship of gametogenesis and irradiance between 10 and $60 \mu\text{E m}^{-2}\text{s}^{-1}$, and that fertility depended on a blue-light dose of at least $260 \mu\text{E cm}^{-2}$ (141). Kain (119) reviews the evidence that gametogenesis is triggered by blue light generally between 360–500 nm, and Lüning (138) emphasizes the importance of a quantum dose rather than instantaneous irradiance. He also found that the irradiance need increased exponentially with temperature. Deysher & Dean (56), working with

Macrocystis, adjusted quantum irradiances in various photoperiods to provide equal daily irradiation dosages to study the interactions between quantum irradiance and quantum dose. The lowest daily quantum dose for gametogenesis was $0.2 \text{ E m}^{-2} \text{ day}^{-1}$. This threshold doubled when instantaneous irradiance was less than $5 \mu\text{E m}^{-2}\text{sec}^{-1}$. These are laboratory studies, but Deysher & Dean have field data showing that morning and evening irradiance rates are below the threshold values and midday rates can be above the saturation levels; clearly these threshold values are critical to the proper interpretation of field measurements. Dean (48) measured the daily photon flux density in a southern California kelp bed and found strong seasonal differences. These densities were lowest in winter and spring and highest in summer; kelp canopy cover and suspended sediments attenuated light transmission. In addition, phytoplankton probably often absorb light.

Once gametogenesis occurs, fertilization depends upon the proximity of male and female gametophytes because the male gametes have very limited dispersal (1, 40, 44, 120, 156, 197). Short-range male dispersal is overcome in many species by drifting fertile sporophylls or sori (32, 190) that are caught by benthic animals such as tube worms, sea urchins, abalones, and even small chitons; all of these capture and hold fertile drift long enough to inundate the immediate area with spores (44). This appears to result in a sufficiently high density of gametophytes to ensure fertilization.

In one of the few gametophyte field studies, recruitment of macroscopic sporophytes was limited by environmental pressures on the embryosporophytes rather than on gametogenesis (108). This emphasizes the need for additional innovative field work.

PRODUCTIVITY

Productivity studies and population approaches to community or ecosystem studies have been quite disparate. Most work on community structure and organization is based on demography and population interactions with an explicit or implied focus on evolutionary relationships. These processes are studied directly, usually with little or no reference to production rates or energy fluxes. Unfortunately, natural systems are marked by great variability that limits the general applicability of results. Studies examining the processes of primary and secondary productivity ignore demographic variability within the populations. This approach is well exemplified by work in South Africa (75–78, 206) and Nova Scotia (23, 143–146). Although the two approaches have fundamentally different objectives (evolutionary understanding vs energy flow and mass balance), their basic interdependencies must be recognized. In this section I review generalizations from the complete reviews of Kain (119) and Mann (146).

The productivity of *Laminaria* populations in the North Atlantic and South Africa vary from 120 to 1900 g C m⁻²yr⁻¹, but most values are between 600–1300 g C m⁻²yr⁻¹. *Macrocystis* productivity in California ranges between 350–1500 g C m⁻²yr⁻¹, but most values are well under 1000 g C m⁻²yr⁻¹; and *Ecklonia* systems in South Africa and Australia vary between 620 and 1000 g C m⁻²yr⁻¹ (146). In parallel with phytoplankton research, most studies of kelp forest productivity emphasize the importance of dissolved nutrients (especially nitrogen), light, and temperature. Kelps occur in temperate to polar habitats where seasonality is important. Dissolved nutrients tend to be low in the summer, the period of maximum photosynthesis and carbon storage. Kelps grow rapidly in the autumn when the concentration of dissolved nitrate in seawater increases by utilizing stored carbon. With reduced winter temperatures, a surplus of photosynthate accumulates that is utilized in spring growth (146). This general model varies depending on local conditions. For example, *Laminaria solidungula* in the high Arctic draws on stored reserves to complete over 90% of its linear growth in the complete darkness of winter (24, 67). As with *Laminaria* species elsewhere (75, 76, 146), *Macrocystis* growth in southern California depends upon availability of dissolved nitrogen, which can be stored for a few weeks (84, 109, 110, 209–211).

Field, Velimirov, and associates in South Africa have demonstrated the strength of this approach by explaining the relationships between levels: The mechanisms of local upwelling and kelp productivity result in detritus essential to mussel populations; mussels are crucial food for lobsters, that in turn are important to several vertebrate populations (75–77, 206). Other sets of questions might come from evaluating the importance of the nutritional value of drift to herbivores (146). Both approaches have proven useful on land and may yield important insights into kelp-based systems.

POPULATION DYNAMICS

Population dynamics are fundamental to understanding community and evolutionary processes. Unfortunately few data exist for kelp forests. Ultimately an understanding of population dynamics must be based on rates of birth, death, immigration, and emigration. Because kelps are attached to the substrata, immigration and emigration are usually rare; however, drifting adult *Macrocystis* can live many months and disperse spores over at least hundreds of meters (38, 44, 73). Birth and death rates also have proven difficult to quantify. Birth rates are especially hard to evaluate because the spores and gametophytes are nearly impossible to monitor in the field. Assuming that zygote formation represents the birth of a kelp sporophyte, it too is practically impossible to evaluate in the field; it may be a rare and unpredictable event (44, 50, 57), depending upon sufficient light, nutrients, and temperature (49, 57). Even after

the juvenile sporophyte appears, species cannot be identified for several weeks. Thereafter the survivorship or mortality rates can be evaluated directly (35, 44, 90, 91): When the age of kelp can be determined, static age structure can be obtained and converted into survivorship curves (21, 55, 119, 130), given the unlikely assumption of a stable age distribution. Such survivorship data can be compared between habitats to evaluate the effects of physical stress on population dynamics. As expected, higher physical stress is associated with higher mortality and faster turnover (44, 119, 130). I find it interesting that lower physical stress can result in density-dependent reduction of recruitment and higher survivorship of adults (44, 124).

In most cases physical and biological disturbances result in different mortality patterns. For example, gametophytes and juvenile sporophytes are susceptible to scour and burial by sediment, several levels of grazing (such as by polychaetes, crustacea, fishes, and sea urchins), competition for light, and mortality due to storms and entanglement. As mentioned earlier, sediment burial and scour can cause high mortality of gametophytes and tiny blades (44, 49, 54). Most grazing studies have been directed to the well-known effects of sea urchins (133, 145, 160, 187, 204) and fishes on kelps (29, 158). In addition, recent field studies (44, 97, 121) appear to corroborate laboratory work (14) demonstrating the important grazing effects of microherbivores such as small polychaetes, crustacea, and especially crabs on small kelps. In most natural situations these grazers are reduced by the abundance of small picker fishes (14, 30, 121). Dayton et al (44) excluded fishes and echinoderms and observed an initial increase of small algae compared with numbers on unprotected plates, although there was an eventual increase of small invertebrates and an elimination of algae (see also 121). On a much larger scale, the common capability of some species of sea urchins to eliminate kelps locally and maintain "urchin barrens" is well known (52, 68, 92, 145) and is discussed below. Finally, intra- and interspecific competition for light can have a major negative impact on kelp recruitment (44, 181). In nature these factors often reduce recruitment, and some disturbances such as storms and sea urchins can eliminate adult kelps over large areas. In most kelp communities the demography of the component populations reflects such episodic events.

Our recent paper (44) exemplifies some practical problems inherent in kelp demography. First, as discussed below, a valid measure of reproductive output is complex and difficult (130) and was not attempted. But even the calculation of survivorship tables of macroscopic sporophytes involved practical problems and assumptions, and three approaches were used. First, the *Macrocystis* survivorship was calculated by following a cohort from germination. Because the original recruits occur in very dense patches, quadrats of different areas had to be sampled for several age classes, and the survivorship table included the implicit assumption of a homogeneous dispersion over the study area.

Although not likely to be important to most generalizations, the assumption is probably never valid at the smaller scales. Second, for long-lived plants that can be aged (*Pterygophora* and *Eisenia*), the static age structure was estimated and the survivorship of the recruits and the adults followed over several years. The survivorship calculations included two age classes and the stable-age-distribution assumption that their survivorship was similar. Third, species with relatively fast turnovers (*Laminaria farlowii* and *Cystoseira*) offered enough observations of growing and dying recruits to test for year-to-year differences. When none was found, many cohorts were lumped in the survivorship calculation. This is perhaps the ideal approach because the stable-age-distribution assumption can be evaluated (at least over a decade). It emphasizes a rapid turnover for those species, but this masks the important observation that some adults survived for 7 years (and more recent surveys indicate that a few of these plants survived over 10 years through an El Niño episode). The first and third approaches follow cohorts and are relatively free of stable-age-distribution assumptions, the second approach is not. An important component of the first and third approaches is the fact that intraspecific competition with the established cohorts prevents recruitment and thus forces an episodic component into the long-term demography of the populations. Interpretations of such studies must be done with regard to the emerging generalization of the importance of episodic recruitment, from whatever causes (44, 46, 55), to kelp populations.

In addition to stable-age-distribution assumptions, which we know are rarely true, many studies implicitly assume spatial homogeneity in survivorship patterns. Others compare survivorship in different habitats (44, 55, 90, 91, 130) in hopes of deducing the population consequences of various environmental stresses. Certainly one must be careful when generalizing from field population studies of kelps, but population responses are very sensitive to many environmental factors and are most appropriate for a mechanistic evaluation of these variables. Finally, population biology is the foundation for most evolutionary understanding. Hence, kelp biologists must recognize but not be thwarted by these problems.

LIFE HISTORY

Evolutionary life-history studies (19, 25, 194) represent an interesting extension of basic demography and dispersal tactics. The only kelp example I know is that of Klinger (130), who emphasizes some basic differences between kelps and higher plants and animals. Perhaps the most important difference is the alternation of haploid and diploid generations that renders an analysis of overall fecundity difficult. The dioecious gametophytes in particular may offer many reproductive options. One important example is the filamentous vegetative

growth and fragmentation of female gametophytes that potentially allow them to become perennials with indefinite gamete production (119); this allows comparison with the theoretical treatment of semelparous vs iteroparous habits (25) at the gametophyte level. Another important difference from higher plants is that sporophylls, sporangia, and even liberated meiospores are pigmented and capable of assimilating nutrients and photosynthesizing; translocation of the photosynthate towards reproductive tissue may occur in some species. Thus the physiological costs associated with reproduction in other organisms are not necessarily relevant in kelps and the existence of a reproductive cost has not been demonstrated. Klinger (130) examined reproductive effort (in terms of allocation of blade surface) to the production of meiospores and attempted to evaluate semelparous and iteroparous reproductive tactics of *Laminaria ephemera* and *L. setchellii*, respectively. She found no significant differences between the estimated fecundities of the two species, but the much faster maturation of *L. ephemera* resulted in a potentially higher rate of population increase.

The seasonality of reproductive activities is another interesting life-history issue. For example, what selective factors might cause *Macrocystis* to be fertile all year, while other kelps (such as *Laminaria*) are reproductive in the fall and winter (149), and some (such as *Pterygophora*) vary over their geographic ranges?

PATCH DYNAMICS

Like most natural communities, kelp forests are often characterized by patches composed of guilds with different canopy adaptations; these include: (a) a floating canopy with fronds at or near the surface, (b) a stipitate, erect understory in which the fronds are supported above the substratum, (c) a prostrate canopy in which the fronds lie on or immediately above the substratum, (d) various turf-forming associations usually composed of articulated coralline algae or foliose and filamentous red algae, and (e) encrusting coralline algae often associated with sea urchins. Neushul and associates (154) have developed hydrodynamic models that offer first-order explanations for many of these adaptations; other explanations include competition for light (41–44, 78, 119, 125, 128, 203) and adaptations to enhance nutrient absorption (211).

Stability of Patches

Study of the stability and dynamics of such patches may be a key to the integration of population level phenomena (recruitment and mortality patterns) and community level processes (interspecific competition, predation, succession, etc). That is, understanding patch resistance (for more than one generation), the actual mechanism of the persistence (e.g. the patch persists despite

being challenged) and resilience (succession to original composition), can clarify much of the uncertainty inherent in purely demographic studies. In three kelp forests in central and southern California (44) where patches were monitored, the main sources of mortality of adult kelps were related to storms and/or sea-urchin grazing. The patches usually persisted for more than one generation. The resistance to invasion resulted from canopy competition for light and limits of spore dispersal. The resilience or recovery of a particular species after being displaced by a different patch type was rarely seen because the patch resistance to invasion was effective. When succession did occur, it was mediated by several factors: seasonal spore production in relation to storm-related mortalities; mechanisms of kelp dispersal, especially via drifting plants and fragments of fertile material held against the substratum by invertebrates; presumed survivorship of gametophytes and small sporophytes, influenced by light and temperature regimes; local scour; and grazing. Within a particular area the relative patch stability was determined by biological relationships; between large-scale areas, the patch patterns were attributable to physical differences (see also 123).

These conclusions regarding the patch stability were severely tested at Point Loma, California, in the winter of 1982–1983 when 11 unusually powerful storms struck southern California (47). These storms essentially eliminated more than 600 hectares of *Macrocystis* surface canopy and accounted for a considerable amount of disturbance on the bottom due to rolling boulders and drifting kelp holdfast bundles. Despite this disturbance, the long-term effects on the understory patches were moderate (47). A subsequent massive recruitment of *Macrocystis* and remaining adults had low survivorship in the summer high-temperature, low-nutrient waters of the 1983 California El Niño (110). In addition to causing mortality among the recruits, the El Niño was associated with summer mortality of the normally robust 2–3-year-old *Macrocystis*. Thus, the storms and El Niño seem to have exerted a strong impact on the large *Macrocystis* patches but very little on the understory patches, the borders of which had been marked ten years earlier (47). Some of the old *Macrocystis* patches subsequently were invaded by perennial understory species such as *Acrosorium uncinatum*, *Laminaria farlowii*, and *Pterygophora californica* in small (square meter to tens-of-square-meter) areas where sporogenous drift material accumulated or was being held by invertebrates. By late 1984 most of the old *Macrocystis* patches comprised mixed species assemblages including surviving *Macrocystis*. In the absence of additional disturbance, the *Macrocystis* will probably overgrow other kelps and win the competition for light.

Although this discussion is focused on the northeastern Pacific, many of the same patterns exist elsewhere. In the northeastern Atlantic competitive interactions occur between the same (126) and different species of *Laminaria* (119, 161) and are affected by currents (68, 164), unstable substrata (119), and

siltation (161). Sea-urchin grazing can prevent kelp growth (92, 116, 126, 160). While competitive patterns may not be so well developed in the northwest Atlantic, the large-scale effects of sea-urchin grazing can be dramatic (22, 145, 146). Similar competitive and grazing phenomena appear important in some New Zealand and South American kelp communities (31, 43, 152, 184).

Adaptive Tactics

Patch dynamics in California (44), Washington State (203), and Amchitka, Alaska (42) have demonstrated alternative morphological adaptations of the different canopy guilds in which exploitation of light is enhanced in taller canopies, whereas the shorter canopy guilds are better adapted to tolerate stress from wave surge. Still others appear adapted to tolerate sea-urchin predation. The adaptations of algae appear to constitute four distinct tactics. (a) Ruderal or opportunistic species such as *Laminaria ephemera*, *Nereocystis*, or *Costaria* are ubiquitous, especially in frequently disturbed areas; (b) large plants with floating canopies such as *Macrocystis* or *Alaria fistulosa* are adapted for exploitative competition for light and/or nutrients but are susceptible to disturbance from wave stress and grazing; (c) kelps such as *Pterygophora*, *Eisenia*, *Dictyoneurum*, or *Laminaria longipes* are adapted to physical stress but potentially outcompeted for light by higher level canopies; and (d) algae such as corallines, *Codium*, *Agarum*, or *Thalasssiophyllum* appear to be adapted to withstand or avoid heavy grazing but seem poorly adapted to competition for light (203). In general, within a particular area the patch composition and stability seem determined by biological relationships, especially competition, but between larger-scale areas the patch patterns seem attributable to physical differences or the presence or absence of effective sea-urchin grazing (44, 68, 72, 164, 204).

Future research should rigorously test these generalizations. If they withstand the test, it would be interesting to evaluate the trade-offs involved in such evolutionary compromises.

DISPERSAL

The dispersal of kelps is perhaps the most important phenomenon integrating population dynamics, life-history biology, and patch dynamics. Because male gametes have limited dispersal, the successful fertilization of the oogonia necessitates a high density of gametophytes. Despite this pivotal importance, very little research has attempted to define and understand the maintenance of dispersal patterns of kelps. Once the spores are released, their dispersal is influenced by physical processes such as currents, internal waves, surge, etc, and by survivorship in the water column and availability of suitable substrata. Tactics available to kelps involve the location of spore release, and behavioral

and physiological adaptations of the spore. Most of the available kelp seed-shadow data suggest that effective spore dispersal is limited (1, 40, 44, 55, 130, 166, 197); hence it is important to evaluate some of these tactics.

Stipitate and prostrate plants release spores near the substratum, and spore dispersal per se should be limited. Some larger kelps such as *Macrocystis* spp. and *Alaria fistulosa* have their sporophylls near the substratum with the fronds floating to the surface. While the above growth forms probably result in relatively limited dispersal shadows, the spores settle in high densities within the limited area and vastly increase their fertilization success. Other large kelps such as *Nereocystis luetkeana* and *Pelagophycus porra* form the sori near their distal end, far above the substratum. If the spores were merely released, there would be a large spore dispersal shadow with low sporophyte recruitment because of low probability of fertilization; both species, however, utilize a tactic in which patches of sporogenic material fall from the fronds and drift along the bottom where they inoculate small areas with high densities of spores.

Do the physiological and physical characteristics of the spore affect the dispersal biology? Kelp spores are relatively short-lived in the water (119), and few studies have sampled the water column for algal spores (58, 107). Ebeling et al (68) discuss heavy *Macrocystis* recruitment on newly cleaned rock faces following severe storms. There were no adult plants in the vicinity; thus long-distance spore dispersal is a possible hypothesis, but the storms may have temporarily deposited fertile drift. Another example of spore dispersal in the water column is an anecdotal report (T. Klinger, personal communication) from British Columbia of consistent recruitment of *Pterygophora* on new nylon lines that were mooring rafts over deep water. In this case many shallow-water *Pterygophora* grew a few hundred meters away, and offshore winds may have caused a local surface-water movement toward the rafts. Other brown algae such as *Dictyopteris* and *Desmarestia* are extremely effective dispersers by mechanisms as yet completely unstudied. The pioneering studies of Coon et al (32) on size and settling behavior of kelp spores should be more widely recognized and integrated into kelp dispersal research programs.

Drifting fragments of fertile reproductive material probably represent the most important mode of intermediate-scale (meters to kilometers) dispersal for kelps (38, 44, 73). *Laminaria farlowii* effectively dispersed in this way over tens to hundreds of meters (44), and in this case small pieces of sori appear to slough off the blade. Preliminary evidence suggests that the entrapment of the drift for at least several hours, or long enough for the local substratum to be inoculated with spores, is an important component of drift dispersal. Grazing animals can thus enhance local kelp recruitment (44). On a still larger (but rarer) biogeographic scale, drifting plants represent very effective propagules; here species such as *Macrocystis*, *Nereocystis*, etc, with pneumatocysts or other floating material, should have much better dispersal than others, and probably wider geographic ranges and more gene flow.

GRAZERS

Kelps are exposed to various suites of predators through their life-history stages. Kelp spores, gametophytes, and tiny sporophytes are probably consumed by a host of grazers such as protozoans and meiofauna, filter feeders such as bivalves and tunicates, detritus feeders of all sizes, ranging from small crustacean and polychaetes to gastropods (such as limpets and littorines) and chitons, and even holothurians and some asteroids (e.g. *Parastichopus* and *Patiria*; P. K. Dayton, personal observation; 189). As the small plants grow they escape some of the smaller herbivores but acquire new ones such as larger polychaetes (e.g. *Diopatra*, 44); gastropods (*Tegula* or *Lacuna*, 114); crustacea (some idoteids, 115); Amphithoe; and various crabs, (103), fishes (8, 106), and some sea urchins (133, 134). Some of these smaller herbivores are themselves effectively preyed upon by fishes (30, 44, 97, 121). With growth the kelps begin to escape predation by many of the smaller herbivores but become exposed to still others. The isopod *Phycolimnoria* can burrow into and weaken the haptera of large plants, facilitating detachment (5, 184). *Phycolimnoria* may contribute to plant mortality in the relatively fast turnover observed in Argentina (93). Certainly *Phycolimnoria* outbreaks seem unpredictable in time and space and deserve more study. Grazing fishes such as *Medialuna californiensis*, *Girella nigricans*, and rarely *Oxyjulis californica* cause kelp mortality in southern California (158). However, examples of fish grazing are usually restricted to relatively isolated plants, or sometimes plants at the periphery of kelp forests. While this can seriously deter the establishment of new kelp patches or forests, grazing by fishes rarely if ever kills plants over a large area. Elsewhere in the world, fish grazing seems unimportant to kelp forests (29, 137).

Kelp communities appear unique among the world's macro plant communities because almost all the plants can be heavily grazed by one type of herbivore: sea urchins. Not all species of sea urchin have this potential, but in most temperate areas at least one species does (133). Often areas of many hectares to many kilometers of coastline are periodically denuded of macroalgae by sea urchins. This has been observed in the north Pacific from Japan [Yendo 1903; cited in (92)] through the Aleutians (72) to the Chuckchi Sea (P. K. Dayton, personal observation) to southeastern Alaska (64–66), through Washington (168, 204), and California (52, 160); in the north Atlantic from New Hampshire and Maine to Nova Scotia and Newfoundland (22, 145), to the North Sea (92, 116) and the Barents Sea (174). Denudation by sea urchins also occurs in the southern hemisphere in Australia (S. Shepherd, T. Dix, personal communication), New Zealand (4, 31), Chile, and Argentina (43); occasionally in South Africa (76), and several sub-Antarctic islands (C. Hay, personal communication). Not surprisingly this phenomenon has been described by many terms, beginning with "Isoyake" in 1903 through the current "barren ground" (133).

The frequency of barren ground situations varies widely, but they appear uncommon in Australia and South Africa.

Whereas the literature has been well reviewed (31, 92, 133), the dynamics of sea-urchin populations and the actual mechanisms by which “barren grounds” are established and invaded by kelps are not understood. In the eastern Pacific, barren grounds appear to result, at least in part, from a release of sea-urchin populations from predation by sea otters north of Point Conception, California, (reviewed by 71) and in patches south of Point Conception by lobsters and sheephead fish (33, 199) and asteroids (189). Predators also may be important in the north Atlantic—for example, lobsters, crabs, and fishes in Nova Scotia (9, 10); eider ducks and wolffish in Norway (92); and crabs in the United Kingdom (126, 129). In most other areas important predators on sea urchins are absent or appear incapable of exerting such a heavy “regulating” effect on sea-urchin populations (2, 31, 187). Sea-urchin populations may be released by human fishing of abalone (*Haliotis*), which appears to free space for urchins (136, but see 200) in California, in Australia (191) and in New Zealand (B. Skinner, personal communication). Another important cause of barren grounds is fluctuation in drift algal abundance, the usual source of nutrition for sea urchins. In California a decrease in the availability of drift food results in urchins’ becoming hungry (as indicated by reduced gonads and a marked shift in foraging behavior) and their subsequent foraging away from crevices and other refuges from predators (33, 44, 52, 68, 98, 179, 200, 201). This often causes barren ground patches that can be maintained for several years. Environmental factors that stress kelp plants, such as pollution, storms, or reduced nutrients, can result in an initial pulse of drift algae usually followed by a reduction in available drift. With a reduction in drift, hungry urchins forage much more actively and barren grounds begin to develop. Under most conditions the behavioral shift to active foraging contributes more to the formation of barren grounds than does urchin density per se (52, 68, 92, 98). Barren grounds are invaded when the urchin populations are affected by alternative foods (65), storms or strong surge (34, 43, 68, 105), and disease (92, 150, 170). The etiology of such disease is not known, but at least in some cases it seems associated with elevated water temperatures (186).

The stability of kelp–sea urchin relationships is one of the most interesting unresolved questions in kelp ecology. Most urchins have broad diets and do not overexploit kelps (18, 52, 133, 152, 184). But once established, some barren zones seem stable and persist for many years (22, 31, 192). More amenable to experimental study are the relatively unstable situations in which urchin barren grounds and kelps are in flux (34; 98; 171; 199; cf the 10 meter zone in 44, and the exposed South American areas discussed in 43). In these cases, many environmental factors, such as urchin larval availability, settlement choice, and survivorship of young; food availability; wave stress; refuges from predators,

etc, all contribute to the urchin-kelp relationship. Interesting but relatively unexplored questions involve chemical (195) and physical defenses against herbivores and, presumably, the nature of the coevolutionary dance between the kelps and their grazers.

SCALE IN TIME AND SPACE

Temporal Variability

Kelps like all other organisms show aggregated distributions on a wide range of temporal and spatial scales. The proper integration of these phenomena is perhaps the most important challenge in ecology today. Historical records of California kelp forests have been summarized by Harger (95), and, for the data tabulated by W. J. North on the Point Loma kelp forest, by Dayton et al (44). Although the data for the first half of the century were fragmentary, they do show that the kelp forest at Point Loma has occupied roughly the same area for almost a century. Following an almost complete loss of *Macrocystis* canopy in the late 1950s and early 1960s, the kelp forest recovered in the late 1960s and was relatively stable until the 1982–1983 storms and El Niño (47, 74, 158). However, more intensive monitoring through the 1970s showed that the *Macrocystis* canopy cover has varied considerably. Temporal unpredictability, especially episodic recruitment events, should be considered characteristic not only of kelps, but of many if not most coastal fish and invertebrate populations (37, 45, 46). On a larger time scale (decades to centuries), extreme climatological shifts have far-reaching effects (37, 45, 132).

Spatial Variability

On a small spatial scale (centimeters to one meter) kelp recruitment tends to be patchy because spores settle at the edges of surfaces where there is turbulence in boundary currents (27, 96, 156, 173). An additional small-scale patchiness results from depressions or other areas where fertile sporophylls may accumulate, and from small disturbances such as the bare areas left by detached plants, broken rocks, or grazed places (44, 68). On a larger scale (square meters to hectares), patches composed of particular species of kelps are capable of resisting invasion by other kelps in adjacent patches (42, 44, 68, 119, 161, 181, 203). Often this resistance to invasion can be evaluated by experimental canopy removal. The mechanism is assumed to be competition for light, but many other factors may be involved. These include limits of spore dispersal and various sources of plant mortality such as storms and entanglement, scour, grazing, whiplash; fouling by epibionts, etc (41–44, 46, 68, 214).

On a still wider intermediate scale, patches of kelps and kelp forests can contribute to changes in the physical oceanographic regimes that can be important to kelp forests. Long ago Kitching et al (127, 128) demonstrated a

reduction of the current velocity by the canopy of *Saccorhiza polyschides*. Like so much of Kitching's work, this observation seems to have been premature (sensu 196), and its general message that kelps can affect the ocean around them was not appreciated until Jackson (109) demonstrated some cases of nutrient depletion inside a large kelp forest. In addition, plankton and larval recruitment differ between outer and inner edges of large kelp forests (8, 15, 199).

Coastal Currents and Kelp Forests

Laminaria stands may reduce the currents within the kelps as opposed to immediately above them (128), but what effects exist on a larger scale? Coastal currents are affected by bottom friction, pressure gradients, and wind shear. Longshore currents dominate the water motion in shallow southern California regions while bottom drag reduces this current in shallower depths (113). Jackson (109–111, 113) found these currents strongest with semidiurnal frequencies. The drag on the large Point Loma kelp forest slows this current by almost a third. Perhaps the most important cross-shore movement is via internal waves, but they too are damped by the kelp drag (110).

The drag area for *Macrocystis* at Point Loma where the plant densities are approximately 0.1m^{-2} was about $0.15u^2$ (cgs), compared to the nonkelp bottom drag coefficient of 10^{-3} to $10^{-2}u^2$, where u is the velocity (113). This high drag will slow the current and cause most of the water to flow around the kelp stand; the transition from nonkelp, to kelp flow regimes should take place over about 100 m (110). The combination of increasing offshore depths and the high kelp drag creates large current gradients. Jackson (110) describes longshore currents outside the Point Loma kelp forest in a water depth of 28 m with a mean flow of 2 cm/sec (Root mean square (RMS) = 10 cm sec^{-1}), while inside the kelp forest at a depth of 14 m the flow was essentially 0 (RMS = 2 cm/sec). Mean cross-shore motions were nonexistent in either case, but the RMS velocities decreased from 4 to 1 cm/sec. This reduced water motion affects the supply of nutrients and larvae in a large kelp forest. For example, water moving at 1 cm/sec will take 220 hr to move through the 8-km-long Point Loma forest. Indeed, mean currents in the water there range from 0.1 cm/sec during a month-long summer deployment to 2 cm/sec (110, 113). With the very low summer cross-shore movement, there is little transport into the kelp forest during the summer when nutrients tend to be depleted and invertebrate larvae are higher than in the winter (110). Relevant biological and physiological rates can be compared with these water replacement rates.

In addition to creating relatively stagnant water in the center of a large kelp forest, the physical drag of the kelps can contribute to a marked edge effect. All naturalists appreciate the importance of such heterogeneity, and it is well known that the peripheries of forests (both terrestrial and marine) are areas of much biological action (70, 180). One mechanism contributing to the edge effect is a simple aggregation at the edge from which individuals forage, the

structure serving as refuge from predators. This is true for forests (70), chaparral (6, 94), and coral reefs (102, 165). Another typical edge effect is the concentration of predators (such as web spiders and insectivorous birds) at the periphery because it facilitates filtration of food from the environment. This has been documented for planktivorous and generalized picker fish (8, 16, 106) and experimentally (15). In such cases the fish are feeding on plankters or on animals encrusting kelp fronds (59), concentrated at the periphery, or the fish are using the kelp forest for orientation and/or predator protection. In addition, the effects on the currents may alter the behavior of the plankters so that they accumulate at the edge of the kelp patch. For example, the reduction of the current sharpens the spatial gradients in shade, turbulence, nutrients, etc, and the edge of a kelp forest can represent an abrupt transition from the pelagic realm. In this sense it must have many chemical and physical cues that initiate settling behavior of competent larvae (113).

Another phenomenon involves the minimum size threshold for the establishment of a southern California *Macrocystis* patch. Kelp fronds can be heavily grazed by fishes such as *Medialuna californiensis*, *Girella nigricans*, or *Oxyjulis californica*, which consume the fronds directly or, more commonly, in the course of feeding on encrusting organisms (8, 158). Isolated or small patches of *Macrocystis* are often heavily encrusted and are particularly susceptible to overgrazing by fishes that consume the fronds at a rate much higher than their replacement growth rate (59). On the other hand, the lack of such picker fishes in southern South America occasionally allows encrusting organisms, especially bivalves, to sink entire forests of *Macrocystis* (43). Thus a 100–200-m-edge effect (110) may serve as a threshold size in this area for the establishment of a *Macrocystis* patch. Another extreme edge effect, the nutrient absorption by the outermost plants can reduce the survival of interior plants in a large kelp forest and, theoretically, can determine the maximum area of a kelp forest.

Kelp communities are not isolated systems; they are driven by unpredictable and much larger mesoscale (hundreds of kilometers) events such as El Niños (28, 47, 68), eddies or rings (100, 169), long-distance larval transport (112, 185, 201), and large-scale interannual anomalies of boundary currents such as the California current (7, 28). The mysteries of episodic recruitment will probably be resolved by analyses coupling such large-scale (169, 172), intermediate-scale [kelp forests (46, 111)] and small-scale [holdfast scars and understory patches (44)] phenomena with a much more sophisticated understanding of physiological phenomena (48–51, 57, 138).

DISRUPTION AND RECOVERY OF KELP COMMUNITIES

The ecological consequences of different levels of disturbance present a basic problem that transcends kelp forest ecology. Ecologists have long appreciated that a mosaic of local disturbance is an integral part of community organization

(70, 167, 193). Clearly there are gradients in severity of such local perturbations, yet the consequences of the very rare catastrophic disturbances such as hurricanes, severe droughts, volcanos, etc, are fundamentally different. Such catastrophes overwhelm the quiltwork of patches of different seral stages and disturbance histories, and shift the communities into different recovery modes. These catastrophes also are part of the natural system, but because of their rarity and large scale, they are poorly understood.

Catastrophic disturbances with long-lasting effects in kelp forests seem associated with unusual storms or with the establishment (or disruption) of stable sea-urchin barrens. Large kelp forests and sea-urchin barren grounds off eastern Nova Scotia may switch or cycle back and forth, since both situations have periodically been seen since the mid-1850s. The extensive barren grounds of the 1970s appeared stable for at least a decade (22, 145) but were recently altered by a massive urchin mortality associated with an amoeboid parasite and record high temperatures (150, 186). Very large (tens of kilometers) urchin barrens existed in the Chilean fjords (43), but such urchin barrens in Chile are not common in the areas north of the fjords (152) or in the far south (43, 184). The sea urchin–sea otter–kelp relationship—in which the otters eat the urchins and release the kelp—is well known in the western Aleutian Islands, Alaska (42, 72), and both urchin barren and kelp communities appear to have persisted, depending on human predation of otters (192). The sea urchin–kelp relationship in southeast Alaska can be transitory as when the kelps were released for one season because the urchins had an alternate food source (65). Before the arrival of white men, the coastal Indians in southern California may have reduced the sea otters to a level so low that their shellfish prey were released (46) as they were at Amchitka, Alaska (192). More recent studies suggest that active foraging and establishment of urchin barrens are influenced by the amount of drift algae available to urchins (see reviews in 52, 68, 98). For example, an unusually severe storm in 1980 in Santa Barbara destroyed the kelp forest and eliminated drift algae; hungry and more active, the urchins formed an apparently stable barren ground that was in turn perturbed by the storms of 1983 so that kelps recovered (68).

The storms and California El Niño had selective disruptive effects at Point Loma, and these might be further enhanced if the urchin populations either forage more actively or have a strong recruitment. The foraging behavior depends upon the amount of drift; but the urchin recruitment is more complicated because it depends upon the availability of the larvae, their settlement, and their subsequent survival. The availability of sea-urchin larvae, which spend at least 4–6 weeks in the plankton, depends upon mesoscale oceanographic patterns. Most of the larvae come from the north and depend upon the southern California eddy for advection to Point Loma (46), but this current system apparently was blocked through 1983 and 1984 by the mass of

southern water associated with the California El Niño (47, 74). The urchin larvae in the water column may have starved in the oligotrophic waters (148). In any case, urchin recruitment at Point Loma in 1983–1984 was very low or zero (M. J. Tegner, P. K. Dayton, personal observation). However, the elimination of the edge effect after the storms destroyed the canopy may eventually facilitate urchin settlement throughout the forest.

The recovery phase at Point Loma is influenced by two interacting factors. First, patterns of algal recruitment, growth, and survival vary among the species. The development of particular patches is influenced by dispersal, usually via drift of reproductive material (44), and by gametogenesis, juvenile growth and survivorship that seem influenced by light, temperature, nutrients, scour, and micrograzers (44, 49, 50, 97). This may result in stochastic founder effects (215) and subsequent canopy competition (44). Second, but perhaps more important, is the balance between sea-urchin populations and the supply of algal drift. Recall that the 1980 Santa Barbara storm killed the kelps and washed the drift from the area, and this resulted in an urchin barren that maintained itself until the 1983 storms killed the urchins and released the kelps (68).

BIOGEOGRAPHICAL PATTERNS

A vast but usually regional phytogeographical literature is reviewed by Druehl (63) and Gaines & Lubchenco (82). Here I briefly describe kelp communities in temperate geographical regions with the objective of discussing unifying and contrasting patterns in the structure and organization of the communities and, perhaps, the evolution of the component populations. Kelp communities in the northern hemisphere are relatively well studied and a recent burst of research activity in the southern hemisphere allows a balanced if superficial treatment of that area.

The northern Pacific is especially diverse. Druehl (61–63) lists the ranges of 21 species of kelps in the northeastern Pacific. In addition to the remarkable species richness, many of these species assume different morphologies and ecological roles in different areas. For example, the Alaskan *Alaria fistulosa* is an opportunistic perennial at Amchitka (42) and an annual at Glacier Bay (66); *Costaria costata* can be either annual or perennial (63); *Cystoseira osmundacea* can form floating canopies or short prostrate turfs, and *Eisenia arborea* can be bush-like, stipitate, or prostrate (44; P. K. Dayton, personal observation).

The northern Atlantic kelp communities are much less diverse (22, 119, 146). While the large *Macrocystis* analogues are missing, *Laminaria longicuris* does float in the water column and can form dense forests. Many Laminariales in this area appear to be interfertile (139). Under most environmental conditions the stipitate *L. hyperborea* is the competitive dominant and forms

dense forests on appropriate habitats (>50 adult plants m^{-2} ; but 8–15 m^{-2} seems a more common density). Other species can compete with *L. hyperborea* when it is stressed by strong water motion (*L. digitata*) or perhaps sedimentation on unstable substrata (*L. saccharina*). The complicated relationships between salinity, surge, sedimentation, sea urchins, and kelps are reviewed by Kain (119) and Kitching and associates (126, 129).

Although one would expect the Westwind Drift and other southern hemisphere currents to disperse kelps to all temperate habitats, the southern hemisphere seems characterized by a surprising provincialism of furoid and kelp distribution. All kelp habitats are characterized by species of *Ecklonia* or *Lessonia*, but the furoids are especially prominent in Australia and New Zealand. South Africa is characterized by *Ecklonia maxima*, which forms a floating canopy, and *Laminaria pallida*, an understory kelp. The only species with circumpolar distributions are the intertidal *Durvillea antarctica* and *Macrocystis pyrifera*.

Although *Macrocystis* is ubiquitous in the southern hemisphere, it is rarely a competitively dominant species. There are large forests in Tasmania (36) and southern Australia (213) and smaller, widely scattered forests in New Zealand (P. K. Dayton, personal observation). In South America *Macrocystis pyrifera* forests in areas along the Chubut Province of Argentina are relatively ephemeral, with one to three year cycles (93) and similar forests exist in Valdivia, Chile (152). In both cases storms, perhaps in association with weakened holdfasts, regularly destroy the kelp forests. Somewhat more stable *Macrocystis pyrifera* forests occur in the Tierra del Fuego–Cape Horn region (18, 184). The forests in South America have relatively few species (reviewed in 43). Most of the sub-Antarctic Islands have *Macrocystis pyrifera*, and in some cases—such as the Chathams, Gough, Tristan de Cuna, Kerguelen, Macquarie, and the Auckland Islands—there are relatively large *Macrocystis* forests (3, 122; C. Hay, personal communication). Marion Island has a new species of *Macrocystis* (101). Probably because the unidirectional Westwind drift sweeps away the long-lived sea urchin larvae, these island kelp communities rarely have large sea-urchin barrens.

The convergence to the five canopy guilds is an especially striking feature of kelp forests. In the northern Pacific, for example, the floating canopy is represented by *Alaria fistulosa*, *Nereocystis luetkeana*, and *Cymothere triplicata* in northern areas, plus *Macrocystis integrifolia* and *Egregia menziesii* from southeastern Alaska down through northern California. *Macrocystis pyrifera*, *M. angustifolia*, *Cystoseira*, and to a small extent *Egregia* form large forests of floating canopies south of San Francisco through central Baja California. *Macrocystis* is the common canopy species in the southern hemisphere; however, *Ecklonia* forms a floating canopy in Africa. Stipitate kelps are well represented by *Ecklonia* and *Laminaria* species in the western Pacific, and in the

northern and northeast Pacific by many species of *Laminaria*, *Pterygophora californica*, and *Eisenia arborea*. Similar canopies are formed by fucoids, *Ecklonia* and *Lessonia* in Australia and New Zealand, *Laminaria* in Africa, and *Lessonia* spp. in South America. Many species have the prostrate life form; these include species of *Laminaria*, *Agarum*, *Thalassiophyllum*, *Costaria*, *Ecklonia*, *Dictyoneurum*, and many fucoids. The turfs and coralline pavements are ubiquitous, the latter usually associated with sea-urchin grazing. In exposed or frequently disturbed areas this patch structure breaks down to a mixture of especially ephemeral species (34, 41, 43). In some such areas *Nereocystis* forms dense forests with floating canopies, but it is a poor competitor (203) and is usually maintained by disturbance. Alternatively, *Macrocystis integrifolia*, *Laminaria longipipes* and *Dictyoneurum californicum* have rhizomatous holdfasts and are exceedingly robust.

Perhaps the most interesting biogeographical issues are unanswered questions such as: Why are there so many species in the North Pacific? How did *Laminaria* and *Macrocystis* cross the warm tropical barriers? Note that the tropical barrier is bridged by both *M. pyrifera* and *M. integrifolia*; *M. pyrifera* is widespread in the south but has a limited distribution in the north. Also, *M. integrifolia* goes well poleward of *M. pyrifera* in the northern hemisphere but is spread toward the equator in the southern hemisphere (153). Why is there such strong brown algal endemism in the southern hemisphere where the Westwind Drift might be expected to disperse the species? What selects for the parallels in canopy structure? What sorts of coevolutionary relationships exist among kelps, sea urchins, and sea-urchin predators? Did the presence of the sea otter release the kelps from invertebrate grazers and allow the high number of species in the northern Pacific (V. A. Estes and P. D. Steinberg, personal communication)? An equally plausible explanation is that the northeast Pacific has higher and more reliable nutrients. This relation between essentially continuously nutrient-rich water and the presence of large kelp communities is supported by distribution patterns in the southern hemisphere. In either case, what mechanisms were involved in the speciation? What are the effects of introduced species such as *Sargassum muticum* (58) or *Macrocystis*, deliberately introduced for commercial reasons? The resolution of these and other such questions will depend upon a much better integration of small- and large-scale research.

SUMMARY

My principal objective has been to outline how various environmental processes are integrated to produce patterns in kelp communities. Many of the small-scale physiological problems, especially those important to the spore-gametophyte–tiny sporophyte phases, must be studied in the laboratory, yet the

interpretation of these studies must be integrated with measures of the relevant field data. In the same sense, the larger-scale research such as community ecology and biogeography must be built on an understanding of both the oceanographic processes, especially with advection of nutrients, and the smaller-scale processes and thresholds that define realistic limits. Nature integrates all levels, and while we are forced to specialize, to be relevant our research must be planned with an appreciation of this integration.

ACKNOWLEDGMENTS

I first acknowledge the pioneering work of J. A. Kitching and co-workers who fifty years ago were grappling with most of the problems considered in this review. I appreciate the continuing education and stimulation I receive from my colleagues, especially C. Barilotti, J. Barry, R. Butler, R. Cowen, T. Dean, L. Deysher, A. Ebeling, J. Estes, R. Gunnill, G. Jackson, T. Klinger, R. McPeak, B. Mordida, M. Neushul, W. North, D. Rivera, R. Searles, M. Tegner, and G. Van Blaricom. I thank T. Dean, L. Deysher, P. Frank, G. Jackson, T. Klinger, D. Reed, M. Tegner, and G. Van Blaricom for comments on the manuscript. My research has been supported by the NSF and Sea Grant.

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