

The Population Biology of Large Brown Seaweeds: Ecological Consequences of Multiphase Life Histories in Dynamic Coastal Environments

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Key Words

demography, Fucales, kelp, Laminariales, life history, microscopic phases, population biology

Abstract

Seaweed population biology has received far less attention than trophic dynamics, yet is critically important in establishing and maintaining algal communities. Complex life histories of habitat-forming kelps and furoids, including spores, gametophytes, gametes, and microscopic and macroscopic benthic stages, must be considered within the context of their highly dynamic nearshore environments. We evaluate differences within and between kelps and furoids in life histories as they affect population biology; dispersal and potential limitations in population establishment; macroscopic stages and variations in survival and longevity affecting stand structure; and microscopic stage responses to disturbance and variation in the physical environment. We suggest that the commonly made comparisons of seaweeds with terrestrial seed plants are misleading because of large differences in morphology, environments, and the ephemeral nature of propagule banks in the sea. We conclude that progress in understanding algal populations depends on better knowledge of microscopic stages and on feedback through density-dependent reproductive processes, dispersal, and settlement.

Kelp: large brown seaweeds of the Order Laminariales

Fucoid: large brown seaweeds of the Order Fucales

Population biology: incorporation of ecology, demography, and life history characteristics and requirements of seaweeds

INTRODUCTION

Seaweeds, particularly large brown algae in the Orders Laminariales (true kelps or laminarians) and Fucales (fucoids), commonly dominate intertidal and subtidal rocky reefs and, like terrestrial plants, provide much of the three-dimensional structure, biomass, habitat, and food for associated species. They are influenced by and also affect environmental factors such as light, turbulence, nutrients, and, in the case of intertidal species, moisture and temperature, thereby affecting myriad species in their associated communities. Understanding the population dynamics of marine algae, however, is enormously complicated because their life histories are multiphasic and occur in complex and variable coastal environments. Although seaweed populations have long been considered analogues of terrestrial plants (Darwin 1860), important differences between algae and seed plants tend to be obscured by a relatively poor functional understanding of algal life history requirements, particularly of early life phases, and a continuing focus on trophic dynamics in the environments they dominate (Jackson et al. 2001) rather than the population dynamics of the seaweeds themselves. It is our premise that understanding seaweed population biology critically underpins an ecological understanding of the communities they dominate.

Parallel research traditions, especially in ecology and phycology, have influenced perspectives on structuring process of algal stands, often reflecting different historical interests, questions, and approaches (cf., Fagerstrom & Westoby 1997). Ecologists most commonly have studied associated animals, especially barnacles, mussels, sea urchins, and fish, and top-down interactions that can affect stand structure (e.g., Estes & Duggins 1995, reviewed in Schiel 2004, Schiel & Foster 1986). In contrast, phycologists traditionally have been concerned with the taxonomy, biology, and physiology of the seaweeds themselves. Given the differences in focus between disciplines, it can be difficult to make ecological sense of complex macroalgal life histories and their environmental interactions, including intraspecific, density-dependent effects. This review attempts to resolve this by evaluating the population biology of large seaweeds, incorporating their entire life histories in an ecological context.

We build on past perspectives on algal community structure (Chapman 1995, Dayton 1985, Schiel & Foster 1986) by evaluating the population biology of kelps and fucoids in the broad sense through the incorporation of ecology, demography, and life history characteristics and requirements of the seaweeds themselves in their dynamic nearshore environments. We begin with a background to algal population biology, contrast critical features of life histories, and evaluate the differences in demographics of micro- and macroscopic stages of kelps and fucoids across four themes.

- Comparisons of seaweeds and seed plants: are they misleading with respect to seaweed population biology?
- Early life stages: is knowledge of their biology and density-dependent processes the key to understanding the population biology of kelps and fucoids?
- Dispersal: does this limit seaweed recruitment and population replenishment?
- Disturbance and variation in the physical environment: how do these factors influence seaweed populations through settlement and recruitment processes?

We conclude by highlighting approaches that may provide a better understanding of algal-dominated communities by incorporating the unique aspects of their life history attributes.

BACKGROUND

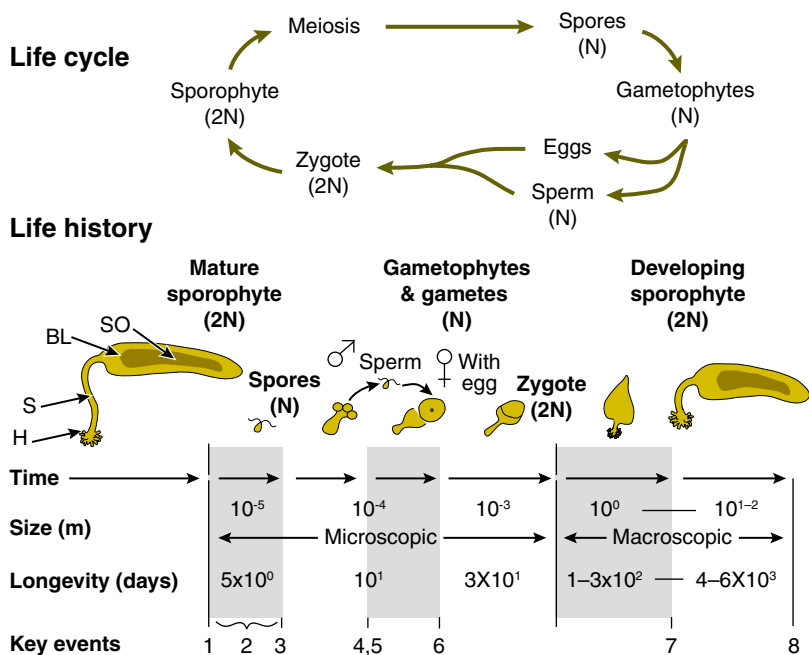
There are at least 100 species of kelps and 500 species of fucoids worldwide (Guiry et al. 2006), and good overviews of their biology and ecology can be found in recent texts (e.g., Graham & Wilcox 2000). Kelps and fucoids occur almost entirely on hard reefs from the intertidal zone to depths of over 100 m but usually shallower than 30 m. They are particularly abundant where the water temperature is generally lower than 20°C, often forming dense stands over large areas, with individuals of some species reaching 30 m in length. They clearly have considerable ecological importance in their distinctive communities as foundation (Dayton 1972) or autogenic (Lawton 1994) species. Both kelps and fucoids have free-living microscopic and macroscopic stages (**Figure 1**) that have different resource requirements and environmental needs. Their population biology and ecology, therefore, can be understood only in the context of their entire life histories, including all of the morphological, cytological, and reproductive phases, and the environments in which they live.

The characteristics that have traditionally described the Order Laminariales are being re-examined (Druehl et al. 1997), but the basic features that define their life histories remain unaltered and we refer to the traditional genera (Guiry et al. 2006) as “kelps.” The great majority of kelps occur subtidally, whereas most fucoids occupy the intertidal and very shallow subtidal zones, usually having high light requirements that exclude them from deeper waters (Chapman 1995). Consequently, there are considerable differences between these algal groups in their responses to environmental variables, including desiccation, waves, sediments, temperature, often high grazer abundances (Vadas et al. 1992) and, increasingly, human disturbances (Kautsky et al. 1986, Keough & Quinn 1998, Malm et al. 2001), which vary considerably in scale and intensity along depth gradients. As a result, survival of all life stages can be highly variable.

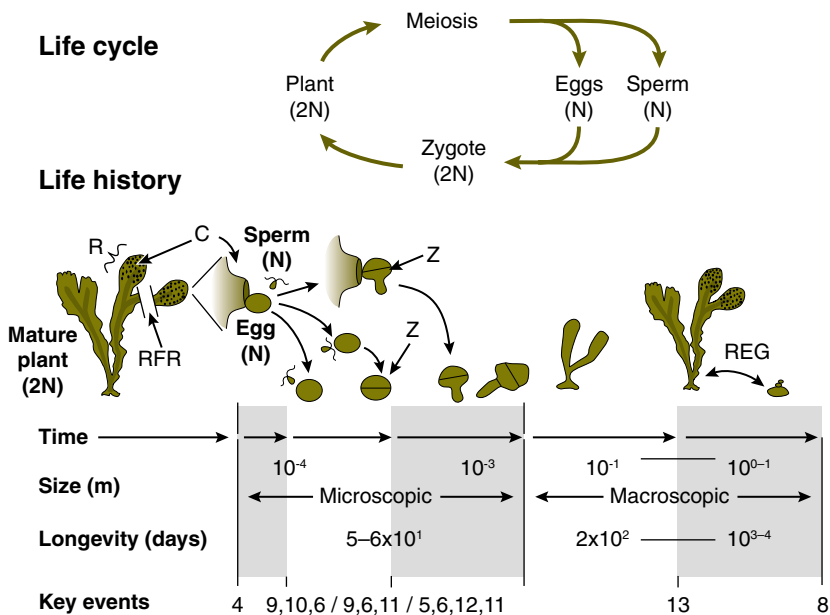
Comparisons with Seed Plants

Seed plant population models, such as in Harper's (1977) classic book, *Population Biology of Plants*, often provide a conceptual context for seaweed studies. However, because of the considerable differences in the structure, life histories, and environments of the two groups, terrestrial plant models may not be well-suited to seaweeds, many of which have free-living microscopic stages (versus seeds and related seed banks), produce enormous quantities of spores and gametes with little documented “cost” (0.1–4% of total adult plant biomass; Joska & Bolton 1987, Neushul 1963, Vernet & Harper 1980), have rapid growth rates and maturity, relatively small dispersal distances, short life spans, and no known animal fertilization (“pollinators”) or dispersal vectors. Although many ecologists and phycologists recognize these distinctive features, their relative importance for the maintenance of seaweed populations is not well established in the ecological literature.

a Kelps



b Fucoids



Harper (1977) emphasized the necessity of considering the entire life history or cycle of seed plants and the demographics of all stages to understand population dynamics. He considered the diploid stages of seed plants (i.e., seeds and plants as genets or genetically distinct individuals made up of modules or ramets) as the primary stages in population dynamics because their recruitment, survival, and fecundity are affected directly by the environment. In contrast, kelps and fucoids expose both their diploid phases (from microscopic zygotes to large, mature plants) and haploid stages (microscopic spores, gametophytes, gametes) to the environment. None of the microscopic stages is protected or nourished within the individuals that produce them or protected by specialized coverings analogous to seeds or seed coats. Generally all stages are photosynthetic, free-living individuals, and fertilization is external to adult plants (Graham & Wilcox 2000). Both 1N and 2N stages, which occur over four to five orders of magnitude in size (**Figure 1**), can therefore be of primary importance in different habitats and at different times. Although there are interesting similarities between portions of kelp and fucoid life histories and those of some seed plants (e.g., sperm dispersal by water and wind pollination), the differences reviewed here are much more ecologically informative.

Gametophyte: the microscopic haploid (1N) life stage of kelps that produces gametes

LIFE HISTORIES OF KELPS AND FUCOIDS

To understand the role of life histories in population biology it is necessary to recognize the distinctive features of large brown algae. Kelps have an extremely heteromorphic life history that is usually considered an adaptation to large, seasonal changes in the environment, including grazing (review in Clayton 1988). They often grow side-by-side with fucoids and other large algae that have very different life histories, so the kelp life history must also reflect phylogenetic constraints and perhaps unique characteristics of the environments in which it arose. Kelps have macroscopic diploid sporophytes that even in nonfloat-bearing species can be 15 m long (e.g., *Laminaria angustata*, Kawashima 1972), tiny haploid stages (spores and sperm) that can be planktonic, and microscopic benthic stages that are either haploid (gametophytes and eggs) or diploid (young sporophytes) (**Figure 1a**). Adult sporophytes produce flagellated spores (~7 μm in length) with a 1:1 sex ratio (e.g., Kain 1979). These settle and develop into free-living, dioecious gametophytes that are self-fertile. Eggs are extruded

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Figure 1

Kelp (*a*) and fucoid (*b*) life cycles and life histories with emphasis on stages, sizes (plant length), longevity, and events of particular relevance to population dynamics. The fucoid life history illustrates three possible sequences leading from gamete production to attached zygotes or embryos. C, conceptacle (cavity in which gametangia develop); BL, blade; H, holdfast; R, receptacle (terminal portion of branch bearing conceptacles); REG, regeneration; RFR, reproductive frond release (in some fucoids); S, stipe; SO, sorus; Z, zygote. 1, spore production; 2, spore dispersal; 3, spore settlement; 4, gamete production; 5, sperm dispersal; 6, fertilization; 7, sporangia development; 8, sporophyte/adult plant mortality; 9, sperm and egg dispersal; 10, egg settlement; 11, zygote settlement; 12, zygote dispersal; 13, development of gametangia.

Sporophyte: the diploid (2N) stage of kelps

from the oogonium but remain attached to it, and are fertilized by sperm. In all species examined, eggs release a pheromone that induces sperm release and attracts sperm to eggs over distances of about 1 mm (Maier & Muller 1986, Muller 1981). The microscopic zygote grows on the female gametophyte and develops to become the mature, macroscopic sporophyte.

In contrast to kelps, meiosis in fucoids results in gametes instead of spores; fucoids do not have a free-living gametophyte phase. Fertilization is external (Graham & Wilcox 2000) and plants can be either monoecious or dioecious, depending on species. Gametangia are produced within sunken chambers (conceptacles) that develop as the diploid plants mature (**Figure 1b**). Eggs and biflagellated sperm are extruded in mucilage through a pore in the conceptacle, often still contained within their respective gametangia. Eggs of different species are 64–250 μm in diameter (Clayton 1992), considerably larger than the spores or eggs of kelp, which has consequences for the survival rates of early life stages. As in kelps, there is no obligate period of development from release to fertilization, but this process is more variable in fucoids than in kelps. Fertilization has been studied in a few fucoids, in which it occurs rapidly on or very near parent plants (Serrão et al. 1996). In the common intertidal *Fucus distichus*, for example, eggs can be fertilized while still loosely attached by mucilage to the parent, or in the water column or on the benthos after they are fully released (**Figure 1b**; Pearson & Brawley 1996). Low intertidal and subtidal populations of *Sargassum* and *Cystoseira* develop deciduous receptacles or fronds with receptacles that bear reproductive conceptacles (**Figure 1b**). Fertilization appears to occur primarily while eggs are still attached to the parent plants by mucilage envelopes or mucilagenous stalks (Namba 1995), and the fertilized eggs begin development on the outside of receptacles (Chapman 1995).

Microscopic Stages

Most of what is known about the development and potential longevity of the microscopic stages of kelp comes from laboratory studies. In culture, spores develop into gametophytes, gametophytes produce gametangia, and gametangia produce gametes with little or no cell division if light (including blue light in most species), temperature, and nutrients are sufficient, each female producing one or two eggs (Lewis 1995, Luning & Neushul 1978). Annual giant kelp populations in Chile are an exception, as female gametophytes become filamentous even in good growth conditions, and can produce more than two eggs (Muñoz et al. 2004). These developments and fertilization can occur in as little as 10 days (**Figure 1a**; Lewis 1995). Under suboptimal conditions gametophytes can divide and grow to become multicellular filaments, with some capable of surviving 16–20 months in complete darkness, and reproducing if returned to optimal growth conditions (tom Dieck 1993, Yoneshigue-Valentin 1990). The growth rate of microscopic sporophytes can also vary depending on culture conditions (Kinlan et al. 2003, Norton & Burrows 1969). In fucoids, the microscopic zygotes and young juveniles take up to several months to develop to macroscopic size under optimal conditions, and growth may be delayed under less favorable

conditions (Ang 1991a, Gunnill 1980). The potential for delayed growth in early life stages has important implications for population replenishment, especially following disturbances (discussed below).

Macroscopic Stages

Although some kelps are annuals (e.g., *Alaria marginata*, McConnico & Foster 2005; *Postelsia palmaeformis*, Dayton 1973; *Nereocystis luetkeana*, Amsler & Neushul 1989), most by far are perennial (e.g., most *Laminaria* species, Kain 1963; *Macrocystis pyrifera* in the northeast Pacific, Neushul 1963). At least one species is biennial (*Laminaria angustata* var. *longissima*, Kawashima 1972). Some perennial species with annual growth rings in the stipe have maximum ages around 15 years (*Pterygophora californica*, Hymanson et al. 1990, *Laminaria hyperborea*, Kain 1979). Growth and maturation of perennial sporophytes vary considerably within and among species, but all species appear to produce spores during their first 1–2 years and every year thereafter under suitable conditions. Most kelp sporophytes occur as distinct individuals. If ramets occur (e.g., the fronds of giant kelp), they can be vegetative or spore-producing (sporophyll) blade-stipe modules that arise from a common holdfast (illustrations and phylogenetic relationships in Druehl & Saunders 1992). Sporophytes can grow very fast (5–40 cm day⁻¹; Kawashima 1972, McConnico & Foster 2005, North 1972).

The morphology of mature sporophytes varies considerably among species but Neushul (1972) pointed out that the morphology of 1- to 5-cm tall juveniles is very similar, all resembling immature *Laminaria* spp. (the macroscopic sporophyte in **Figure 1a** but without a sorus). This has a bearing on field studies because juveniles of different species can be difficult to distinguish in mixed stands. Cell divisions in the meristematic region between the stipes and blades lead to the production of thallus parts; with few exceptions (e.g., *Laminaria sinclairii*, Markham 1968), blades and stipes are not initiated from other parts of the thallus and cannot regenerate if the meristematic region is lost. In stipe-bearing kelps, severe grazing in this region can result in plant death (Andrew & Jones 1990).

Fucoids are almost all perennials but individual biomass may vary greatly because of losses from grazing and turbulence, or the annual loss of most of the thallus (e.g., *Sargassum*, Kendrick & Walker 1994) or of large reproductive fronds (e.g., *Cystoseira osmundacea*, Schiel 1985b). Individuals of many species live 5–10 years (Chapman 1995; Gunnill 1980, 1986), and some like *Ascophyllum nodosum* may live over 100 years (Åberg 1992b). However, longevity is unknown for most species. Growth in fucoids is initiated by one or a few meristematic cells at the ends of fronds, and vegetative cells can become meristematic (Graham & Wilcox 2000). Unlike most kelps, fucoids have the ability to regenerate from holdfasts or even holdfast fragments (Kendrick & Walker 1994, McCook & Chapman 1992), which no doubt reduces their mortality from grazing and other disturbances. In some species, therefore, a single individual may alternate between macro- and microscopic forms, a variation in size within one generation similar to that between the two generations in kelps (Regeneration in **Figure 1b**).

DEMOGRAPHICS

Microscopic Stages

There has been a recent surge of interest in population inputs and the factors responsible for settlement, recruitment, and population maintenance (e.g., Kinlan & Gaines 2003, Schiel 2004). In large brown seaweeds, this process involves the supply, survival, and growth of microscopic stages from the release of spores, eggs, or sperm through to visible recruits in field conditions. Despite the life history of kelps being known for over 90 years (Sauvageau 1915), in situ studies of the microscopic stages are relatively few. Such studies are inhibited by the small size of these stages, morphological similarity among kelps and between kelps and other taxa, and the myriad other microscopic organisms, sediment, organic particles, and low-lying algae that occur in the same microenvironments. Therefore, these microscopic stages have commonly been lumped together in a “black box,” with inputs of spore abundance and outputs of visible “recruits.” This approach can be informative (e.g., McConnico & Foster 2005) but cannot determine where key demographic changes occur. If, for example, abundant spore release is followed by poor sporophyte recruitment it could be due to poor spore survival in the water column; low spore settlement; poor gametophyte development, survival, or maturation; reduced fertilization success; or high mortality of microscopic sporophytes. Here we evaluate what is known about these stages of development and survival through them.

Kelps are extremely fecund, producing up to 10^8 – 10^{12} spores individual⁻¹ year⁻¹ (DeWreede & Klinger 1988, Joska & Bolton 1987, McConnico & Foster 2005). In a dense stand of subtidal giant kelp, Graham (2003) found up to 54,000 spores L⁻¹ at 3 cm above the benthos. Stands of *Alaria marginata* synchronously release up to 10^9 spores individual⁻¹ hr⁻¹ and probably saturate the area beneath adults with spores (McConnico & Foster 2005). Spore release in annual populations generally occurs in late autumn before sporophytes die (Buschmann et al. 2004, Dayton 1973, McConnico & Foster 2005). Of the few perennial species studied, some (e.g., *Pterygophora californica*) have discrete periods of spore production, some produce spores continuously (e.g., *Laminaria digitata*), or continuously but with seasonal peaks (e.g., *Macrocystis pyrifera*, *Ecklonia maxima*; Chapman 1984, Joska & Bolton 1987, Reed et al. 1997). It is unknown whether the spores are equally viable in all seasons.

Survival from spore to juvenile sporophyte is very difficult to determine, but a few studies provide some general estimates. McConnico & Foster (2005) found that densities of about 10^{10} spores m⁻² produced around 400 visible (> 1 cm) sporophytes m⁻² of *Alaria marginata* on an intertidal reef in central California. Assuming that half the spores were female and one egg is produced per female gametophyte, proportional survival would be 8×10^{-6} . The only estimate of survival from spore release to settlement is from Chapman (1984), who used sporangial densities in two perennial *Laminaria* species in Nova Scotia to estimate spore release over a year; he estimated spore settlement from the number of visible sporophytes on ceramic tiles placed monthly into kelp stands and then cultured in the laboratory. Each species released about 10^{10} spores m⁻², and proportional survival from release to settlement was

2×10^{-3} for *L. longicruris* and 10^{-4} for *L. digitata* (**Figure 2a**). Deysher & Dean (1986) seeded small ropes with giant kelp spores at a density of $\sim 3.3 \times 10^8$ spores m^{-2} , outplanted the ropes, and then counted the microscopic sporophytes produced after 42 days in the field. In repeated experiments, the highest microscopic sporophyte density was 5×10^6 m^{-2} . Reed (1990a) seeded rocks with varying densities of spores, outplanted the rocks, and counted the number of visible sporophytes of *Macrocystis pyrifera* and *Pterygophora californica* produced. His results were also highly variable, but the greatest survival at spore densities of 10^6 m^{-2} (1 spore mm^{-2}) and 10^8 m^{-2} resulted in sporophyte densities of 10^2 and 10^4 m^{-2} , respectively, for the species (**Figure 2a**). At spore densities > 10 mm^{-2} , proportionately fewer female gametophytes produced sporophytes but there were far more recruits overall.

Fucoid propagules (zygotes and embryos) begin at a considerably larger size than those of kelps; an egg is 10–40 times greater in diameter than a typical kelp spore. Newly settled embryos and germlings can be identified readily in the field under low-power magnification (Brawley & Johnson 1991), and are visible to the unaided eye from when they are weeks (Gunnill 1980) to a few months old (Ang 1991a). Consequently, there is more information on the survival of microscopic stages of fucoids than kelps under a variety of environmental conditions.

Like kelps, by far the greatest mortality in fucoids is in the microscopic stages, as illustrated by a few species for which detailed data could be derived (**Figure 2b**). Schiel (1988) found that 2×10^6 ova of adult *Sargassum sinclairii* produced around 3×10^4 benthic settlers and 1.5×10^3 visible recruits (**Figure 2b**). Therefore, about 5% of settlers made it through to recruitment. Ang (1991a,b) estimated that *Fucus distichus* produced around 1.4×10^7 eggs m^{-2} years $^{-1}$, 30% of which were released from conceptacles; about 1–10% of eggs in receptacles became settlers and of these 0.4–12% became visible recruits (Chapman 1995). In one of the only published accounts of detailed survival of fucoid embryos to juvenile stages in the field, Dudgeon & Petraitis (2005) found that across numerous treatments, survival ranged from about 0.3–3.8% over 400 days (**Figure 2b**). Mortality was greatest in the first few days before attachment was secure, and average life expectancies of initial germlings were only 4–25 days. Even though *Ascophyllum nodosum* stands may produce 10^9 eggs m^{-2} years $^{-1}$ (Åberg & Pavia 1997), Dudgeon & Petraitis (2005) estimated a minimum period of 13 years for an individual to replace itself. *Fucus gardneri* had similarly poor but highly variable survival of recently settled embryos, with only 2 of 5395 embryos surviving to visible recruits (Wright et al. 2004). These survival rates, although small, are still several orders-of-magnitude greater than for the microscopic stages of kelps (**Figure 2a** versus **2b**). Most deleterious interactions occur in these and the early postrecruitment juvenile stages and are discussed below.

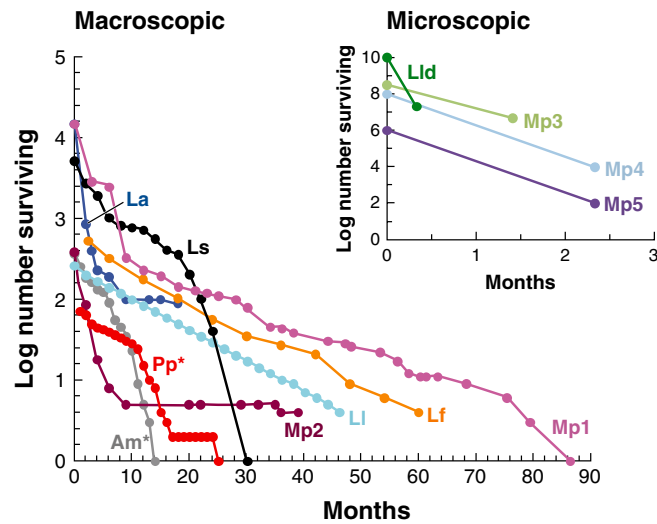
Macroscopic Stages

There are few studies that assess the survival of macroscopic stages of kelps by following cohorts, and most were done at a single site for one cohort. Furthermore, studies are difficult to compare because the starting size (commonly referred to as “visible”) has varied from 1–30 cm and mortality is usually highest in smaller plants. As

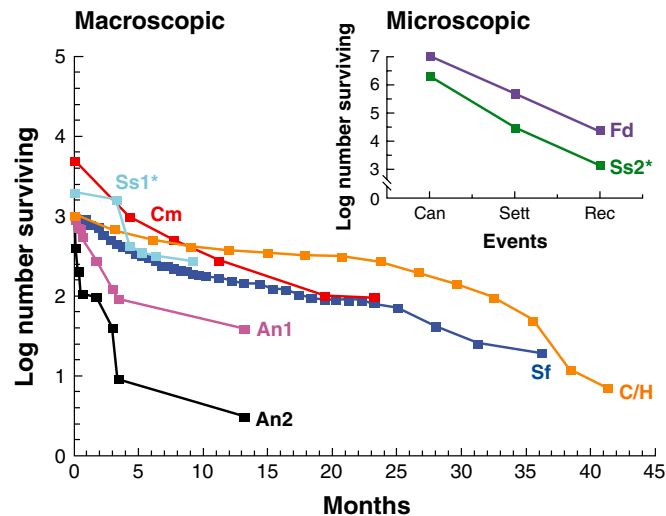
pointed out by De Wreede (1986) and Chapman (1993), the lack of standardization, combined with sparse information on the demography of microscopic stages, density-dependent mortality, and size variation within age groups diminishes the generality and usefulness of some demographic analyses, especially matrix models.

Despite these problems, some informative general trends have emerged (Figure 2*a*). Most kelp cohorts had greater mortality when plants were small,

a Kelps



b Fucoids



especially when initial densities were high. Black (1974), for example, found in an annual population of *Egregia laevigata* that, at a natural density of 2000 juveniles m^{-2} , density-dependent mortality occurred as clusters of plants with intertwined holdfasts were removed in clumps by water motion. Mortality of giant kelp juveniles can also be density-dependent (Dean et al. 1989). Many of the survival curves indicate a roughly constant rate of mortality after juveniles begin to reach adult size, and some maintain this rate for all or a great portion of their lives. This may be followed by increased mortality of the oldest plants in some perennial populations (e.g., Mp1 in **Figure 2a**). In other perennial populations, mortality rates may decline as plants mature and dominate a cohort [**Figure 2a**; *M. pyrifera* (Mp2), *L. angustata*]. For giant kelp, there is considerable variation in the different segments of survivorship curves between sites (**Figure 2a**) and for larger plants within sites and among years (Dayton et al. 1992) and regions (Buschmann et al. 2004). Although variable, these data suggest that macroscopic sporophyte demography might best be understood if this portion of the life history is divided into three stages: small juveniles, large juveniles to young adults, and old adults. It is not surprising that very high sporophyte fecundity is needed to maintain dense stands of mature plants given the low survivorship of microscopic stages and young juveniles. The demographic patterns described above for various kelps are more similar to those of terrestrial ferns (Cousens 1988) than seed plants.

Studies of the dynamics of adult kelp stands composed of multiaged plants make up the bulk of the ecological literature on marine algae and have been reviewed thoroughly (Dayton 1985, Schiel & Foster 1986). However, their demographics have received far less attention. Surprisingly, the spatial distribution and density of stands within local sites can be relatively constant from year to year in annual populations, most likely the result of when spores are produced, their microhabitat requirements, and the facilitative effects of high adult densities on their microscopic stages, including

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Figure 2

Survivorship curves for cohorts of kelps (a) and furoids (b). Macroscopic cohorts began with juveniles 1–10 cm long for kelps and 1–3 cm for furoids. Microscopic kelp cohorts began and ended with microscopic stages described below for each curve. Microscopic furoid cohort abundance plotted against events rather than time: zygotes/embryos released at canopy height (Can), number settled (Sett), and number of recruits (Rec, 1–3 cm long). *denotes annual population. Kelps: Am, *Alaria marginata* (McConnico & Foster 2005); La, *Laminaria angustata* (Kawashima 1972); Lf, *L. farlowii* (Dayton et al. 1984); Ll, *L. longicuris* (Chapman 1986); Lld, *L. longicuris* and *digitata* (average, spores in water to spores settled; Chapman 1984); Ls, *L. saccharina* (Parke 1948); Mp1, *Macrocystis pyrifera* (Dayton et al. 1984); Mp2, *M. pyrifera* (Rosenthal et al. 1974); Mp3, *M. pyrifera* (settled spores to microscopic sporophytes; Deysher & Dean 1986); Mp4, *M. pyrifera* (high density of settled spores to visible sporophytes; Reed 1990a); Mp5, *M. pyrifera* (low density of settled spores to visible sporophytes; Reed 1990a); Pp, *Pelagophycus porra* (Coyer & Zaugg-Haglund 1982). Furoids: An1, *Ascophyllum nodosum* (best survivorship; Dudgeon & Petraitis 2005); An2, *A. nodosum* (worst survivorship; Dudgeon & Petraitis 2005); C/H, *Cystoseira osmundacea/Halidrys dioica* (Gunnill 1986); Cm, *Carpophyllum maschalocarpum* (Schiel 1985a); Fd, *Fucus disticus* (Ang 1991b, Chapman 1995); Sf, *Silvetia fastigiata* (Gunnill 1980), Ss1 and Ss2, *Sargassum sinclairii* (Schiel 1985a).

reduction of potential competitors (Dayton 1973, McConnico & Foster 2005). It would be informative to know if similar consistency is maintained in low-density stands of these species. In a very thorough depletion study (survivorship of a “cohort” composed of all plants in a stand) of kelps, Chapman (1984) found replacement rates of 1–2 plants m^{-2} years^{-1} in stands of two perennial *Laminaria* spp. with densities of 1–3 plants m^{-2} . These densities are at the low end of the range of densities for mature, perennial, stipitate kelps (e.g., 0.3–7 m^{-2} for *Laminaria farlowii* (Dayton et al. 1984), 2–45 for *Ecklonia radiata* (Schiel & Choat 1980), 1.5–58 for *Pterygophora californica* (De Wreede 1984, Hymanson et al. 1990). This gradual loss and continual replacement was similar to that described for giant kelp at protected sites where densities of adult plants were about 0.1 m^{-2} (Graham et al. 1997). Adult giant kelp densities can, however, be highly variable within and among stands (Schiel & Foster 1986). Population age frequency distributions have been obtained for some long-lived kelps and used to intuit population dynamics (De Wreede 1984, Kain 1963, Klinger & De Wreede 1988). These show that age distributions can be unimodal (dominated by middle-aged or young plants), multimodal or stable, indicating that, as in giant kelp, different population dynamics occur within and among species.

As for kelps, there are few complete life tables for any fucoid species. Compiling these can be difficult because of the very high densities at which many populations occur, the entwinement of holdfasts and branching of plants that can make ramets difficult to distinguish from genets, and their often turbulent environment. Survival curves for several species (**Figure 2b**), therefore, are indicative only because there is such wide variation in survival depending on conditions (Chapman & Johnson 1990, Wright et al. 2004).

Fucoid life histories can be considered in four stages: (a) production of gametes, fertilization, and presettlement, (b) settlement and development through microscopic benthic phases, (c) the juvenile period when many density-dependent processes are manifested, and (d) mature adults. From the visible stage of recruitment (~ 1 cm), plants generally appear to have an order-of-magnitude-greater survival than kelp recruits in their first year or two. For example, Gunnill (1980) generated survivorship curves for numerous cohorts of intertidal *Silvetia* (= *Pelvetia*) *fastigiata*. Over 700–1200 days, survival from visible recruitment ranged from about 1–24%, with 50% mortality typically occurring in the first 120 days and relatively little mortality after one year (**Figure 2b**). Similarly, mortality of a *Cystoseira/Halidrys* complex was initially high, then stabilized for a year before increasing again (Gunnill 1986). Subtidal, primarily annual *Sargassum sinclairii* that recruited at around 2000 m^{-2} had 13% survival after one year, when plants died back following reproduction (**Figure 2b**, Schiel 1985a). A perennial fucoid, *Carpophyllum maschalocarpum*, that recruited at 5000 m^{-2} had only 2% survival after two years (but still 95 plants m^{-2}) when plants became reproductive. For 15 cohorts of *Fucus distichus*, Ang (1991a) found that survival over one year ranged from about 5–10%, and after three years from 0.2–5%, with wide variation in the slopes of survival curves. Mortality was generally greater (40%) in the first two months than at later times. For the intertidal *Fucus gardneri*, monthly survival of large plants over one year averaged >90%, yielding about 28% survival after 1 year, but during periods of long daytime exposure the average monthly survival was <65%

(Wright et al. 2004). Some fucoids, such as the intertidal *Ascophyllum nodosum*, can be extremely long-lived as adults, and have little population turnover. Åberg (1992a,b) estimated that individuals can live 50–60 years where ice scour affects habitats and >120 years without ice effects. The greatest annual mortality of *A. nodosum* of about 60–80% occurred in the smallest recruits (Åberg 1992a).

Studies on both kelps and fucoids show that by far the greatest mortality occurs in the early life stages and that, except where grazing by macroinvertebrates such as sea urchins is intense (Chapman & Johnson 1990, Schiel & Foster 1986), the patterns of algal stand structure are largely determined in the microscopic early life stages. We evaluate some of the factors affecting these stages below.

LONG-LIVED MICROSCOPIC STAGES OR SEED BANKS?

Some “storage” of microscopic stages, often referred to as “banks” (Chapman 1986, Edwards 2000, Hoffmann & Santelices 1991), undoubtedly occurs in large brown algae but it is far different from the seed banks found in the terrestrial environment. In large brown algae, prolonged development of microscopic stages is critical to the population dynamics of annual species, because macroscopic plants may be absent for several months (Dayton 1973, McConico & Foster 2005), and of perennial species, because of the often catastrophic loss of plants from grazing, severe water motion, and other abiotic stresses (Dayton et al. 1992, Underwood 1999). Unlike seeds, however, kelp and fucoid propagules have no protective structures [the exception is Saito’s (1975) observation of *Undaria pinnatifida* gametophytes forming thick-walled “resting stages” at high temperatures] or known innate dormancy, are far more transitory, and the surrounding medium offers none of the protection afforded seeds in terrestrial soils. Rather than true dormancy, algal propagules simply appear able to delay or prolong development when conditions are unfavorable.

In culture, kelp gametophytes can be long-lived and reproduce if returned to optimal conditions, and the growth of microscopic sporophytes can be delayed (discussed earlier). However, there is little evidence that this occurs in the field (for a possible exception, see Ladah et al. 1999). Delayed development can occur in the embryo or germling stages of fucoids in very cold water (Worm et al. 1999) or when other seasonal conditions are unfavorable (Clayton 1988, DeWreede 1986). Most species, however, probably go through their microscopic stages within a few months in the field. Deysher & Dean (1986), for example, found that densities of microscopic sporophytes on outplanted substrates seeded with giant kelp spores peaked at about 40 days and then declined. Given the numerous intrinsic and extrinsic factors that affect early life stages, including grazing, scour, sediment, temperature stress, shading, and overgrowth (Vadas et al. 1992), the ability to persist in adverse benthic conditions is probably not great.

At present, it would seem best to understand better how long these microscopic stages may persist in nature, the relative contributions of older versus younger stages to juvenile plant abundance and, after disturbances of various degrees, how these contribute to population replenishment and persistence in such variable environments. A stretched and perhaps inappropriate analogy to terrestrial seed banks could inhibit

more scientifically fruitful investigations that simply consider these algal stages as what they are, microscopic plants.

DENSITY-DEPENDENT EFFECTS

Kelps and fucoids have complex density-dependent relationships and, as for terrestrial plants, most of the literature in this area involves thinning and growth processes of postrecruitment stages across densities. From an early paper showing positive effects of density on growth and reproduction of postrecruits in a kelp and a fucoid, and comparisons with terrestrial plants (Schiel & Choat 1980), the role of density-dependence in seaweeds has been controversial, with varying degrees of positive and negative effects being reported (Ang & Dewreede 1992, Cousens & Hutchings 1983, Creed et al. 1998, Kendrick 1994, Neushul & Harger 1985, Reed 1990b, Scrosati 2005). However, the demographic and population consequences of different densities are far from clear in most species, particularly when entire life histories are considered. The dominance and suppression effects seen in terrestrial plants occur at high densities in algae (Ang & DeWreede 1992, Reed 1990b), but there are positive effects of high densities that are often ignored. Elevated local densities may increase dispersal distances and gametophyte densities (discussed below), enhance fertilization (Pearson & Brawley 1996), reduce physical stress in intertidal habitats by retaining moisture (Johnson et al. 1998), dampen water motion (Schiel 1985b), reduce per capita loss from fish (Dayton & Tegner 1984) and sea urchin grazing (Harrold & Reed 1985, Konar 2000, Mattison et al. 1977), reduce juvenile sea urchin densities (Andrew & Choat 1985), and suppress recruitment and growth of competitors (Choi & Norton 2005, Reed 1990b).

A major distinction between terrestrial plants and large brown algae is that high densities of the latter are generally required to achieve fertilization. In kelps, high adult densities lead to increased spore densities, and peaks in the latter occur when adult densities are high and spore release is synchronous (McConnico & Foster 2005, Reed et al. 1997). Such high densities may be critical because fertilization requires male and female gametophytes to be in very close proximity. High spore densities, in combination with increased water motion, also increase the probability of long-range dispersal (Gaylord et al. 2002, Reed et al. 2006). Conversely, when water motion is severe and plants sparse, dilution of spores may greatly compromise recruitment processes (Gaylord et al. 2002). Fucoids require critical sperm concentrations for high fertilization rates (Berndt et al. 2002). These may be achieved in some species through retention of gametes by mucilage on parent conceptacles, thereby enhancing chances of successful fertilization in dense stands of dioecious species (Pearson & Brawley 1996) and perhaps outbreeding in monoecious species. Fertilization is also enhanced in some fucoids by the release of gametes during calm seas, a process that can be turned on and off over remarkably short time periods (Pearson & Brawley 1996). If generally true, such mechanisms may be important to the turnover and persistence of populations in a wide range of turbulent conditions.

As for the macroscopic stages, numerous negative effects of high density have been documented for germlings (Choi & Norton 2005, Steen & Scrosati 2004), but

considerably more work is needed to understand density-dependent processes from gamete release to settlement and recruitment, and how these vary among species. The retention of moisture and amelioration of desiccation in dense aggregations (Johnson et al. 1998), elongation similar to the etiolation of terrestrial plants (Reed 1990b), and the quick formation of closed canopies may allow some species to compete more effectively with others (Choi & Norton 2005). It may well be the case that given their life histories, kelps and fucoids may require high adult densities to persist, and that negative effects such as inbreeding from self-fertilization (Raimondi et al. 2004) and thinning as populations develop are consequences of requirements of their early life stages.

Dispersal

The ability of species to disperse and replenish marine populations is an important area of research receiving much attention by ecologists (e.g., Kinlan & Gaines 2003). It was long thought from observations of recruitment around isolated kelp stands that spore dispersal was limited to a few meters, and this seems to be true for *Postelsia palmaeformis* based on recruit distribution (Dayton 1973) and genetic relatedness (Coyer et al. 1997). Reed et al. (1988) and subsequent studies by Gaylord et al. (2002), however, showed that propagules of the kelp *Macrocystis pyrifera* and the furoid *Sargassum muticum* can disperse >1 km, and genetic data indicate long-distance dispersal in the kelp *Alaria marginata* (Kusumo & Druehl 2000). Such dispersal depends on the intensity of turbulence of waves, the sinking speed of propagules and their release height above the substratum. Gaylord et al. (2002) noted that the dominant feature distinguishing passive dispersal on land from that in the sea is the density of the surrounding medium. Air is far less dense than seeds, but the densities of seawater and macroalgal propagules may differ by only a few percent (Denny 1993). Therefore, algal propagules tend to sink slowly and can be carried great distances before reaching the sea floor.

Spores likely behave as passive particles at scales greater than a few millimeters in moving water (Graham 2003). They lack cell walls, are photosynthetic, and have nutritional reserves that enable them to swim for up to five days in the light (Clayton 1992, Reed et al. 1992). However, they do not have an obligate planktonic period and may settle, attach, and begin development immediately after release (reviewed in Santelices 1990). Spores have behaviors that aid in settlement; they can be positively chemotactic to nutrients, are stimulated to settle by them (Amsler & Neushul 1990), and may exhibit thigmo- and rheotaxes (Fletcher & Callow 1992, Santelices 1990). These abilities are probably effective only at scales of a few millimeters or less under typical water motion conditions because spores are tiny and water is viscous to them (Gaylord et al. 2002). They may serve mainly to concentrate spore settlement in favorable microsites and increase the success rate of gametophyte development and fertilization. Spore attachment processes, especially how they vary among species, substrates, and water motion conditions, are largely unknown, but knowledge of them should provide valuable insights into the nature of microenvironmental settlement sites.

Gaylord et al. (2002) distinguished between colonization potential and dispersal potential. Where a minimum density of kelp spores is required for fertilization, the decline in density with distance may obviate effective colonization even if spores disperse far. A model by Kinlan et al. (2005) shows that algal propagules have far less ability for long-distance dispersal than other taxa such as invertebrates and fish, mainly because of their very short planktonic period. They comment that this is at odds with the known rapid spread of many algal species, to which other mechanisms must contribute. Reed et al. (2006) argued that dense colonization at moderate distances (kilometers to tens of kilometers) is more likely to result from the dispersal of spores from large aggregations of attached plants (i.e., kelp beds) than from a few drifting plants. This was shown by colonization patterns on an artificial reef (Reed et al. 2004). Although kelp drifting at the sea surface may produce viable spores (Macaya et al. 2005), the spores are so small and sink so slowly that the probability they will reach the sea bed in sufficient densities to colonize is likely to be low. Furthermore, severe inbreeding depression (Raimondi et al. 2004) may compromise survival and fecundity of plants resulting from drift dispersal of isolated individuals. Most kelps may rely primarily on spore dispersal via water motion to establish populations.

In all fucoids studied, zygotes or germlings appear to be the primary dispersal phase, but can disperse while still attached to detached, drifting, fertile parts of parental plants (Deysher & Norton 1982, Schiel 1985a). Fucoids, therefore, may be generally more effective than kelps at dispersing long distances and colonizing through rafting of reproductive material (**Figure 1b**, reproductive frond release). Unlike many kelps, most fucoids float or are neutrally buoyant (e.g., Norton & Mathieson 1983), and their propagules need only to attach and grow after release. Zygotes and germlings produce adhesives that aid in attachment to the substrate (Fletcher & Callow 1992). Some species, such as *Sargassum muticum*, *S. sinclairii*, and *Cystoseira osmundacea*, have fronds bearing reproductive structures that dehisce seasonally and float along the coast (Chapman 1995, Norton 1992). Some propagules may be released before reproductive structures become planktonic, enabling colonization of both local and distant sites (Deysher & Norton 1982, Schiel 1985a). Given the much larger mass of fucoid propagules relative to kelp spores, however, and that many fucoids release them near the substratum (e.g., *Fucus* spp.), it seems likely that propagules produced by attached fucoids do not travel far from parent plants (e.g., Johnson & Brawley 1998). Where large tracts of fucoids have been removed, for example, it can take many years for populations to recover (Jenkins et al. 1999, 2004; Underwood 1999).

DISTURBANCE AND ENVIRONMENTAL EFFECTS

Coastal marine environments are characterized by disturbances of different intensities and frequencies, from waves over a matter of seconds, to seasonal storm events and temperature fluctuations, episodic grazing, El Niño periods over years, and decadal oscillations (e.g., Dayton & Tegner 1984). These have numerous effects on communities, but most importantly on the demographic characteristics of growth, reproduction, and survival of species. Furthermore, the marine environment varies by

tidal height, depth, and boundary-layer effects near the substratum. Here we consider some of the intrinsic and extrinsic factors highlighted by Vadas et al. (1992) that act on different life stages and still require work. The emphasis is on the early life stages before visible recruits appear. These stages are where most mortality occurs, and the combination of favorable circumstances define the “windows” of recruitment that maintain populations.

Water Motion

Water motion has long been recognized as having a major influence on the distribution and abundance of seaweeds (Lewis 1968). The removal of large stands during storms and resulting piles of wrack on the shore are the most spectacular manifestation of this, but there is a broad correlation between species distributions and wave exposure along coastlines (e.g., Bustamante & Branch 1996). Water motion has numerous documented effects on adults (Schiel & Foster 1986) and, no doubt, early life stages of kelps and fucoids. The latter are in the early stages of investigation. For many fucoids there is an apparent paradox of living in highly turbulent shallow environments and yet having relatively poor ability to fertilize eggs and attach in such conditions. This is solved by at least some fucoids by releasing gametes only in calm conditions. Serrão et al. (1996) found, for example, that *Fucus vesiculosus* had a high release of gametes and about 100% fertilization when water velocities were below 0.2 m s^{-1} and that greater water motion inhibited release by *F. distichus* and *Silvetia* (= *Pelvetia*) *fastigiata*. These results are supported by other studies on fucoids (Pearson & Brawley 1996), but it is still unclear the extent to which some species release gametes at low tide or if other mechanisms such as buoyancy by mucilage (Clayton 1992) allows effective release in turbulent conditions. Furthermore, the timing required for fertilization, only a matter of a few hours, may be inadequate for secure attachment of zygotes. Vadas et al. (1990) showed that even a low-velocity wave removed 99% of 15-minute old zygotes of *Ascophyllum nodosum* from experimental tiles. Even with refuges and postsettlement times up to 4 hours, 75–90% of zygotes were removed by a single wave. Beyond current speeds of 20 cm s^{-1} , attachment of this species was poor, whereas another fucoid, *Fucus evanescens*, attached more securely (Vadas et al. 1992). Similarly, Taylor & Schiel (2003) showed that the ability to attach across wave gradients was broadly correlated with the distribution of adult populations. The sheltered coast fucoid *Hormosira banksii* could attach effectively only in the calmest conditions and when zygotes remained undisturbed on the substratum for 12 hours. Only 5–8% of zygotes remained on exposed shores after a single tidal cycle. In contrast, the exposed coast species *Durvillaea antarctica* had >90% successful attachment in all conditions, even when zygotes were just an hour old. A fucoid characteristic of intermediate conditions, *Cystophora torulosa*, had intermediate survival in all conditions.

Fucoid zygotes attach initially by mucilage before rhizoids are formed to anchor them securely to substrata, a process that can take a couple of days (Clayton 1992, Pearson & Brawley 1996). Because of the time necessary for effective attachment, therefore, there is a very narrow window of opportunity during the calmest of

conditions for some species to become established. This probably applies mostly in intertidal and very shallow subtidal environments where constant wave impacts are greatest. It may also apply to kelps as well as fucooids; Gaylord et al. (2002) found that spore attachment of giant kelp declined 30-fold between velocities of 15–25 cm s⁻¹. The processes involved in secure attachment and their role in the demography of species across environmental gradients is a fruitful area for further investigation.

Canopies

The suppressive effects of algal canopies on intra- and interspecific recruitment of large brown algae has been shown in many studies; removing algal canopies usually is followed by a burst of recruitment of many species owing to an increase in light (Reed & Foster 1984). Light reduction is exacerbated for microscopic stages on the sea bed where many low-lying species occur. In intertidal areas, however, direct exposure to sunlight and associated temperature stress can affect seaweeds adversely (e.g., Dethier et al. 2005), so the presence of a canopy can also be positive.

Tall algal canopies and dense patches of much shorter, highly branched species (turfs) can modify relationships between settlement of propagules and recruitment. Johnson & Brawley (1998) found that orders-of-magnitude-more settlement occurred beneath rather than just outside canopies of *Pelvetia compressa*, but subsequent recruitment was three times more common outside. Most recruits occurred in red algal turf, especially when compared to bare rock where no recruits were found. McConnico & Foster (2005) found greatest recruitment of the kelp *Alaria marginata* in patches of coralline algal turf and on residual *A. marginata* holdfasts even though spores probably saturated numerous other available benthic habitats. In the absence of tall canopies, juvenile kelp survivorship may be facilitated by subtidal algal turfs that protect the kelps from fish grazing (Harris et al. 1984). A disconnection between settlement and recruitment is probably common, not only because of suppression or facilitation by canopies but through interactions with grazers and other features of the benthic environment (e.g., Chapman & Johnson 1990). Given the generally high levels of disturbance to algal communities and the highly localized dispersal noted in most large algae, it seems that saturating the parental environment with propagules is an essential life history attribute.

Grazing, Sediments, and Nutrients

The effect of grazers on algal assemblages has been one of the most studied aspects of early postsettlement mortality (Vadas et al. 1992) and provides the basis for “top-down” models of trophic control of algal assemblages. Most knowledge about the interactions of consumers and resources in controlling algal communities comes from work on adult stages. Numerous studies show that grazing can exert strong localized control of algal community structure through selective or complete removal of large algae, but it is also highly variable in space and time (Chapman & Johnson 1990, Schiel & Foster 1986). Furthermore, grazing may interact with water motion, sedimentation, and many other variables, perhaps especially acting on the highly

vulnerable early life stages on the substratum (Bertness et al. 2002), which are prey to a wide range of grazers (e.g., small crustaceans, snails, sea urchins), and potentially unfavorable nutrient and sediment conditions near the boundary layer. The recent discovery of kelp gametophytes living in situ as endophytes within the cell walls of other algae (Garbary et al. 1999) is significant as it suggests a possible means of protection from some adverse microenvironmental effects.

Sedimentation is potentially one of the most pervasive factors affecting colonization and survival of early life stages of marine algae (Airoldi 2003). Deviny & Volsøe (1978), in one of the few studies of sediment effects on spores and gametophytes, found that sediment concentrations of only 10 mg cm^{-2} could prevent giant kelp spores from settling and developing successfully, probably because they settled on unstable sediment grains. At a much larger scale, it is likely that the massive loss of giant kelp forests along the southern California coast in the late 1950s and 1960s was caused in part by increased sedimentation associated with sewer outfalls (Grigg & Kiwala 1970). Sediment chemistry and smothering can greatly affect the growth and survival of fucoid germlings, especially in organically rich deposits (Chapman & Fletcher 2002). However, the greatest effect of sediment is probably to prevent attachment, as shown by studies on kelp spores. Even fine sediments can reduce attachment of fucoids by $>90\%$ relative to controls, and there can be species-specific differences in the ability to attach to primary substrata in the presence of fine sediments (Schiel et al. 2006). On a large scale, changes in sedimentation have resulted in long-term changes in the distribution and abundance of fucoid species in the Baltic Sea (Kautsky et al. 1986). Seasonal influxes of sand can alter communities through differential tolerances of species to abrasion and burial (D'Antonio 1986), but the effects of sedimentation may be ameliorated by grazers in some situations (Bertness 1984).

Nutrients can have large effects on the dynamics of adult kelp populations, particularly at range margins where nutrients are variable (reviewed in Schiel & Foster 1986). At smaller spatial scales, a nutrient enrichment (N-P-K) and grazing experiment by Lotze et al. (2001) showed a grazing effect but no nutrient effect on *Fucus* germlings, although grazers caused a shift in dominance of benthic species that was enhanced by an increase in nutrients. Steen (2004) found in lab experiments that there was a significant interaction between temperature, nutrients, and competitor density on the survival of *F. serratus* and *F. evanescens* germlings. At a high temperature and a high level of nutrients (nitrate and ammonia) the green alga *Enteromorpha* outgrew the fucoids, potentially displacing them in eutrophic conditions. However, in another study, grazers had a positive effect on the establishment of *Fucus* species by reducing benthic algae such as *Enteromorpha* (Worm et al. 1999). In other experiments on *F. serratus* and *F. evanescens*, Steen & Scrosati (2004) concluded that among even-aged germlings, nutrient competition was more important than competition for light in early life stages, especially at higher temperatures when fast growth increases nutrient demands. At larger scales, light attenuation from coastal eutrophication can potentially eliminate deep water kelp populations (Spalding et al. 2003).

In one of the earliest examples of interactive effects of environmental factors on recruitment windows for kelp in the field, Deysher & Dean (1986) showed that high

recruitment of giant kelp in southern California occurred only when temperatures were lower than 16.3°C and light levels greater than $0.4 \text{ Einsteins m}^{-2} \text{ day}^{-1}$, a coincidence that happens only occasionally in this environment. Artificially adding nutrients increased recruitment only in the late summer when natural temperatures were higher than 16°C and nutrients were low.

CONCLUSIONS

The recent ecological literature shows a welcome increase in studies that focus on early life stages and inputs to algal populations. These studies suggest that although there are interesting analogies between large brown algae and seed plants, differences between their life histories and environments require different conceptual approaches to understanding their population ecology. In both fucoids and kelps, the microscopic stages are morphologically distinct from diploid adults, exist in environments in or near the boundary layer that are very different from those of adults, can be tremendously abundant near dense stands of adults, and are hugely variable in their survival to recruit and juvenile stages. The “bottlenecks” of these stages are only beginning to be understood, and for relatively few of the dominant species on rocky reefs worldwide. These microscopic stages are directly dependent on dispersal and settlement of propagules, processes that also require much further investigation. Current knowledge also suggests interesting and important links between the density of macroscopic plants and the distribution, abundance, and survivorship of microscopic plants. Further progress in all these areas requires innovative techniques that cross ecological, physiological, physical, and chemical disciplines to be applied in field situations.

Despite this emerging literature, most models involving the dynamics of stands of large brown algae are based on trophic control through top-down processes. Although the generality of these models has been questioned (Elner & Vadas 1990, Foster 1992, Foster & Schiel 1988), they continue to be applied with little consideration of alternatives (e.g., Jackson et al. 2001). There is considerable evidence that even with great reductions in major predators, climatic and related physical and nutrient effects still have the greatest overall impacts on many kelp forests (Dayton et al. 1998). At this stage, it is difficult to resolve the parity of the scales of these different processes (Dayton & Tegner 1984). All act locally on algal stands but their pervasiveness along coastlines and with depth can be very different. These influences are not mutually exclusive but operate in different frames of time and space, most dramatically focussing on large losses rather than microscopic inputs. Understanding the feedbacks between these highly variable processes and reproductive output, dispersal, and survival through recruitment still requires considerable work.

Kelp and fucoid stands are affected globally by degradation of coastal habitats, especially through increased sedimentation and eutrophication, and potentially through seawater warming (Schiel et al. 2004). There is an increasing social mandate for science to help solve these problems (Hughes et al. 2005). Theory provides a context within which research can focus questions, but it is comparatively barren if it ignores the individual characteristics of important foundation species, their demographics, and how they make their living in complex and dynamic coastal environments.

SUMMARY POINTS

1. The population biology of large brown seaweeds is usually absent from models of algal community structure, yet the differing life histories, ecology, and demographics of kelps and fucoids from spores/gametes, through microscopic stages to settlement, recruitment, and maturity are critical to the establishment and persistence of algal stands.
2. Terrestrial plant models are not well suited to kelps and fucoids, which have life histories with free-living microscopic stages, produce enormous quantities of spores and gametes with little documented cost, have rapid growth rates and maturity, relatively small dispersal distances, short life spans, no known animal fertilization or dispersal vectors, and no true “seed banks” but rather delayed development for usually no more than a few months.
3. In comparison to kelps, fucoids often occur in highly turbulent nearshore environments, may release gametes during calm conditions when they are more likely to fertilize and attach, have no obligate period of development to fertilization after release from parent plants, produce far fewer, much larger propagules than kelps, and often have orders-of-magnitude-better survival through early life stages.
4. Density-dependent factors are critical for the establishment and maintenance of both kelps and fucoid stands, especially in the close proximity of gametes required for fertilization, dispersal processes that may require high densities of spores/gametes to establish populations, and feedbacks between adult densities, reproductive output, settlement, and recruitment.
5. Recruitment windows in both kelps and fucoids require the coincidence of critical levels of several conditions, especially of nutrients, light, temperature, and water motion, but are often limited by sedimentation, grazing, degree of canopy development, and microsite conditions.

FUTURE ISSUES

1. Dispersal: What are the feedbacks between generations and over what scales? To what degree do metapopulations exist? What barriers exist and over what scales do they operate? How do these relate to propagule movement, attachment, and water motion? Under what conditions can microstages be long-lived in nature? What can population genetics reveal about population isolation and connectivity?
2. Density-dependent effects on early life stages: What are the critical densities for effective settlement, fertilization, and recruitment and how do they vary among species? How do these relate to adult stand densities, reproductive timing and output, and dispersal distances?

3. Boundary layer effects: What critical interactions (physical, chemical, biological) occur at the level of microsites, and how do these scale up to wider processes to produce recruitment?
4. Species invasions: What critical features of life history stages, propagule distribution, and environments enable kelps and fucoids to get traction and spread in new habitats or, conversely, resist invasion by other species?
5. Multiple stressors: How do changing coastal environments, including nutrients, temperature, light, and water motion affect population dynamics through stage-specific processes?

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