



SEVENTEEN

Shallow Rocky Reefs and Kelp Forests

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Introduction

Kelp forests are among the iconic ecosystems of California despite most people having experienced them only remotely. From shore, viewers are captivated by the forest canopy formed at the ocean surface and the associated marine birds and mammals. Some observers have experienced kelp forests in public aquaria, but most are familiar with these ecosystems only through photographs and video. Nonetheless, these glimpses impress one with the extraordinary three-dimensional structure and biodiversity characteristic of kelp forest ecosystems. These impressions are captured in Charles Darwin's exuberant description of the forests of giant kelp (*Macrocystis pyrifera*) around the coast of Tierra del Fuego, even though his observations were largely limited to the surface and samples brought to him aboard the RV *Beagle*:

The number of living creatures of all Orders, whose existence intimately depends on the kelp, is wonderful. A great volume might be written, describing the inhabitants of one of these beds of sea-weed. . . . Innumerable crustacea frequent every part of the plant. On shaking the great entangled roots, a pile of small fish, shells, cuttle-fish, crabs of all orders, sea-eggs, star-fish, beautiful Holothuridae, Planariae, and crawling nereidous animals of a multitude of

forms, all fall out together. Often as I recurred to a branch of the kelp, I never failed to discover animals of new and curious structures. . . . I can only compare these great aquatic forests of the southern hemisphere with the terrestrial ones in the intertropical regions. Yet if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp. Amidst the leaves of this plant numerous species of fish live, which nowhere else could find food or shelter; with their destruction the many cormorants and other fishing birds, the otters, seals, and porpoises, would soon perish also. (C. Darwin, 1839)

Globally, a variety of species of kelp establish forests along margins of continents and islands in the temperate oceans of both the southern and northern hemispheres. Kelp forests also develop in some subtropical areas that experience considerable OASTA UP E NG. The distribution of these kelp forests is generally limited to areas where rocky reefs occur at shallow depths (generally <40 meters) and are consistently or intermittently bathed in cool, relatively nutrient-rich waters. Along the west coast of North America are five canopy-forming kelp species that extend from the rocky bot-

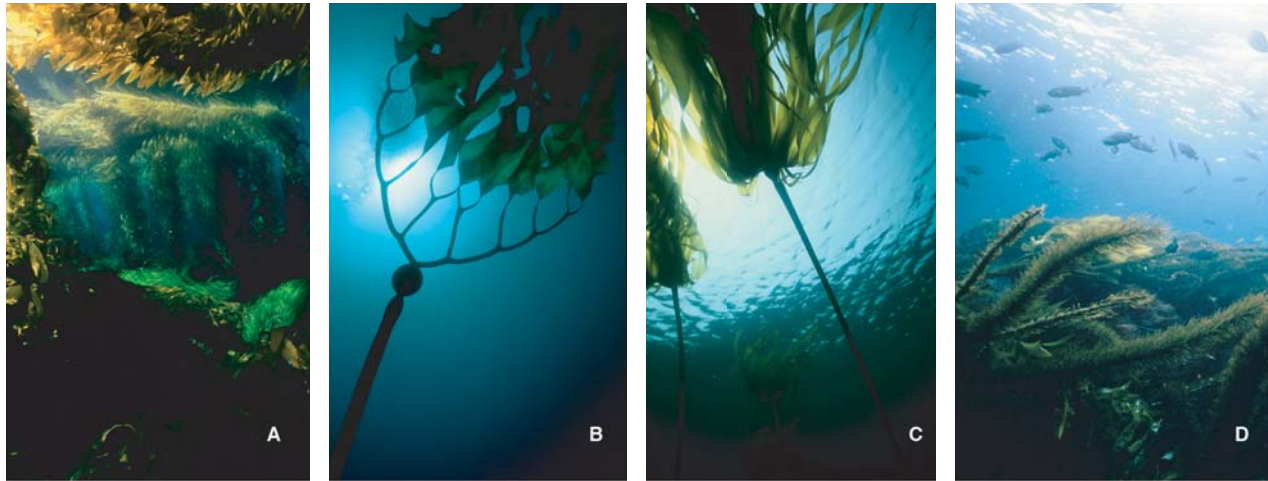


FIGURE 17.1 Images of the various species of kelps (family Laminariales) that form surface canopies in kelp forests along the coast of California. Photos: (A–D) Ronald McPeak.

- A Giant kelp (*Macrocystis pyrifera*)
- B Southern elk kelp (*Pelagophycus porra*)
- C Bull kelp (*Nereocystis luetkeana*)
- D Feather boa kelp (*Egregia menziesii*)

tom to the ocean surface, including the giant kelp (*Macrocystis pyrifera*), bull kelp (*Nereocystis luetkeana*), elk kelp (*Pelagophycus porra*), and the feather boa kelp (*Egregia menziesii*) (Figure 17.1). The dragon kelp (*Eualaria fistulosa*; formerly *Alaria* and *Druehllia*) is limited to waters along Alaska (Figure 17.2). Of these, several are limited to colder, deeper, or shallower waters; thus giant kelp and bull kelp are the primary species that form surface canopies along the coast of California.

Canopy-forming kelps exhibit markedly high rates of productivity, which reflect the combined effects of both the unique conditions in which they grow and the evolution of a form and physiology that enable kelps to capitalize on their aqueous environment. Attached firmly to the reef substrate by a tenacious holdfast, canopy-forming species of kelp extend to the sea surface to access sunlight and translocate the products of photosynthesis to deeper parts of the plant that can be in near darkness. Buoyed by seawater and, for several species, gas-filled structures referred to as pneumatocysts, most kelp biomass is allocated to leaflike

blades rather than the structural trunks, limbs, and leaves of terrestrial plants. The large surface area of these blades serves as the primary tissue for photosynthesis and nutrient absorption. The numerous blades and upright structure of these massive algae create habitat used by the myriad invertebrates and fishes that Darwin described. The biodiversity attained in kelp forests rivals that of any marine or terrestrial ecosystem in temperate latitudes. For example, counts by divers of conspicuous species in three kelp forests along the mainland of southern California produced an average of 53, 191, and 44 species of macroalgae, invertebrates, and fishes, respectively (Reed, personal observation). But these counts only included the larger more conspicuous species typically recorded by kelp forest ecologists, and not the

great diversity of smaller cryptic taxa (e.g., mesocrustaceans and microcrustaceans, polychaetes, and mollusks) that seek refuge in kelp forest ecosystems. One especially thorough examination of giant kelp forests in southern California and northern Baja California, Mexico, listed 130 species of algae and almost 800 species of animals (introduction in North 1971).

Because kelp forests are highly productive, species-rich, and close to shore, they provide a variety of ecosystem services to California's coastal communities and beyond. Commercial and recreational fishing and kelp harvesting are economically and culturally important consumptive services provided by kelp forests. Nonconsumptive services include ecotourism such as scuba diving, kayaking, and wildlife watching from shore as well as a variety of spiritual and cultural experiences. But the proximity of kelp forests to shore also exposes these ecosystems to a variety of anthropogenic impacts. These include overfishing, sediment from runoff, and a variety of pollutants and contaminants including shore-borne diseases.

Several excellent and comprehensive reviews exist of the ecology of giant kelp (North 1971, Graham et al. 2007), the ecosystems these kelp forests support (North 1971, Dayton 1985, Schiel and Foster 2015, Schiel and Foster 1986, Schiel and Foster 2006, Graham et al. 2008, Foster et al. 2013), and the ecosystems associated with bull kelp forests (Springer et al. 2010). In this chapter we draw from these reviews and more recent literature to provide an overview of kelp forest ecosystems along the coast of California and the biotic and abiotic processes that influence them. We discuss how regional variation in species composition and ecosystem function translates into regional differences in the services kelp forests provide and the anthropogenic threats they face. We close with a discussion of future challenges and opportunities for ensuring the sustainability of services generated by these highly productive and species-rich ecosystems in the face of growing coastal human populations and a changing global climate.

Photo on previous page: The great diversity of flora and fauna commonly portrayed by underwater photographs of California kelp forests. Photo: Chad King.

Geographic Distribution of Kelp Forests

The distribution of kelp in California is limited to a narrow coastal band, whose width is determined largely by the combined effects of depth, water clarity, wave action, and availability of the rocky bottom to which kelps attach. In clearer water, light penetrates deeper, allowing the forest to extend to greater depths. Likewise, an ocean floor that slopes gradually away from shore provides shallower habitat in which kelp can flourish. Within the typically narrow band along the shore that supports kelp forests, the presence of individual kelp species varies along a latitudinal gradient, corresponding to changes in abiotic and biotic conditions that determine their range limits. In this section we describe the geographic ranges of surface and subsurface, canopy-forming kelps in California, and the latitudinal differences in forest species composition that result from them. Where the various species of surface, canopy-forming kelps and upright and prostrate subcanopy-forming kelps co-occur, they create multiple layers of forest canopies above the rocky reef.

Surface Canopy-forming Kelps

Giant kelp occurs in both the southern and northern hemispheres but is restricted to cool, temperate latitudes and some subtropical areas that experience considerable coastal upwelling. In the northern hemisphere along the west coast of North America, giant kelp extends across California and from Mexico to Alaska (Table 17.1, see Figure 17.2). In northern California, however, giant kelp forests are sparse and restricted to sites well-protected from ocean waves (Schiel and Foster 2015, Seymour et al. 1989, Graham 1997, Graham et al. 2007). The southern extent of giant kelp forests is thought to be limited by both low nutrient availability, especially of nitrogen, and increasing water temperature (Ladah et al. 1999, Hernández-Carmona et al. 2000, Hernández-Carmona et al. 2001, Edwards 2004, Graham et al. 2007) or competition with warm-tolerant species (Edwards and Hernández-Carmona 2005). Historically, three species of *Macrocystis* were recognized in California—*M. pyrifera*, *angustifolia*, and *integrifolia*—with *angustifolia* at a few subtidal locations in southern California and *integrifolia* in the low intertidal and subtidal from central California to Alaska. More comprehensive morphological and genetic comparisons now indicate these are ecotypes of one species, the giant kelp *M. pyrifera* (Demes et al. 2009).

The latitudinal range of bull kelp extends from Point Conception, California, to Alaska. Where the southern range of bull kelp overlaps with giant kelp, giant kelp appears to out-compete bull kelp, restricting it to either the outer, deeper edge of the giant kelp forest or the shallow inshore where water turbulence prevents the retention of giant kelp (Foster and Schiel 1985, Graham 1997, Graham et al. 2007). Along the more exposed coastline north of Santa Cruz, California, bull kelp becomes the predominant surface canopy-forming kelp throughout the open and protected coast where shallow rocky reefs occur (Figure 17.2; Springer et al. 2010).

The geographic range of elk kelp extends from Mexico to the California Channel Islands. Because some stands of elk kelp do not form surface canopies, its distribution within its range is not well-known. Like bull kelp, elk kelp is limited to the deeper offshore edges of giant kelp forests where they co-occur. The shallow depth limit of elk kelp could be influenced

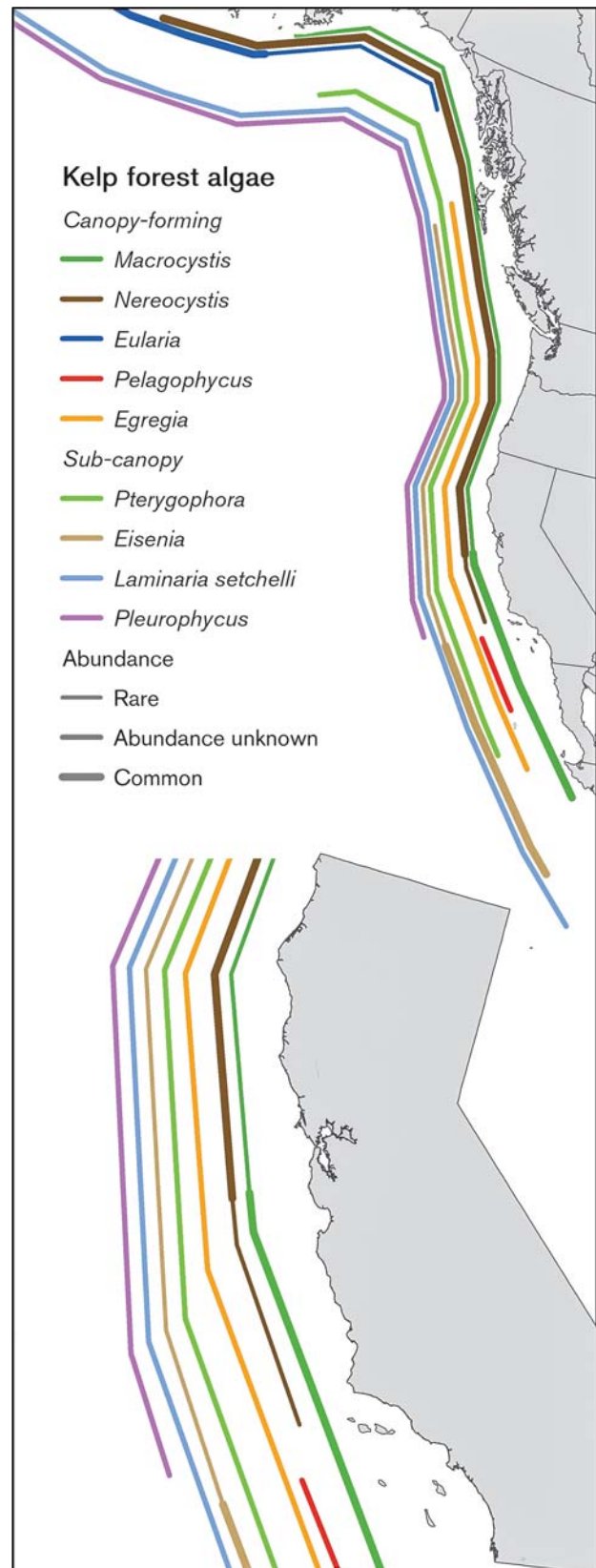


FIGURE 17.2 Geographic range of the canopy and subsurface canopy-forming macroalgae that constitute the vertical structure of kelp forests along the coast of North America. The thickness of each line reflects the relative abundance of a species across its geographic range. This figure illustrates how the species composition and relative abundance of structure-forming macroalgae vary along the coast. Source: Illustration by Emily Saarman.

TABLE 17.1
Geographic range of canopy forming and subsurface canopy-forming kelp species along the west coast of North America

Species	Southern limit	Northern limit	Most abundant	References
<i>Macrocystis pyrifera</i>	Punta San Hipolito, Baja California, Mexico	Kodiak Island, Alaska	South of Santa Cruz, California	Foster and Schiel 1985, Schiel and Foster 1986, Seymour et al. 1989, Graham 1997, Edwards and Hernández-Carmona 2005, Graham et al. 2007, B. Konar pers. comm.
<i>Nereocystis luetkeana</i>	Point Conception, California	Unimak Island, Alaska	North of Santa Cruz, California	Druehl 1970, Abbott and Hollenberg 1976, Miller and Estes 1989, Springer et al. 2010
<i>Eularia fistulosa</i>	British Columbia	Aleutian Islands	Aleutian Islands	Citations reviewed in Springer et al. 2010
<i>Pelagophycus porra</i>	Isla San Benito and San Quintin, Baja California, Mexico	Santa Cruz Island, California Channel Islands, California		Abbott and Hollenberg 1976, Miller and Dorr 1994, Miller et al. 2000, M. Edwards pers. comm.
<i>Egregia menziesii</i>	Punta Eugenia, Baja California, Mexico	Queen Charlotte Islands, British Columbia, Canada		Abbott and Hollenberg 1976, Henkel and Murray 2007
<i>Pterygophora californica</i>	Bahia Rosario, Baja California, Mexico	Cook Inlet, Alaska		Abbott and Hollenberg 1976, Matson and Edwards 2007
<i>Eisenia arborea</i>	Bahia Magdalena, Baja California, Mexico	Graham Island, British Columbia, Canada	South of Point Conception, California	Edwards and Hernández-Carmona 2005, Matson and Edwards 2007
<i>Laminaria setchelli</i>	Baja California, Mexico	Attu Island, Alaska		Abbott and Hollenberg 1976, Lindeberg and Lindstrom 2012
<i>Pleurophycus gardneri</i>	Piedras Blancas, San Luis Obispo County, California	Aleutian Islands, Alaska		Abbott and Hollenberg 1976, VanBlaricom et al. 1986, Lindeberg and Lindstrom 2012

by exposure to ocean waves, competition for light with giant kelp, or the low light-tolerance of microscopic stages (Fejtek et al. 2011). In contrast, the feather boa kelp is tolerant to great wave energy in the very shallow subtidal and is therefore almost ubiquitous wherever shallow rocky reef occurs along the coast of California.

Subsurface Canopy-forming Kelps

Several other kelp species reach heights of <3 meters above the bottom, forming a subsurface canopy a few meters above the reef. Like those species that form surface canopies, these kelps are restricted to shallow rocky reefs, establishing subsurface canopies either in the presence or absence of taller kelp species. Four of these kelps stand upright with a stiff but flexible trunk-like stem. Of these, the northern sea palm (*Pterygophora californica*) (see Figure 17.3a) and southern stiff-blade kelp (*Laminaria setchelli*; see Figure 17.3c) are broadly distributed across California from Mexico to Alaska. The southern sea palm (*Eisenia arborea*) (see Figure 17.3b), is prominent on rocky reefs from Mexico to Point Conception, California, though it occurs in low abundance on reefs across California and as far north as British Columbia, Canada. The fourth

species, *Pleurophycus gardneri* (see Figure 17.3d), ranges from the Point Conception, California, to Alaska. In central California it occurs in deeper water, usually below the lower limit of giant kelp (Spalding et al. 2003). Many other kelp species common to California kelp forests are characterized by a very short stipe that supports a long, wide blade that drapes over the rocky reef. These more prostrate species include *Laminaria farlowii*, *Agarum fimbriatum*, *Costaria costata*, and *Dictyonium californicum* (Figure 17.4).

Environmental Determinants of Kelp Distributions within Their Geographic Range

The kelp species introduced in the preceding section share common key environmental drivers of distribution within their geographic ranges. However, the relative influence of these drivers differs among species due to their markedly different growth forms and physiologies. These differences in turn determine the upper and lower depth distributions and relative vulnerability of these species to removal by wave action. For example, light is the primary constraint on the maximum depth of kelps, and differences in minimum and maximum light tolerances can explain differences in the rel-

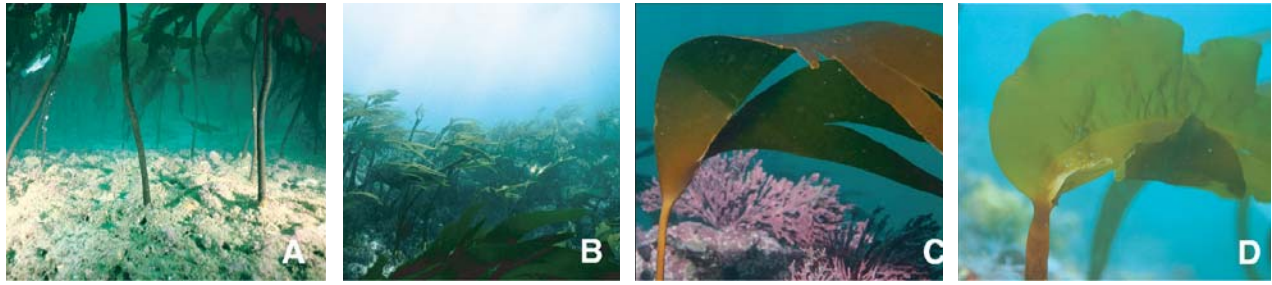


FIGURE 17.3 Images of the common species of macroalgae that form subcanopies 1 to 2 meters above the reef surface and contribute to vertical structure of forests along the coast of California. Photos: (A, B) Ronald McPeak, (C, D) Steven Lonhart.

- A Northern sea palm (*Pterygophora californica*)
- B Southern sea palm (*Eisenia arborea*)
- C Southern stiff-blade kelp (*Laminaria setchelli*)
- D Broad-ribbed kelp (*Pleurophycus gardneri*)



FIGURE 17.4 Images of the common prostrate species of kelp whose blades lie across the surface of the rocky reef, forming habitat for fishes and invertebrates. Photos: (A, B) Ronald McPeak, (C, D) Steven Lonhart.

- A (*Laminaria farlowii*)
- B Fringed sieve kelp (*Agarum fimbriatum*)
- C Seersucker kelp (*Costaria costata*)
- D (*Dictyoneurum californicum*)

ative depth range of species (Schiel and Foster 2015, Schiel and Foster 2006). However, somewhat like the seedling stages of terrestrial plants, it is the light requirements of the microscopic GAMETOPHYTE life stages and the young SPOROPHYTE stages that determine their successful germination and early growth under low light conditions (reviewed by Schiel and Foster 2006, Matson and Edwards 2007). The growth form of giant kelp (i.e., multiple FRONDS each possessing multiple blades distributed through the water column) greatly enhances the acquisition of light as compared to kelp species possessing a single stipe and fewer blades (e.g., bull kelp and several shorter upright species such as northern sea palm, southern sea palm, and *Laminaria* spp.). However, the growth form of giant kelp greatly increases its drag and susceptibility to being torn from the reef by wave action. Thus the single stipe species occur in more exposed sites while giant kelp is generally restricted to more protected sites (Foster and Schiel 1985).

Physical factors such as topography, substrate geology, and wave exposure can interact in ways that greatly increase their individual effects on the distribution of kelp species. For example, kelps attached to more friable sedimentary reefs are more likely to be detached by wave action than individuals

of similar size attached to harder granitic or basaltic reefs. Similarly, the erosion of sedimentary reefs increases turbidity and reduces light penetration, which can limit the depth range and abundance of kelps (Spalding et al. 2003, Shepard et al. 2009). Rocky reefs with low vertical relief, surrounded by or interspersed with sand, are also more likely to experience scouring by ocean waves and thus are characterized by lower densities of perennial kelps and relatively high densities of more ephemeral and rapidly colonizing algae (e.g., *Desmarestia*, many species of foliose red algae).

Another example of a strong interaction between geologic and oceanographic factors is the rare exception where kelps establish on sandy substrata rather than on rocky reef. Historically, an extensive giant kelp forest persisted for decades on sandy seafloor along the mainland just south of Point Conception, in an area protected from waves by the Northern Channel Islands (Thompson 1959). The existence of this forest illustrates how the restriction of kelps to areas of rocky substrate results from their susceptibility to removal by waves. The upper depth range of many macroalgal species can be determined by their tolerance for high wave action (e.g., for bull kelp) (Graham 1997), desiccation, ultraviolet energy (Swanson and Druehl 2000), grazing, and competi-

tion (Graham 1997). One key trait of shallow-dwelling species is a thick, flexible stipe and blades resistant to tearing and abrading against the rocky reef. Kelps that occur at shallow depths often extend into the low intertidal zone, and their thick blades are also more tolerant to desiccation (see Chapter 18, “Intertidal”).

Other factors that influence the distribution and abundance of kelp forests are nutrient availability and water temperature, which are both linked to large-scale oceanographic forcing (e.g., Pacific Decadal Oscillation [PDO], El Niño Southern Oscillation [ENSO]) and more local-scale oceanographic processes (e.g., OASTA UP E NG, currents, thermal stratification of the water column), some of which are influenced by the geomorphology of the coastline. For example, the profound influence of the 1976 PDO that altered oceanographic productivity in southern California (Roemmich and McGowan 1995) was manifest in reduced productivity in surf perch populations, which Holbrook et al. (1997) attributed to reduced production of invertebrate prey and the benthic algae that supported those prey. More episodic climatic events such as El Niño and La Niña can also have profound effects on regional patterns of distribution and abundance of kelps that persist for multiple years (see the “Disturbance, Forest Dynamics, and Shifts in Community Structure” section later in this chapter). At regional scales, Broitman and Kinlan (2006) used an archive of aerial surveys to identify the spatial correlation between kelp forest biomass and upwelling associated with coastal headlands. Similarly, chronic increased water temperature in a bull kelp forest due to discharge from an adjacent nuclear power plant in central California led to a decline in bull kelp and a concomitant increase in giant kelp. A wholesale change in community structure took place, including dramatic changes in understory algae (Schiel et al. 2004). A strong east-west geographic gradient in the structure of kelp forest communities, including the algal assemblage, in the Northern Channel Islands corresponds with a marked cline in water temperature (Hamilton et al. 2010).

Kelp Forest Phenology

Kelp forest phenology is shaped by the typically brief lifespan of the species that constitute the forest; its annual cycles of spore production, recruitment, and growth; and the loss of adults during winter storms (Figure 17.5). Some California kelp forest species are annuals, such as *Nereocystis luetkeana* (Amsler and Neushul 1989), but most are perennials, including most *Laminaria* species (Kain 1963), northern sea palm (Hymanson et al. 1990), and giant kelp (Neushul 1963). Graham et al. (2007) describe how the predictable seasonality of giant kelp growth at higher latitudes is influenced by seasonal variation in sunlight availability and wave exposure (Foster 1982, Harrold et al. 1998, Graham et al. 1997). At lower latitudes like southern California, seasonal growth rates correspond with variability in ambient nitrate concentrations, such that frond growth was greatest during winter-spring upwelling periods and reduced during summer-fall nonupwelling periods (Zimmerman and Kremer 1986).

Thus the phenology of giant kelp forests varies across its geographic range. More recently, by comparing net annual primary production of giant kelp forests in southern and central California, Reed et al. (2011) found that productivity of the southern forests was greater because of their reduced wave disturbance and prolonged growing season, despite their



FIGURE 17.5 Giant kelp (*Macrocystis pyrifera*) that has been torn from offshore reefs by storm waves and deposited on a sandy beach near Santa Barbara, California. Photo: Shane Anderson.

lower nutrient availability and greater abundance of grazers. The importance of insulation and wave exposure on seasonality of forest production at higher latitudes is also reflected by bull kelp, whose sporophytes can grow at extremely high rates, up to 6 cm day^{-1} (Scagel 1947). Maximum photosynthesis occurs in summer and early fall, and mortality of bull kelp sporophytes reaches a maximum in winter, primarily due to dislodgement by winter storms. This phenology of giant kelp and bull kelp contributes to and is embedded in a complex suite of drivers of forest dynamics that markedly influences ecosystem dynamics.

Trophic Structure and Functional Attributes of Kelp Forest Ecosystems

Kelp forest communities are characterized by a trophic structure unique to shallow reef ecosystems in that the primary space holders (i.e., macroalgae and sessile suspension-feeding invertebrates) occupy different trophic levels. Macroalgae are primary producers that derive their nutrition from sunlight and dissolved nutrients, whereas sessile invertebrates are consumers nourished by filtering plankton and other organic matter from the water column. This trophic structure leads to two different pathways in the kelp forest food web: one derived from primary production of benthic algae and the other from primary production of phytoplankton in the water column. These different trophic pathways contribute to complex trophic interactions within kelp forests that includes omnivory and carnivory across multiple trophic levels. The prey composition of many kelp forest species changes as they grow, resulting in individuals occupying multiple trophic levels over their lifetime. Taken together, trophic webs and interaction networks in kelp forests are very complicated and difficult to characterize accurately within the simplified categories generally used to describe the structural and functional relationships in communities. While we are aware of this complexity, we nonetheless present the structural and functional relationships among species in a simplified organization to illustrate qualitative differences in the species composition of trophic groups along the coast of California.

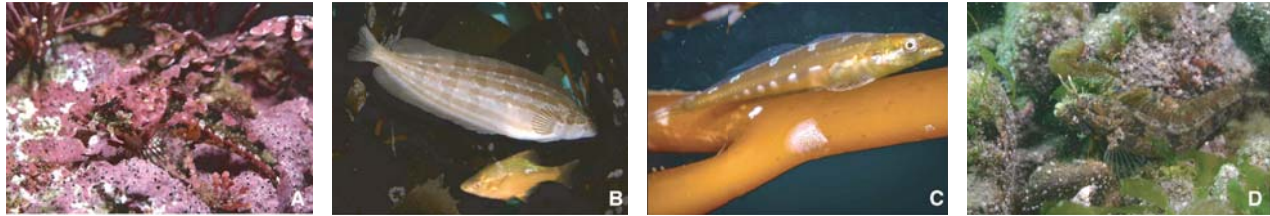


FIGURE 17.6 Examples of the cryptic coloration of kelp forest fishes, reflecting their strong association with algal habitats. Cryptic coloration enhances the ability of these species to avoid predation or ambush their prey. Photos: (A–D) Steven Lonhart.

- A Coralline sculpin (*Artedius corallines*)
- B Giant kelpfish (*Heterostichus rostratus*) and kelp perch (*Brachyistius frenatus*)
- C Manacled sculpin (*Synchirus gilli*)
- D Onespot fringehead (*Neoclinus uninotatus*)

Primary Producers

Much like the trees of forests on land, canopy-forming kelps serve as the structural species of submarine forests in the ocean. Their fast-growing, three-dimensional structure extends from the ocean floor to the sea surface and provides food and shelter for a diverse array of species (Graham 2004, Graham et al. 2008, Byrnes et al. 2011). As such, kelps are important AUTOGEN E OSYSTEM ENG NEERS of shallow rocky reef ecosystems. Beneath the overlying surface canopy, multiple vegetation layers of different algal forms occur in a patchwork mosaic competing for light and space on the bottom. Short-statured kelps with nonbuoyant, rigid stipes (e.g., southern sea palm, southern stiff-blade kelp, and northern sea palm) often grow in dense patches, forming a subsurface canopy 1–2 meters above the bottom (Dayton et al. 1984, Reed and Foster 1984, Reed 1990a). Smaller foliose, branching and filamentous forms of red, brown, and green algae produce a low-growing, bushy understory that attains its greatest biomass in areas where the surface and subsurface canopy kelps are less dense (Pearse and Hines 1979, Kastendiek 1982, Reed and Foster 1984, Miller et al. 2011). Canopies in competitive equilibrium can persist for many years by resisting invasion from other species (Dayton et al. 1984, Reed and Foster 1984) because once established, the adult plants are dominant competitors for light and space and provide the nearest source of spores when small disturbances thin their ranks (Tegner and Dayton 1987).

The geographic distribution of kelp species described in the previous section sets the stage for geographic variation in the species composition of the key primary producers within kelp forests. South of Point Conception, giant kelp is the dominant surface canopy-forming kelp with elk kelp forming subsurface canopies in some areas (Figure 17.7c). The subcanopy is composed primarily of the cosmopolitan northern sea palm and the more restricted southern sea palm and *Laminaria farlowi* (Figure 17.3). In this region major contributors to the understory layer of the forest are brown algae in the genera *Desmarestia* and *Dictyota*, *Sargassum* on the offshore islands, and various species of filamentous, branching, and foliose red algae. Crustose ORA NE A GAE are particularly abundant, especially in association with UR H N ARRENS. In central California, *Macrocystis* and *Nereocystis* both contribute to the surface canopy, with *Nereocystis* typically confined to wave-exposed sites and the offshore and inshore edges of *Macrocystis* forests (see Figures 17.2 and 17.7B). The subsurface canopy-forming kelps include northern sea palm and *Laminaria*

setchelli, and the understory algae are dominated by extensive assemblages of foliose red algae and erect articulated corallines. The articulated corallines are particularly abundant where water motion is moderate to high.

In northern California, bull kelp is by far the predominant surface canopy-forming species, whereas giant kelp only forms small stands at protected, shallow water sites. In addition, *Egregia* and *Stephanocystis* (formerly *Cystoseira*) can form a surface canopy in very shallow (<5 meters) depths (see Figure 17.1d). Like central California, subsurface canopy species are primarily northern sea palm and *Laminaria setchelli*, with an increased abundance of *Pleurophyucus gardneri* (see Figures 17.3a, b, d and 17.7a). Because of the great exposure of reefs to ocean waves and the increased numbers of sea urchins, the understory algae on these reefs is largely erect and crustose coralline algae. These geographic patterns reflect both temperature differences and the strong species interactions described below.

Annual rates of net primary production (NPP) for giant kelp vary regionally, from 2.15 kg dry mass m⁻² yr⁻¹ in southern California to 1.05 kg dry mass m⁻² yr⁻¹ in central California (Reed et al. 2011). While other algae within forests add to this annual productivity, giant kelp is by far the major source of production where it occurs. Much like terrestrial forests, the fate of primary production in kelp forests follows two principal pathways: grazing of live kelp and other macroalgae by herbivores, and consumption of kelp litter by detritivores. However, in contrast to terrestrial forests, a much greater portion of the primary production generated by kelps is also exuded into the water column in the form of dissolved or particulate organic matter. Kelp-derived dissolved organic matter (DOM) and particulate organic matter (POM) can be consumed directly by many species of planktivores, which have evolved to feed on dissolved substances or minute particles suspended in the water.

Another critical difference between these forests and terrestrial forests is the high degree to which kelp forest primary production is exported to other ecosystems (e.g., Gerard 1976). Algal fragments, whole algae, and even entire forests can be exported from their natal rocky reefs and transported shoreward by currents and waves to rocky intertidal and sandy beach ecosystems (see Figure 17.5), where they supply nutrients (Dugan et al. 2011) and fuel detrital pathways just as they do within kelp forests (Dugan et al. 2003, Revell et al. 2011, Robles 1987). On sandy beaches shorebirds feed on amphipods

that consume kelp detritus, or “wrack,” and the abundances of shorebirds and their prey are correlated with the abundance of wrack delivered from offshore forests (Dugan et al. 2003). Alternatively, detached macroalgae (also referred to as “drift” or “litter”) can be swept offshore along the bottom, where it eventually collects on deeper rocky reefs, depressions in deep sandy bottoms, and especially in deep submarine canyons where it can account for up to 80% of the particulate carbon reaching the sea floor (Harrold et al. 1998, Vetter and Dayton 1998). Kelp litter provides an important source of dietary carbon for many consumers in these deep habitats as well as structure within which small animals such as crustaceans, snails, and young fish can find shelter.

Yet another fate of detached kelp plants is to float for long periods (several months) at the ocean surface, potentially transported great distances by ocean currents (Hobday 2000a). These “kelp rafts” form habitat structure, attracting small fishes and invertebrates. These in turn attract larger fishes and marine mammals, creating floating islands or localities of intensified feeding interactions. When many of these rafts are ultimately transported back inshore, they carry with them small fishes, including the opaleye (*Girella nigricans*) and juveniles of many species of rockfishes. Thus, during these excursions, kelp rafts become vectors of transport and delivery of young to their nearshore adult habitats (Kingsford 1993 and 1995, Hobday 2000b). This “ecosystem connectivity” whereby nearshore kelps contribute various functional roles to other coastal ecosystems underscores the broader importance of kelp forests in California’s coastal ecosystems.

Kelps and other forest algae create habitat structure that is used by other species in various ways. The habitat (biologically created) formed by macroalgae adds enormous amounts of structurally complex surface area upon which other algae (EPHYTES), microbes, fungi, and invertebrates (EPHONTS) attach. Epibionts on kelp represent a variety of trophic guilds, including grazers that feed upon the kelp (e.g., amphipod crustaceans, gastropod mollusks), sessile invertebrates that feed on plankton swept near the kelp throughout the water column (e.g., caprellid amphipods, nudibranchs, and the very common encrusting bryozoan, *Membranipora*), and mobile invertebrate (e.g., crabs) and fish predators that feed on the epibionts. The structural complexity of the algae provides refuge from predation for juvenile fishes and adults of small species. The strength and importance of these associations is reflected in the cryptic coloration that fish species of a wide variety of families have to match algal habitats (Figure 17.6), the strong relationships between the relative abundances and composition of fishes and algae in a forest (Carr 1989), and the correspondence of interannual dynamics of recruitment of young fishes with year-to-year variation in abundance of species like the giant kelp (Anderson 1994, Carr 1994, others reviewed in Carr and Syms 2006, White and Caselle 2008).

Foliose and articulated coralline algae (see Figures 17.6A and 17.7A, B) form important and structurally complex habitat inhabited by a myriad of small invertebrate species (see Kenner 1992 and Dean and Connell 1987 for an intertidal example). Many small, mobile invertebrates including a diverse array of crustaceans, polychaetes, mollusks, and echinoderms seek food and shelter in the understory assemblage and in turn serve as prey for fish. Coralline algae are long-lived and more predictable in occurrence through time, and they produce chemical cues that induce settlement and metamorphosis in the larvae of many invertebrate species such as

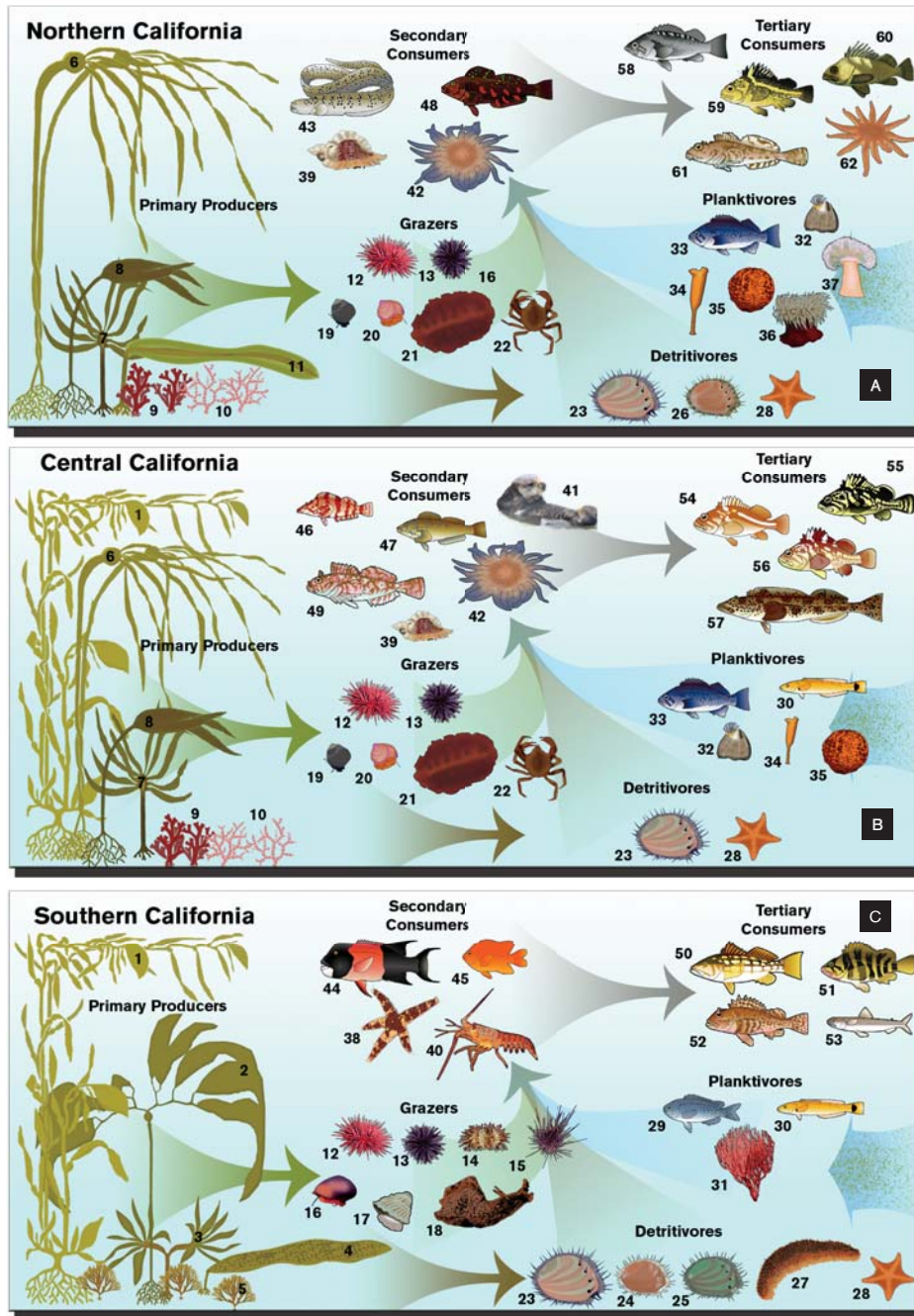
abalone (Morse and Morse 1984). Similar to the way coral erosion leads to the formation of sand habitats in tropical latitudes, the calcium carbonate structures of articulated coralline algae within kelp forests contribute to the physical structure of adjacent, soft-bottom seafloors.

Grazers

The great productivity and diversity of forms of kelp forest algae support an abundant and taxonomically diverse group of herbivores and omnivores. Among the most important are sea urchins, which depending on the abundance of kelps and production of litter are more typically relegated to roles as detritivores. However, when the supply of litter is reduced, sea urchins can switch from passive drift feeding to active foraging on attached algae. They can form dense aggregations or “fronts” that move across rocky reefs consuming all algae they encounter, including kelp holdfasts (Dean et al. 1984, Ebeling et al. 1985, Harrold and Reed 1985, Harrold and Pearse 1987). Four species of sea urchins inhabit kelp forests of California, and their relative abundance varies geographically. Kelp forests in southern California are inhabited by the highest diversity and numbers of sea urchins: red (*Strongylocentrotus franciscanus*), purple (*S. purpuratus*), white (*Lytechinus anamesus*), and the more tropical-associated crowned (*Centrostephanus coronatus*; see Figure 17.7c). Neither the crowned nor the white urchin occurs north of Point Conception. Along the central coast, with large numbers of sea otters, the abundance of sea urchins is greatly diminished; the numbers of red and purple sea urchins do not increase again until north of Santa Cruz, coinciding with the northern extent of sea otters (see Figure 17.7b). In northern California, both red and purple sea urchins are abundant in the absence of sea otters.

A diversity of herbivorous mollusks, including snails, limpets, and chitons, graze on the kelps, and red and green algae; and the relative abundances of these grazers vary along the coast. In southern California forests four species are of notable occurrence, including the smooth turban snail (*Norrisia norrisii*), wavy turban snail (*Megastrea undosa*), giant keyhole limpet (*Megathura crenulata*), and California sea hare (*Aplysia californica*) (see Figure 17.7c). The smooth turban is particularly abundant on giant kelp in southern California but rare north of Point Conception (Lonhart and Tupen 2001). The large California sea hare grazes on red algae throughout reefs of southern California but is far less abundant north of Point Conception. In central California other turban and top snails (genera *Tegula* and omnivorous species of *Calliostoma*) become very abundant and are distributed broadly throughout kelp forests (Watanabe 1984; see Figure 17.6b). Also more abundant in central and northern California forests is the large gumboot chiton (*Cryptochiton stelleri*) (see Figure 17.7a,b), an important grazer of turf algae. Throughout southern, central, and northern California kelp forests, crustaceans ranging in size from small amphipods to larger crabs graze directly on kelps and understory algae (Davenport and Anderson 2007). Especially in central and northern California, spider crabs (family Majidae) are particularly abundant and distributed up and down kelps and among the understory algae (e.g., the northern kelp crab, *Pugettia producta*) (Hines 1982).

The many species of snails and small crabs that graze on kelps and understory algae have been shown to compete with one another for this food resource. For example, two species of small turban snails, *Tegula aureotincta* and *T. eiseni*, exhibit



KEY

PRIMARY PRODUCERS

1. *Macrocystis*
2. *Pelagophycus*
3. *Eisenia*
4. *Laminaria farlowi*
5. *Dictyota*
6. *Nereocystis*
7. *Pterygophora*
8. *Laminaria setchelli*
9. *Foliose red algae*
10. *Erect coralline algae*
11. *Pleurophyucus*

GRAZERS

12. *Strongylocentrotus franciscanus*
13. *S. purpuratus*
14. *Lytechinus*
15. *Centrostephanus*
16. *Norrisia*
17. *Megastrea*
18. *Aplysia*
19. *Tegula*
20. *Calliostoma*
21. *Cryptochiton*
22. *Pugettia*

DETRITIVORES

23. *Haliotis rufescens*
24. *H. sorenseni*
25. *H. fulgens*
26. *H. kamschatkana*
27. *Parastichopus parvemensis*
28. *Patiria*

PLANKTIVORES

29. *Chromis*
30. *Oxyjulis*
31. *Lophogorgia*
32. *Balanus nobilis*
33. *Sebastes mystinus*
34. *Styela*
35. *Tethya*
36. *Urticina*
37. *Metridium*

SECONDARY CONSUMERS

38. *Kellitia*
39. *Ceratostoma*
40. *Panularis*
41. *Enhydra*
42. *Pycnopodia*
43. *Anarrhichthys*
44. *Semicossyphus*
45. *Hypsypops*
46. *Oxylebius*
47. *Hexagrammos decagrammus*
48. *H. superciliosus*
49. *Scorpaenichthys*

TERTIARY CONSUMERS

50. *Paralabrax*
51. *Sebastes serriceps*
52. *Sebastes guttata*
53. *Synodus*
54. *Sebastes caurinus*
55. *Sebastes chrysomelas*
56. *Sebastes carnatus*
57. *Ophiodon*
58. *Sebastes melanops*
59. *Sebastes nebulosus*
60. *Sebastes maliger*
61. *Hemilepidotus*
62. *Solaster*

FIGURE 17.7 Geographic variation in species composition of trophic groups that constitute kelp forest communities and trophic pathways in kelp forests of California. Shown are the abundant and distinctive species that constitute each trophic group in (A) northern California (the mouth of San Francisco Bay to the Oregon border), (B) central California (Point Conception to the mouth of San Francisco Bay), and (C) southern California (the Mexican border to Point Conception) kelp forests. Artwork by Emily Saarman, Claire Saarman, Larry Allen, and Rodrigo Beas.

exploitative competition for the fine microalgae they graze from rock surfaces in southern California forests (Schmitt 1985, 1996). This competition is intensified by their co-occurrence in cobble habitat that provides the two species a refuge from their shared predators (sea stars, lobster, and octopi) (see Schmitt 1982, 1987). Their coexistence in this refuge habitat reflects trade-offs in their different grazing techniques at different densities of the algae (Schmitt 1996). The studies on these two snails have generated fascinating insights into the complex interactions of predation and competition in determining the distributions and coexistence of these two competitors (Schmitt 1987). Similarly, different species of *Tegula* exhibit different habitat associations within central California kelp forests: some distributed at different heights along kelp plants, others in the understory algae and each at different depth strata (Watanabe 1984). These spatial patterns of the snails (Watanabe 1984) and crabs (Hines 1982) are considered examples of resource partitioning by which the species use algal resources in different areas so as to avoid competitive exclusion by one another.

Detritivores

The great production of litter by kelps and other algae supports a diverse, abundant, and economically important assemblage of detritivores. Detritivores are divided between those mobile species that actively forage for algal litter (e.g., shrimps, crabs, sea stars) and those less mobile (e.g. sea urchins, abalone) and immobile, sessile species (e.g., hydroids, polychaete worms in calcareous tubes) that depend on water movement to deliver detritus to them. The latter are referred to as sessile suspension feeders. The several species of sea urchins described as grazers also consume vast amounts of kelp litter. Of the snails that consume kelp litter, the seven species of abalone are particularly important. Southern California forests have historically harbored large numbers of red (*Haliotis rufescens*), black (*H. cracherodii*), pink (*H. corrugata*), and green (*H. fulgens*) abalone (see Figure 17.7c). Pink, green, and black abalone extend south into Mexico, but black and red abalone are the only large abalone species that typically occur north of Point Conception.

Decades of overfishing, diseases, and expanding sea otter populations have not only resulted in termination of commercial fisheries for all abalone species in California but also restricted recreational take to red abalone (and this only north of San Francisco Bay) and placed the white abalone on the endangered species list. A bacterial disease referred to as the “withering foot syndrome” has caused severe declines of black abalone across its range in southern and central California, leading to its recent listing as an endangered species. Abalone are now far less abundant and restricted to cracks and crevices in the presence of sea otters in central California forests. Here and to the north, two other smaller abalone occur: the flat (*H. walallensis*) and pinto (*H. kamschatkana*) abalone (see Figure 17.7a).

Other important, mobile detritivores include three species of sea cucumbers (*Eupentacta* and two *Apostichopus* spp.); a host of crustaceans including amphipods, crabs, and shrimps; and some sea stars (Asteroidea) and brittle stars (Ophiozoidea). Many of these species, such as the warty sea cucumber (*Apostichopus parvimensis*), are referred to as deposit feeders, collecting small bits of organic matter off the bottom (see Figure 17.6a). The most predominant detritivorous sea star is the bat

star (*Patiria miniata*), distributed throughout California but in greatest numbers north of Point Conception (Figure 17.7a–c). This species everts the five folds of its stomach directly onto the rocky bottom, digesting detritus in place.

A wide variety of sessile species wait for kelp litter to be delivered to them, including many species of tube-forming polychaete worms that extend tentacles to collect detrital material falling from the water above or resuspended from the bottom. Unlike the planktivorous sessile invertebrates described in the following section, these species inhabit horizontal surfaces near the base of the reef where detrital material collects. Of particular importance is the polychaete worm (*Diopatra ornata*) that consumes drift algae and whose mats of worm tubes collect bits of algae and shells that create a complex habitat inhabited by a diversity of crustaceans, worms, snails, and small fishes (Kim 1992).

Planktivores

Like detritivores, planktivores can be sedentary (e.g., sea cucumbers, brittle stars, anemones), sessile (e.g., barnacles, sponges, tunicates, hydroids) or mobile (e.g., fishes). Planktivores can be primary and secondary consumers, feeding on phytoplankton and zooplankton, respectively. The major source of plankton is *ANTHROPIC*, from outside the forest, and planktivores rely largely on delivery of plankton by currents into the forest from offshore. Kelp that extends through the water column causes drag and reduces the movement of plankton into the forest (Jackson and Winant 1983, Jackson 1998). Thus planktivores tend to be more abundant where currents are strongest, where kelp is less dense, and at the up-current end of forests (Bernstein and Jung 1979). In fact, planktivorous fishes like the blacksmith (*Chromis punctipinnis*) in southern California forests will move from one end of a forest to the other as the up-current and down-current end of forests alternate with the ebb and flow of tidal currents (Bray 1981).

The reef substrate used by kelp and algae also serves as substrate for sessile filter feeders, which stay fixed in place and rely on currents to bring plankton to them for feeding. The diversity of strategies and adaptations to filter plankton out of the water column is astounding. Most kelp forest sessile filter feeders rely on extended appendages (e.g., arms, tentacles) with large surface areas that can trap the tiny species of plankton. In many cases, these sessile filter feeders are passive (e.g., brittle stars, polychaete worms, hydrocorals, hydroids, bryozoans), extending these structures into the water column and waiting for plankton to drift into them, then capturing the plankton with slimy surfaces or tiny barbs and hairs. In contrast, some sessile filter feeders are active (e.g., barnacles, *Melibe nudibranch*), actively sweeping their feeding structures through the water. In addition, other filter feeders (e.g., tunicates, sponges, bivalves [boring clams and scallops]) have internal structures to capture plankton and actively draw in plankton-rich water by generating their own currents, pumping the water through internal filtering structures. The many sessile invertebrates mentioned above such as anemones, sponges, bryozoans, hydroids, and tunicates are particularly abundant on the vertical surfaces of high-relief rocks, where they find refuge from competition with algae and can better position themselves to collect particles as currents sweep by. Their abundance is reduced in the presence of subcanopy kelps that reduce the rate of water movement near the surface of the rocky reef (Eckman et al. 1989). A particularly

important planktivore is the colonial polychaete *Phragmatopoma californica*. This tubeworm creates massive reefs of their sand-impregnated tubes that provide habitat for boring clams and other species.

Fishes can be very important planktivores in kelp forest ecosystems, particularly by collecting plankton from the water column and delivering that energy and nutrients to organisms on the reef surface. For example, blacksmith (*Chromis punctipinnis*) feed on plankton in large aggregations above the reef throughout the day, and shelter in cracks and crevices at night where they urinate, defecate, and provide nitrogen that enhances algal production on the reef (Bray et al. 1981). The señorita (*Oxyjulis californica*) also forms large aggregations and feeds on plankton throughout the kelp forest (Hobson and Chess 1976). Kelp perch live mostly up in the surface canopy of kelp forests and feed both on planktonic crustaceans and those associated with the forest canopy (Anderson 1994). Juveniles of some species of rockfishes (genus *Sebastes*) form large aggregations throughout the water column (e.g., blue, black, olive, and yellowtail) and, like blacksmith, seek shelter on the reef at night. Others associate with the forest canopy (copper, gopher, kelp, black, and yellow) and feed on plankton throughout the day and shelter there throughout the night (Singer 1985, Carr 1991, Love et al. 1991). Aggregations of juvenile rockfishes in central California create a “wall of mouths” that likely reduces the delivery of larvae of nearshore species like barnacles to habitats inshore (Gaines and Roughgarden 1987). Aggregations of juvenile and adult blue rockfish (*Sebastes mystinus*) are the most abundant fish in central and northern California forests, where they feed on plankton throughout the water column. Other schooling planktivorous fishes are more ephemeral, passing through kelp forests as they move along shore (e.g., salemma, anchovy, topsmelt, jack mackerel).

As with other trophic groups, the species composition of the predominant planktivores in kelp forests varies geographically. Southern California forests support much greater abundances of particular planktivorous reef fishes, including the blacksmith and the señorita, and sessile and sedentary planktivores including five species of gorgonians (only one of which extends north of Point Conception), particular bryozoans (e.g., *Bugula*, *Crisia*), sea cucumbers (*Pachythyone*), and brittle stars (*Ophiothrix*). In central California forests the señorita is joined by huge schools of the blue rockfish (*Sebastes mystinus*) (Figure 17.8), which is also the predominant planktivorous fish in northern California forests. Central California forests support much greater abundances of barnacles (e.g., *Balanus nubilus*, *B. crenatus*), compound and solitary tunicates (e.g., *Didemnum* and *Styela*, respectively), bryozoans (*Hippodiplosia*), sponges (e.g., the orange puffball sponge, *Tethya*), and anemones (e.g., four species of *Urticina* and the strawberry anemone, *Corynactis californica*). Sessile planktivores in northern California are similar to central California, with exceptions of greater abundances of the sea cucumber *Cucumaria minitata*, and some anemones (e.g., *Urticina* and the large white anemone, *Metridium farcimen*). The greater productivity of plankton associated with coastal upwelling north of Point Conception may explain the greater abundances of sessile planktivores in central and northern California kelp forests.

Secondary Consumers

The tremendous production of grazers, detritivores, and planktivores in California kelp forests fuels a highly diverse



FIGURE 17.8 Clouds of planktivorous blue rockfishes (*Sebastes mystinus*) that are characteristic of central and northern California kelp forests. Photo: Steven Lonhart.

assemblage of secondary consumers. These predators are almost all mobile species that forage across spatial mosaics of algae and sessile invertebrates. Key among these are the great diversity of sea stars that digest their prey externally by everting their stomachs. One of the most important and voracious sea stars in central and northern California is the large sunflower star (*Pycnopodia helianthoides*), which uses its more than twenty rays and hundreds of tube feet to dislodge prey from the reef surface (e.g., turban snails, abalone) or chase down mobile prey (e.g., sea urchins, many species of snails, other sea stars) (Moitza and Phillips 1979, Duggins 1983, Harrold and Pearse 1987, Pearse and Hines 1987, Byrnes et al. 2006). Unlike other sea stars, the sunflower star ingests its prey. Although *Pycnopodia* is also a tertiary consumer, we mention it here because of the prevalence of sea urchins and other primary consumers in its diet.

The mollusks have several adaptations that facilitate consumption of both sessile filter feeders and mobile herbivores and grazers. For example, the leafy hornmouth (*Ceratostoma foliatum*) uses a spine on its shell to pry open barnacles or puncture a hole through the shells of newly settled barnacles. Kellet's whelk (*Kelletia kelletii*) has a highly extensible and prehensile proboscis that moves into the tubes of filter-feeding polychaete worms and shreds soft tissue with a radula full of rasping teeth at the tip of the proboscis. The California cone snail (e.g., *Conus californicus*) uses its proboscis to subdue its prey with a venomous protein, and other predatory snails subdue small mobile prey by enveloping them in their large, fleshy foot. Many dorid nudibranchs specialize on feeding on particular sponges, matching the color of their prey as insects do on terrestrial plants. In southern California, secondary consumers include predatory snails like *Kelletia*, *Ceratostoma nuttalli*, and other muricids. In central and northern California, *C. nuttalli* is replaced by *C. foliatum*. Octopi are also abundant, mobile, voracious predators that feed at night on snails, crabs, and other mobile organisms in kelp forests (Ambrose 1986) throughout California.

In contrast to mollusks, crabs and other crustaceans can attack sessile filter feeders and mobile prey with powerful claws, and either tear or crush the external defenses to access the internal organs and soft tissue. In southern California forests the California spiny lobster (*Panulirus interruptus*) can be an important predator on purple and red sea urchins (Beh-

rens and Lafferty 2004, Lafferty 2004). The extent, distribution, and spatial scales at which spiny lobster limit or control urchin abundance is unclear, with studies in the Northern Channel Islands suggesting that spiny lobster control urchin populations and their distributions (Behrens and Lafferty 2004, Lafferty 2004), whereas other studies along the mainland suggest they do not (Foster and Schiel 2010, Guenther et al. 2012).

California sheephead (*Semicossyphus pulcher*) are also well-known urchin predators in southern California forests (Cowen 1983, Cowen 1986, Hamilton et al. 2011, Hamilton et al. 2014), and urchin density or foraging rates can be inversely related to sheephead density (Cowen 1983, Harrold and Reed 1985, Hamilton et al. 2011). In central California, southern sea otters (*Enhydra lutris nereis*) are important predators of sea urchins (Tinker et al. 2008), and the almost ubiquitous low densities of sea urchins there is thought to reflect the presence of sea otters (McLean 1962, Riedman and Estes 1988, Reed et al. 2011), though examples of changes in urchin abundance independent of otters also exist (e.g., Pearse and Hines 1979, Pearse and Hines 1987, Watanabe and Harrold 1991). The voracious otter consumes 25% to 33% of its body weight per day, and individuals specialize on crabs, abalone, sea urchins, and clams (Costa and Kooyman 1982, Yeates et al. 2007). Sea otters are such effective predators on red sea urchins and abalone that their current numbers have negated commercial and recreational fisheries for these species within their range.

In northern California kelp forests, *Pycnopodia helianthoides* and the wolf eel (*Anarrhichthys ocellatus*) are voracious predators of adult sea urchins, but their influence on sea urchin density or foraging behavior has not been assessed in that region. In central California urchin barrens are rare, whereas in southern California, barrens vary spatially from localized patches to entire reefs and temporally from several months to many years (Dayton et al. 1984, Dayton et al. 1992, Dayton et al. 1999, Dayton and Tegner 1984, Harrold and Reed 1985, Graham 2004). Urchin barrens are also more common in northern California than central California (L. Rogers-Bennett pers. comm.). How strongly the effects of any one of these predators on sea urchins cascade to the spatial and temporal variation in kelp abundance continues to be debated among kelp forest ecologists. Interestingly, Byrnes et al. (2006) found positive correlations between predator diversity and kelp abundance, but not predator abundance and kelp abundance, in kelp forests in the Northern Channel Islands. These correlations were supported by manipulations of predator diversity and kelp abundance in small experimental Meso-OSMs. That study and others (e.g., Cowen 1983) indicate that altered foraging behavior of kelp grazers in the presence of predators could contribute to possible cascading effects.

Predators in kelp forests can influence the structure of communities in adjacent ecosystems as well. For example, both California sheephead and California spiny lobster feed on intertidal mussels. Researchers have shown that lobster foraging on mussels can greatly reduce the abundance of this competitive dominant and alter the community structure of rocky intertidal ecosystems (Robles 1987, Robles and Robb 1993). This example illustrates how predation can enhance the connectivity of kelp forests with adjacent coastal marine ecosystems. Myriad species of reef fishes feed on grazers and detritivores, especially on the great production of small crustaceans (amphipods, mysids) and snails that feed on or asso-

ciate with macroalgae. Many of these fishes are small cryptic species of an amazing diversity of families, including the clingfishes (Gobiesocidae), eelpouts (Zoarcidae), blennies (Blenniidae), clinids (Clinidae), pipefishes (Syngnathidae), poachers (Agonidae), snailfishes (Liparididae), pricklebacks (Stichaeidae), gunnels (Pholididae), gobies (Gobiidae), and sculpins (Cottidae), which in turn are all consumed by larger fishes. These small fishes are akin to the lizards and amphibians that consume insects in terrestrial forests. Because of their small size (usually <10 centimeters long), they are vulnerable to predation by larger fishes and are therefore well camouflaged to match their algal habitats (see Figure 17.6). In addition to these small fishes, larger reef fishes feed on small crustaceans, crabs, and snails, including many species of surfperches (family Embiotocidae) distributed throughout the coast of California.

In southern California small wrasses (*Halichoeres semicinctus*) and California's state marine fish, the bright orange Garibaldi (*Hypsypops rubicundus*), add to the diversity of reef fishes that depend on the great production of herbivorous and detritivorous crustaceans. In central California the painted (*Oxyplebs pictus*) and kelp (*Hexagrammos decagrammus*) greenling also feed on small crustaceans, crabs, and snails. In northern California the rock greenling (*Hexagrammos superciliosus*) and grunt sculpin (*Rhamphocottus richardsonii*) become more abundant. Fishes that target larger invertebrates include the horn shark (*Heterodontus francisci*) and the swell shark (*Cephaloscyllium ventriosum*) in southern California and the bat ray (*Myliobatis californica*). Also more abundant in central California and northern California is the cabezon (*Scorpaenichthys marmoratus*), which yanks abalone from the rock surface, ingests shell and all, and regurgitates the shell after digesting the meat from it.

The high abundances of many of these secondary consumers provide excellent examples of both intraspecific and interspecific competition as a key mechanism structuring kelp forest communities (reviewed by Hixon 2006). Competition for nesting territories among Garibaldi was one of the earlier documented examples of intraspecific competition in regulating the density of reef fishes (Clarke 1970). Intraspecific and interspecific competition within and between the black and striped surfperches has generated some of the most thorough field studies of competition in fishes (reviewed by Hixon 2006). Similarly, the species of small blennies (Stephens et al. 1970) that exhibit distinct depth and habitat associations are thought to reflect more examples of resource partitioning and niche diversification as a means of species coexistence and the maintenance of diversity.

Tertiary Consumers

The great diversity of primary and secondary consumers are fed upon by a diverse assemblage of tertiary consumers, most of which are larger, piscivorous fishes of ecological and economic importance. As mentioned earlier, many of these tertiary predators are opportunistic and feed on a combination of larger invertebrates (e.g., carnivorous gastropods, octopus, sea stars, crabs) and the many smaller fishes described above as secondary consumers. In southern California the most abundant tertiary consumer is the kelp or calico bass (*Paralabrax clathratus*), which feeds on a wide variety of smaller fishes. Additional predatory fishes characteristic of southern California forests are the treefish (*Sebastes serriceps*), the

scorpion fish (*Scorpaena guttata*), and the California lizardfish (*Synodus lucioceps*). Forests located in areas of cooler, upwelled water such as Palos Verdes and the western Channel Islands support species more common to central California, including several species of rockfishes of the genus *Sebastes* (Holbrook et al. 1997, Hamilton et al. 2010).

In central California no fewer than nine species of rockfishes inhabit kelp forests (Miller and Giebel 1973, Hallacher and Roberts 1985, Love et al. 2002), including species that form aggregations in the water column (e.g., blue, black, olive, yellowtail) and more solitary species that lie on the rocky reef (e.g., grass, black and yellow, gopher, copper, vermillion, China) or up in the water column among fronds of giant kelp (kelp rockfish). A particularly voracious predator of other fishes in both central and northern California forests is the lingcod (*Ophiodon elongates*). Although this species and the cabezon also inhabit rocky reefs beyond depths of kelp forests, both species mate on shallow rocky reefs where the male guards nests of eggs. In northern California three species of rockfishes—the black (*S. melanops*), China (*S. nebulosus*), and quillback (*S. maliger*)—are more abundant and major constituents of the kelp forest fish assemblage. In addition, three large (circa 40 centimeters long) sculpins, including the buffalo sculpin (*Enophrys bison*) and the brown and red Irish lord (*Hemilepidotus spinosus* and *H. hemilepidotus*, respectively), are tertiary consumers distinctive to northern California and further north.

In addition to fishes, some invertebrates are tertiary consumers, feeding on the predators of detritivores, planktivores, and herbivores. In southern and central California forests the moon snail (*Euspira*, formally *Polinices*) feeds in the sand adjacent to rocky reefs on reef-associated predatory snails. Several species of crustaceans also consume predatory snails. In southern California crustaceans that feed on predatory snails include the spiny lobster (*Panulirus interruptus*) and rock crabs of the genus *Metacarcinus* (formally *Cancer*). In central California forests the rock crabs *M. antennarius* and *M. productus* prey upon predatory snails, peeling away the aperture of the shell to access the soft tissue within. In northern California forests, *M. magister* is more common in shallow waters and is joined by the voracious morning sun star (*Solaster dawsoni*), which feeds on other sea stars, other echinoderms, and predatory snails. Several species of octopi occur up and down the coast of California, but diversity and abundance is particularly high in southern California forests.

Like the many species of primary and secondary consumers, tertiary consumers exhibit distinctive habitat associations thought to reflect habitat and resource partitioning. The rockfishes, in particular, exhibit distributions stratified throughout the water column and by depth (Hallacher and Roberts 1985). Elegant experimental removals of the shallower- and deeper-dwelling black and yellow (*Sebastes chrysomelas*) and gopher (*S. carnatus*) rockfishes, respectively, have revealed that their depth stratification is a result of asymmetric competition by which the superior black and yellow rockfish excludes the subordinate gopher rockfish from the preferred highly productive shallow reef habitats (Larson 1980a, 1980b).

Apex Predators

Apex predators are species that tend to occupy higher trophic levels; have few, if any, predators of their own; and strongly

influence the abundance of an important prey species or trophic level, such that the loss of an apex predator can cause cascading effects across lower trophic levels. The complex food webs of kelp forests, with many trophic pathways, can support a diversity of potential apex predators such as fishes, invertebrates, marine birds, mammals, and of course human beings. For many of these species, however, the extent to which they actually limit or control the abundance of their prey is unclear. We focus on species that are resident to kelp forests, because the extent to which more transient predators such as the great white shark (*Carcharodon carcharias*), California barracuda (*Sphyrnaea argentea*), white seabass (*Cynoscion nobilis*), and the Pacific electric ray (*Torpedo californica*) determine the numbers of kelp forest fishes is unknown.

Even for the resident predators, such as harbor seals (*Phoca vitulina*), diving Brandt's cormorants (*Phalacrocorax penicillatus*), snowy egrets (*Egretta thula*), and great blue herons (*Ardea Herodias*), which feed on juvenile and adult kelp forest fishes throughout California, the extent to which they control prey populations has not been assessed. Distinctive resident apex predators in southern California kelp forests include the highly evasive California moray eel (*Gymnothorax mordax*) and the now rarely encountered giant seabass (*Stenolepis gigas*). Because of the nocturnal and cave-dwelling behavior of California morays and the paucity of giant seabass as a result of historical overfishing, our understanding of the ecological significance of these species to kelp forest ecosystems is also poorly understood. In central California harbor seals are joined by the sunflower star and the southern sea otter. The primary predator of both harbor seals and the sea otter is the transient white shark. Apex predators in northern California forests include the sunflower star, the morning sunstar, and harbor seals. Although these species of sea stars and the sea otter are notable predators of sea urchins, they also consume a variety of carnivorous gastropods and sea stars. Our lack of knowledge of the ecological significance of many of these potential apex predators in structuring kelp forest communities underscores the need for research on their functional roles.

Determinants of Community Structure

Abiotic Determinants of Community Structure

The many abiotic drivers of species distributions described in the previous section also determine the species composition of kelp forest communities. Large-scale differences in oceanographic conditions driven by interactions among the California Current, nearshore wind fields, and the configuration of the coastline drive regional differences in the prevalence of coastal upwelling and wave exposure. Regional differences in these oceanographic drivers generally correspond with major headlands and create the foundation for the regional differences in macroalgae, invertebrate, and fish assemblages described earlier. Most conspicuous are the biogeographic differences between the Oregonian and San Diegan provinces north and south of Point Conception, respectively (e.g., Briggs 1974). North of Point Conception, notable differences in community structure occur north and south of Point Reyes and the mouth of San Francisco Bay, with additional differences north and south of Monterey Bay (e.g., the transition between prevalence of giant kelp and bull kelp). Between and within each region the topography of the seafloor (reef slope,

rock type, size, and vertical relief) interacts with water movement to shape species composition. In particular, the relative prevalence of sand and sedimentary reefs greatly influences water clarity, which collectively can affect the species composition of algae and sessile invertebrates. These geomorphological and oceanographic conditions set the stage upon which species interactions further shape the structure of kelp forest ecosystems.

Biotic Determinants of Trophic Structure

Because macroalgae and sessile invertebrates occupy different trophic levels, they do not compete for resources other than space. However, competition *within* the two space-holder groups for other resources may indirectly affect the strength of competition for space *between* them. For example, different species of macroalgae compete with one another for available sunlight. Although large, canopy-forming kelps (e.g., giant kelp and bull kelp) occupy relatively little space on the bottom (typically less than 10%), they can monopolize available sunlight and reduce the amount reaching the bottom by more than 90% (Pearse and Hines 1979, Reed and Foster 1984). The large reduction in light caused by the surface canopy suppresses understory macroalgae (Reed and Foster 1984, Dayton et al. 1984, Edwards 1998, Clark et al. 2004), which can have indirect positive effects on the abundance of sessile invertebrates via reduced competition for space (Arkema et al. 2009). Indeed, stands of these subcanopy-forming and low-lying algae can reduce delivery rates of invertebrate larvae and the planktonic prey on which sessile planktivores depend (Eckman et al. 1989). As described earlier, such interactions have implications for higher trophic levels as the composition of understory algae alters the abundance of habitat structure and prey for reef fishes (Schmitt and Holbrook 1990, Holbrook and Schmitt 1984, 1988), which in turn determines the production and survival of young fish (Okamoto et al. 2012) as well as the abundance and species composition of small, cryptic benthic fishes (Carr 1989).

Perhaps the most striking difference between kelp forests and adjacent areas occurs in the mid- and surface waters where canopy-forming kelps can provide the only physical structure above featureless seafloors (Larson and DeMartini 1984, DeMartini and Roberts 1990). Kelp blades provide habitat for a variety of sessile invertebrates, including hydroids and bryozoans, as well as a myriad of mobile crustaceans and gastropods (Bernstein and Jung 1979, Coyer 1985, 1987, Davenport and Anderson 2007). In addition to the many sessile and mobile invertebrates attached directly to the kelp, numerous species of fish associate closely with kelp structure. Adults of several species, such as the kelp perch (Anderson 1994) and manacled sculpin, feed on the invertebrates associated with the algae but also find refuge from predators in the dense forest canopy (Larson and DeMartini 1984, Anderson 2001, Deza and Anderson 2010, Stephens et al. 2006, Steele and Anderson 2006). The distribution, dynamics, and survival of juvenile fishes and the overall patterns of population replenishment of a number of reef fish species can be strongly influenced by the distribution and dynamics of the density of plants and blades that constitute forest structure. A number of experiments demonstrate the influence of the kelp density and forest area on recruitment and population dynamics of kelp forest fishes (reviewed in Carr and Syms 2006, Steele and Anderson 2006, Stephens et al. 2006).

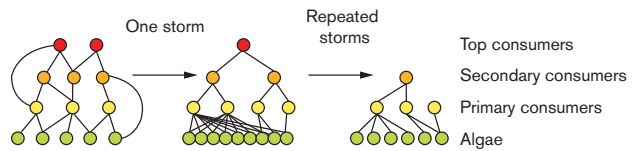


FIGURE 17.9 Model simulations and experiments show that repeated storm disturbance simplifies kelp forest food webs. Species richness goes up following a single storm as increases in the number of species of algae exceed decreases in top consumers. This leads to increases in the average number of feeding links per species. Repeated disturbance leads to less diverse and less complex food webs with fewer trophic levels and fewer feeding links per species. Source: Byrnes et al. 2011.

Interactions between Abiotic and Biotic Processes

The ecological importance of canopy-forming kelps extends far beyond their role as provider of food and shelter. Their mere physical presence dramatically alters the physical conditions of the nearshore environment and creates a habitat very distinct from adjacent waters. In this way, canopy-forming kelps function as classic autogenic ecosystem engineers (sensu Jones et al. 1994) that dramatically reduce the amount of light reaching the bottom (Foster 1975, Heine 1983, Gerard 1984, Reed and Foster 1984, Dean 1985), attenuate and redirect currents and internal waves (Jackson and Winant 1983, Jackson 1984, Jackson 1998, Gaylord et al. 2007, Rosman et al. 2007, 2010, Fram et al. 2008) and enhance mixing and turbulent flow (Rosman et al. 2010, Gaylord et al. 2012). Such modifications of the physical environment can have far-reaching biological consequences for inhabitants of the kelp forest community by affecting nutrient uptake (Wheeler 1980, Fram et al. 2008), morphology and chemical composition (Stewart et al. 2009), primary production (Miller et al. 2011), propagule dispersal (Gaines and Roughgarden 1987, Graham 2003, Gaylord et al. 2004, Morton and Anderson 2013), food supply and growth (Bernstein and Jung 1979, Arkema 2009), foraging behavior (e.g., Bray 1981), and competition (Reed and Foster 1984, Dayton et al. 1984, Clarke et al. 2004). Separately and in combination, these effects influence the productivity and spatial distribution of species, which in turn influence the composition and strength of interactions among species in the forest.

Competition among the different vegetation layers for light (and hence its indirect effects on sessile invertebrates) is very much influenced by storm-induced wave disturbance because an alga's probability of being removed by waves tends to be positively related to its stature in the water column (and hence its ability to compete for light). Unlike the giant kelp, which is dislodged by waves quite easily (Gaylord et al. 2008), many low-lying species of understory algae are able to resist removal by all but the largest of waves (Dayton and Tegner 1984, Ebeling et al. 1985, Seymour et al. 1989). Moderate wave events that remove only the surface canopy of kelp may tip the scale of space competition in favor of understory algae, which flourish in the high-light environment created by loss of the kelp canopy (Cowen et al. 1982, Foster 1982, Miller et al. 2011). Such changes can cascade throughout the entire kelp forest community, as wave disturbance has been linked to measured changes in the structure and complexity of kelp forest food webs. The periodic removal of giant kelp by wave disturbance was shown to increase local species richness and the density of feeding links of food webs by both direct and indirect pathways (Byrnes et al. 2011). Predictions

from statistical simulations of time series data, and results from a multiyear kelp removal experiment designed to simulate frequent large storms, suggested that periodic storms help maintain the complexity of kelp forest food webs. However, if large storms occur year after year, then kelp forest food webs become less diverse and complex as species go locally extinct. The loss of complexity occurs primarily due to decreases in the diversity of higher trophic levels (Figure 17.9).

Disturbance, Forest Dynamics, and Shifts in Community Structure

Kelp forests in California are very dynamic systems that fluctuate greatly in response to a complex of predictable (seasonal) and unpredictable (aseasonal and human-induced) events (reviewed in Dayton 1985, Schiel and Foster 1986, Reed et al. 2011). Frequent disturbance coupled with the relatively short lifespans of the dominant vegetation species thwart progress toward a state of equilibrium and result in a preponderance of postdisturbance succession. Off central California, for example, the thinning of mature plants by large waves associated with winter storms, along with spring upwelling of nutrients and the recruitment of new plants, leads to predictable, seasonal regeneration of kelp forests (Foster 1982, Graham et al. 1997, Harrold et al. 1988). Sea otters and strong wave action control populations of sea urchins that otherwise might graze back new plant growth (McLean 1962, Lowry and Pearse 1974, Pearse and Hines 1979, Hines and Pearse 1982, Cowen et al. 1982), contributing to seasonally lush kelp forests throughout central California.

Off southern California, seasonal fluctuations in kelp forests are less predictable. Although generally weaker, storm disturbance varies greatly from year to year (Ebeling et al. 1985, Tegner and Dayton 1987, Dayton et al. 1989, Seymour et al. 1989, Reed et al. 2011), nutrient regeneration from upwelling is less dependable (Jackson 1977, Gerard 1982, Zimmerman and Kremer 1986, Zimmerman and Robertson 1985), and recruitment events occur more sporadically (Deysner and Dean 1986, Dayton et al. 1984, Dayton et al. 1992, Reed 1990b). The absence of sea otters and the insufficient numbers of other predators of macroinvertebrates make regenerating forests more vulnerable to deforestation by grazing sea urchins (Leighton et al. 1966, Leighton 1971, Dean et al. 1984, Ebeling et al. 1985, Harrold and Reed 1985) or displacement by dense aggregations of suspension-feeding invertebrates (Carroll et al. 2000, Rassweiler et al. 2010). In addition, abundant species of subtropical fishes (kyphosids and labrids), which are rare or absent in central and northern California forests, browse the kelp and under certain circumstances can inhibit forest regeneration (Rosenthal et al. 1974, North 1976, Bernstein and Jung 1979, Harris et al. 1984).

Both the 1982–1984 and the 1997–1998 El Niño Southern Oscillation (ENSO) events demonstrated the large and widespread impact that episodic climatic changes can have on nearshore kelp communities (Gerard 1984, Dayton and Tegner 1984, Zimmerman and Robertson 1985, Ebeling et al. 1985, Cowen 1985, Dayton et al. 1999, Edwards 2004, Edwards and Estes 2006). For example, the 1997–1998 El Niño resulted in the near-complete loss of all giant kelp throughout one-half of the species' range in the northeast Pacific Ocean (Edwards 2004, Edwards and Estes 2006). The effects of ENSO are usually stronger and last longer in southern California than in regions farther north (Paine 1986, Tegner

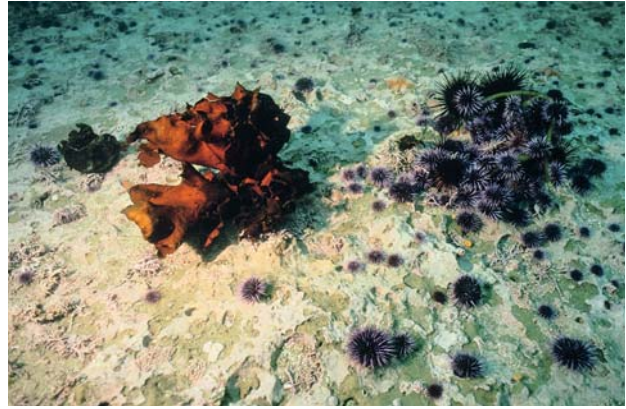


FIGURE 17.10 A barren area in southern California caused by physical disturbance and urchin predation is characterized by an absence of macroalgae and high cover of encrusting coralline algae. Photo: Ron McPeak.

and Dayton 1987, Edwards 2004, Edwards and Estes 2006). These erratic or episodic disturbances in kelp forests can contribute to the formation of barren areas (Figure 17.10) of variable size that persist for indeterminate periods in southern California (Leighton et al. 1966, Leighton 1971, Dean et al. 1984, Harrold and Reed 1985, Ebeling et al. 1985). The regeneration of the forested state in barren areas depends on a fortuitous combination of oceanographic events and biological processes (Harrold and Reed 1985, Rassweiler et al. 2010, Bestelmeyer et al. 2011). For example, Ebeling et al. 1985 chronicled the loss and reforestation of kelp forests off Santa Barbara. Strong storms removed much of the giant kelp on a reef, triggering sea urchins to vacate cracks and crevices and remove much of the algae across the reef. The area remained an “urchin barrens” until a subsequent storm caused mass mortality of the exposed sea urchins, allowing the giant kelp to recolonize and reforest the reef.

Kelp Forest Ecosystem Services

Because of their great productivity, biodiversity, and close proximity to shore, California's kelp forests have a long and diverse history of human use. Kelp forest ecosystems provide humans with a diversity of consumptive and nonconsumptive services, including kelp harvesting for several products, recreational and commercial fisheries, ecotourism (e.g., kayaking, wildlife viewing, scuba diving), shoreline protection, and spiritual and cultural values.

Kelp Harvesting

Kelp beds were favorite fishing grounds of Native Americans living near the coast of California, providing fish and shellfish as important sources of protein in their diets (Landberg 1965). Kelp itself was used by Native Americans to make fishing line (Swan 1870); bottles for storing bait, food, and freshwater (Driver 1939); seasoning for food (Leachman 1921); and medicines (Mead 1976). By the turn of the twentieth century, the United States had become the world's largest consumer and importer of potash, an organic compound found in plants and used to manufacture fertilizers and black gun-

powder. World War I created enormous demands for potash as well as for acetone, a solvent used to manufacture smokeless gunpowder (Neushul 1987, 1989). Enterprising American businessmen developed a new industry designed to extract both potash and acetone from California's giant kelp (Haynes 1954). Although short-lived, California's World War I kelp industry was the largest ever created in the United States for the processing of marine plants (Neushul 1987).

Kelps are also an important natural source of alginate, a PHYCOID used in a wide variety of pharmaceutical, household, and food products. The commercial harvesting of kelp for the production of alginates began in San Diego in 1929 and reached its peak in the 1970s, when annual harvests of giant kelp in California averaged nearly 142,000 metric tons (Leet et al. 1992). The productivity and sustainability of this industry was enhanced by limiting kelp removal to the upper 2 meters of the surface canopy. Specialized vessels with rotating cutting blades literally "mowed the lawn" of the surface canopy of giant kelp forests (Figure 17.11), which allowed young fronds from the same plants to rapidly replace the removed canopy. The kelp alginate industry in California continued until 2006, when International Specialty Products (formerly Kelco), the nation's largest and oldest kelp harvesting company, moved its manufacturing operations to Scotland. Since the termination of California's large-scale commercial harvest of kelp, human harvest has consisted primarily of a small industry that harvests giant kelp to support the abalone mariculture industry along the coast of California. Kelp harvest for this industry involves smaller mechanized vessels and harvest by hand.

The California Department of Fish and Wildlife manages the harvest of giant kelp by leasing beds for commercial harvest. Aerial photographic surveys have been used to assess the state of the resource, and this time series of the spatial extent of the giant kelp forests along the coast has provided a valuable time series of forest dynamics.

Fisheries

California kelp forests have long supported economically and culturally significant recreational and commercial fisheries (see also Chapter 35, "Marine Fisheries"). In southern California invertebrates including several species of abalone (genus *Haliotis*) and the spiny lobster (*Panulirus interruptus*) have been primary targets of recreational fisheries. Private and commercial passenger fishing vessels have supported a highly active hook-and-line recreational fishery (e.g., Love et al. 1998). Several species of abalone also supported a commercial fishery in southern California for several decades until it was realized that stocks of all abalone species were greatly depleted. Consequently, both the recreational and commercial take of abalone have been terminated there since 1997 (Karpov et al. 2000). Now, the only abalone fishery is the recreational fishery confined to the coastline north of the mouth of San Francisco Bay. The commercial and recreational spiny lobster fisheries in southern California continue to today. In addition, a fishery for the warty sea cucumber occurs in southern California kelp forests.

Historically, nearshore shallow (<30 meter depth) rocky reef and kelp forest ecosystems were fished for finfishes more heavily by recreational than commercial fisheries along the California coast (Starr et al. 2002). Nearshore rocky areas became more important to commercial finfish fisheries in the



FIGURE 17.11 A kelp harvester designed with a mower on the bow of the vessel to remove the surface canopy of a giant kelp forest. Photo: Kendra Karr.

early 1980s and later as a result of the more lucrative live-fish fishery (CDFW 2002a). Rockfishes are the predominant component of commercial catches in nearshore rocky reef and kelp habitats; about fifteen rockfish species are commonly caught in these shallow areas, especially in central California. Annual commercial landings of fishes from shallow rocky habitats averaged about 330,000 kg yr⁻¹ from 1991 to 1998, almost twice that of the annual landings in the 1980s. Declines in catch rates in shallow kelp and reef habitats during the 1990s suggest that fishing rates were not sustainable. In the late 1990s commercial landings declined in rocky nearshore habitats, due to a decrease in fish abundance and more restrictive fishery regulations (Figure 17.12). Increased landings of many species, especially cabezon, kelp greenling, and grass rockfish, in the early 1990s have been attributed to the increase in the live-fish fishery. Since 1998, however, more rigorous fishing regulations have reduced landings of several nearshore fishes.

The commercial live-fish fishery began in southern California as a trap fishery primarily for California sheephead but quickly spread up the California coast. In the early 1990s the fishery expanded to central California, and in 1995 the region recorded the highest catches in California, with the majority caught using various hook-and-line and trap methods. The fishery is comanaged, depending on species, by the federal Pacific Fishery Management Council (PFMC) and the California Department of Fish and Wildlife. As of this writing, the fishery is considered "data poor" based on the paucity of stock assessments and difficulty in assessing catch (CDFW 2002b).

Human Impacts to Kelp Forests and Management Responses

Restoration

Kelp forests are potentially at risk from a number of human activities in the nearshore coastal zone. Land uses that alter the amount and constituents of runoff and the coastal discharge of municipal, agricultural and industrial wastes can negatively impact kelp forests by degrading the physical, chemical and biological environment in which they occur (North et al. 1964, Meistrell and Montagne 1983,

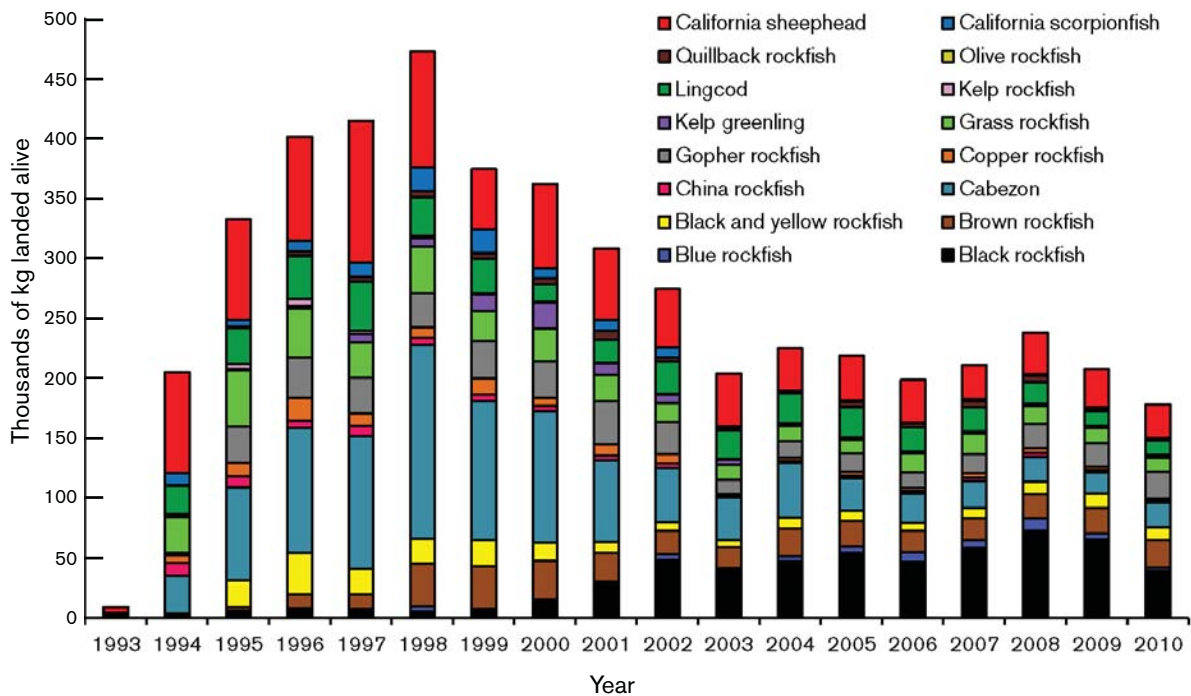


FIGURE 17.12 The trend in commercial landings of fish species targeted by the live-fish fishery in nearshore waters, especially kelp forests. The trend reflects the rapid growth of the fishery in the early 1990s and the subsequent decline due to greater restrictions. Source: Data from PacFIN (Pacific Fisheries Information Network) database.

Ambrose et al. 1996, Airoidi and Beck 2007, Gorman et al. 2009). The most severe effects appear to result from increased turbidity and sedimentation, which cause a reduction in bottom irradiance and loss of suitable rocky substrata needed for kelp attachment (Schiel and Foster 1992). The natural recovery of kelp often proceeds rapidly once human-induced stressors have been removed and the nearshore environment has been returned to its natural state.

The damaging effects of sewage discharge, coastal development, and sedimentation were realized between 1950 and 1970 in kelp forests at Palos Verdes and Point Loma near the rapidly growing cities of Los Angeles and San Diego. Discharge of domestic and industrial wastes and pollutants from the cities of Los Angeles and San Diego increased more than tenfold during this period (Foster and Schiel 2010). Sedimentation from coastal development and harbor expansion further reduced water quality in both areas. Such heightened activities in the coastal zone can adversely affect the reproduction, growth, and survival of microscopic stages of kelp by reducing availability of exposed hard substrate and light on the bottom and increasing concentrations of toxic chemicals (Devlinny and Volse 1978, Deysher and Dean 1986, Schiff et al. 2000). Not surprisingly, dramatic declines in the canopy area of giant kelp occurred at Palos Verdes and Point Loma during this time. Recovery of the kelp canopies at both sites coincided with increases in water quality that resulted from improvements in sewage treatment and extension of the sewage outfall into deeper water (Foster and Schiel 2010).

The construction of artificial reefs has been used to mitigate for the loss of kelp forest habitat in the case where the stressors causing degradation were allowed to continue. The most prominent example of this is a large, artificial reef near San Clemente, California, that was constructed to compensate for the loss of kelp forest habitat caused by the operation of the San Onofre Nuclear Generating Station (Reed et al.

2006a; Elwany et al. 2011). This artificial reef was rapidly colonized by giant kelp and reef fish (Reed et al. 2004, Reed et al. 2006b) and supports populations of many kelp forest species similar to natural reefs in the region. Artificial reefs have also been used to transform soft-bottom habitats into hard-bottom areas in efforts to expand kelp habitat beyond its natural occurrence (Turner et al. 1969, Lewis and McKee 1989). The depth, topography, and bottom coverage of an artificial reef as well as its proximity to existing kelp forests are important determinants of the timing and extent of colonization by kelp and its ability to persist (Reed et al. 2004; Reed et al. 2006a). Although the technology for building artificial reefs that support kelp is largely developed, the large-scale transformation of soft-bottom habitats into hard-bottom kelp forests is expensive and involves trading resources associated with one habitat type for those associated with another. For these reasons, the pros and cons of using artificial reefs for habitat transformation should be carefully weighed and considered.

Invasive Species

Invasive (i.e., introduced) species are a much greater concern in coastal embayments with concentrated vessel traffic, like San Francisco Bay, than in ecosystems along the open coast. Nonetheless, a handful of more prominent algae and invertebrates have successfully invaded kelp forests and shallow rocky reef habitats along the coast of California (Page et al. 2006, Maloney et al. 2007, Williams and Smith 2007, Miller et al. 2011). The brown alga (*Sargassum muticum*) inhabits shallow (<10 meter) depths and ranges from British Columbia, Canada, the likely site of introduction, south to Baja California, Mexico. This species can inhibit the reestablishment of giant kelp where it has invaded after removal of giant kelp

(Ambrose and Nelson 1982). It also invaded former giant kelp forests at some sites after the 1982–1983 El Niño removed giant kelp, but the invader died out over four years as giant kelp recovered (Foster and Schiel 1993).

A more recently introduced congener, *Sargassum horneri* (formally *filicinum*), was first found in Long Beach Harbor on the southern California mainland and now occurs in kelp forests across several islands off southern California (Miller et al. 2011). Another recent invasive alga is *Undaria pinnatifida*, which was restricted to harbors until its recent discovery in kelp forests off Santa Catalina Island in southern California (Aguilar-Rosas et al. 2004, Thornber et al. 2004). Other less conspicuous invasive algae are more abundant in southern California than to the north (Miller et al. 2011 and Miller pers. comm.).

Most of the invasive invertebrates found in kelp forests tend to be inconspicuous species, including the bryozoan *Bugula neritina*, the colonial tunicate *Botryllus schlosseri*, a polychaete worm *Branchiosyllis exilis*, the tube-forming serpulid worm *Hydroides elegans*, and the amphipod *Monocorophium insidiosum*—all of which have been detected on natural reefs (Maloney et al. 2007). One conspicuous bryozoan invader in the genus *Watersipora* is likely a species complex (Mackie et al. 2012) and is growing increasingly abundant in at least one central California kelp forest adjacent to the Hopkins Marine Station in Monterey Bay. Although the invasive algae are starting to receive greater attention, the invertebrates are not, and the geographic distribution and rate of spread of all of these invaders is not being systematically monitored in kelp forests. Only in the case of *Sargassum muticum* have the ecological consequences of invasion in giant kelp forests been assessed.

Ecosystem-based Management and Marine Protected Areas

The recent interest in more ecosystem-based approaches to fisheries management has become more tangible in kelp forest ecosystems in recent years. This is evidenced by the growing number of studies of oceanographic drivers of replenishment and dynamics of species fished from kelp forests (reviewed in Carr and Syms 2006, Caselle et al. 2010); the identification of critical habitat components, including giant kelp and bull kelp forests, for fished species; and a slowly growing understanding of the ecological function of fished species and the potential ecosystem-wide consequences of their removal (Tegner and Levin 1983, Dayton and Tegner 1998, Tegner and Dayton 2000, Steneck et al. 2002, Behrens and Lafferty 2004, Lafferty 2004). In the near future the ecosystem-based approach will turn more attention to better understanding the human dimensions of these nearshore fisheries and the factors sustaining these coupled social-ecological systems, especially in the face of a changing climate.

Because the surface canopy of giant kelp forests creates habitat for a community of invertebrates (Coyer 1985 and 1987, Bernstein and Jung 1979) and fish populations (Anderson 1994) and provides nursery habitat for juvenile fishes (Carr 1989, 1991, 1994, Singer 1985, Johnson 2006a, 2006b, Deza and Anderson 2010), a more ecosystem-based approach to managing kelp harvest considers these potential ecosystem-wide consequences (Springer et al. 2010). The sustainability of giant kelp harvest is based on its growth form; new fronds are propagated from the base of the plant, allowing rapid replacement of the harvested canopy. Moreover, the reproductive



FIGURE 17.13 Map of the statewide network of marine protected areas along the coast of California. Red polygons indicate “no-take” marine reserves and blue polygons indicate marine conservation areas that allow take of some species (e.g., recreational fishing). Source: Illustration by Emily Saarman.

blades (SPOROPHYTES) are located at the base of giant kelp plants, protecting them from harvest. Such is not the case for bull kelp. Removal of the surface canopy of bull kelp essentially removes the entire plant, including the reproductive blades, reducing the ability of a harvested forest to replenish itself (reviewed by Springer et al. 2010).

One of the most notable efforts toward ecosystem-based management of kelp forest ecosystems is the recent establishment of a statewide network of marine protected areas (MPAs) (Figure 17.13). Goals of the MPAs created by the Marine Life Protection Act include: (1) to protect of the natural diversity and abundance of marine life, and the structure, function, and integrity of marine ecosystems; (2) to help sustain, conserve, and protect marine life populations, including those of economic value, and rebuild those that are depleted; (3) to improve recreational, educational, and study opportunities provided by marine ecosystems that are subject to minimal human disturbance, and to manage these uses in a manner consistent with protecting biodiversity; (4) to protect marine natural heritage, including protection of representative and unique marine life habitats in California waters for their intrinsic value; and (5) to ensure that the state’s MPAs are designed and managed, to the extent possible, as a network.

Because of the greater dispersal potential of young organisms, populations in MPAs are more connected to populations outside of protected areas than are populations in terrestrial reserves (Carr et al. 2003). Kelp forests are one of thirteen ecosystems specified for protection by MPAs in California, and the network includes kelp forests distributed across state waters (Saarman et al. 2013). The proportion of kelp forests in each of four regions of the coast in no-take reserves and all MPAs combined varies from 5% and 8% on the North Coast to 28% and 44% on the Central Coast, respectively (Table 17.2; Gleason et al. 2013). Not only are these MPAs likely to contribute to ecosystem-wide conservation (e.g., the functional roles of harvested species and curtailing habitat impacts associated with some fishing methods), but in combination with coupled ecological and oceanographic monitoring programs they also serve as valuable tools for fisheries management (e.g., Schroeter et al. 2001, Babcock and MacCall 2011) and for assessing the combined effects of fishing and climate change on kelp forest ecosystems (Carr et al. 2011). In addition, a federally designated MPA, the Monterey Bay National Marine Sanctuary, contributes to the protection of reef habitats that support kelp forests along the coast of central California. Separate from these management roles, reserves contribute to the aesthetic values of coastal marine ecosystems like their terrestrial counterparts (e.g., national parks and wildlife refuges).

Impending Challenges

California's kelp forest ecosystems face three overarching challenges, each of which is a consequence of ever-growing coastal human populations and a changing global climate. Growing coastal populations and global demands on California's highly productive coastal agriculture look to the ocean as a substantial means of replacing or augmenting dwindling freshwater sources. As coastal power stations close or shift to onshore cooling systems, growing numbers of desalination facilities will continue to extract seawater and the larvae of marine organisms that occupy those waters, though likely at lower rates than historically observed for power stations. Simultaneously, agricultural and urban runoff and wastewater discharge continue to threaten coastal water quality in various ways including eutrophication. Careful management of water withdrawals from and discharge into the coastal ocean so as not to impair the productivity of coastal marine ecosystems will be paramount. Likewise, growing demands for protein will increase pressure on the many existing and emerging fisheries associated with kelp forests.

Simultaneously, climate models predict changes in the magnitude, timing, and distribution of coastal upwelling, which fuels kelp forest productivity (e.g., Snyder et al. 2003, Diffenbaugh et al. 2004). Predicted increases in surface ocean temperatures and associated low nutrients have the potential to shift the southern limit of giant kelp along the mainland from central Pacific Baja to somewhere between Santa Barbara and Los Angeles. Giant kelp might even disappear from the southern islands, from Santa Catalina Island south, that are little-influenced by the cooler California Current. Other coastal manifestations of climate and atmospheric change include hypoxia and ocean acidification, both of which are directly linked to upwelling processes (Grantham et al. 2004). How anthropogenic impacts interact with a changing coastal ocean will influence the ability of kelp forests, like

TABLE 17.2
Proportion of kelp forests within no-take state marine reserves and all marine protected areas (MPAs) combined
Includes both reserves and conservation areas that allow limited take of specified species

Regions	Proportion of kelp forests in no-take reserves	Proportion of kelp forests in all MPAs
North Coast	5.0%	8.4%
North Central Coast	15.4%	39.4%
Central Coast	27.7%	44.1%
South Coast	9.4%	13.2%
Statewide	13.3%	21.9%

SOURCE: Modified from Gleason et al. 2013.

other coastal marine ecosystems, to generate the services we have come to rely upon and expect. The great challenge is to innovate new approaches to understanding and managing the social and ecological relationships that underpin the sustainability and resilience of California's remarkable kelp forest ecosystems and the coastal communities that benefit so much from them.

Summary

Kelp forests are among the most productive and species-rich ecosystems in temperate latitudes. Much like terrestrial forests, kelp forests are often layered with tall, canopy-forming kelps extending from the seafloor to the water's surface (as much as 40 meters) and a variety of shorter algal species that constitute a layered understory. Their complex physical structure creates habitat, food, and refuge for a diverse array of organisms, including a number of commercially and recreationally important fish and invertebrate species. Like terrestrial forests, kelp forests modify the physical environment by reducing light penetration to the seafloor and reducing wave action and current velocity.

The species of kelp, other algae, fishes, and invertebrates that constitute kelp forest communities vary latitudinally, with marked differences among southern, central, and northern California. Within each of these regions the distribution of kelp forests is patchy and determined by the availability of rocky substratum, light, water temperature, exposure to waves, and grazers. The extent and density of kelp forests varies among years, influenced by oceanographic conditions such as El Niños and La Niñas. The magnitude and duration of effects of these disturbances vary geographically and are most pronounced in southern California.

Complex kelp forest food webs are fueled by the great primary and detrital production of the kelps and other algae as well as by a continuous influx of plankton. These sources of production support a phenomenal diversity of invertebrates including herbivores, detritivores, planktivores, and carnivores. In turn, these species are consumed by a great variety of carnivorous invertebrates and fishes. In strong contrast to terrestrial forest ecosystems, the primary producers (algae) and consumers (sessile invertebrates) compete directly

for limited space on the rocky substratum. The strength of these various species interactions (competition, predation, mutualisms) varies geographically with change in the species composition of the forest community. Notably, sea urchins, important grazers of structure-forming kelps, show dramatically different patterns of abundance in southern, central, and northern California. In southern and northern California, intense grazing by large numbers of urchins can eliminate kelp from localized areas. In central California, where greater numbers of sea otters occur, these voracious predators greatly diminish urchin abundance and their impact on kelp.

The great diversity and productivity of species associated with shallow rocky reefs and kelp forests support a variety of human activities and ecosystem services. Nonconsumptive services include tourism, shoreline protection, and spiritual and cultural values that extend back to the period of indigenous Californians. Consumptive services include economically and culturally significant recreational and commercial fisheries and, historically, the harvest of kelp for a variety of uses. Because of their close proximity to shore, kelp forest ecosystems are vulnerable to a number of anthropogenic threats including diminished water quality (e.g., sedimentation, turbidity, contaminants, shore-based water intake and discharge), direct and indirect effects of fishing, invasive species, and a changing global atmosphere and climate. Climate change is manifest in kelp forests in a variety of ways, including changes in the magnitude and frequency of major storm events, sea surface temperature, and the magnitude and location of coastal upwelling—all of which determine nutrient availability and the productivity of the forests. Additional climate-related impacts also associated with coastal upwelling include hypoxia and ocean acidification.

While the climate-related threats to kelp forests are relatively intractable to local management, California is taking bold steps to address threats posed by fisheries and water quality. Examples include a recently established statewide network of marine protected areas and more stringent water-quality regulations. It is hoped that these management actions will protect the structural and functional integrity of kelp forest ecosystems, enhancing their resistance and resilience to the multitude of potential perturbations associated with a changing global climate.

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Glossary

- ALLOCTHONOUS** Input of material to a system or place that originated elsewhere. For example, the influx of plankton to a forest or reef, the influx of drift kelp to a submarine canyon or sandy beach.
- AUTOGENIC ECOSYSTEM ENGINEER** An organism that modifies the environment by its presence and growth. For example, the presence of kelp creates habitat for other organisms, attenuates light, and alters water flow on a reef.
- BIOGENIC HABITAT** Physical habitat structure created by living organisms such as algae, corals, sponges, and the shells of sessile invertebrates (e.g., large barnacles, scallops).
- BLADE** A flat or leaflike multicellular, photosynthetic structure attached to the stipe of an alga.
- COASTAL UPWELLING** The coupled atmospheric and oceanographic process by which coastal winds cause surface waters to move offshore and are replaced by deeper, cooler, nutrient-rich waters from offshore.
- CORALLINE ALGAE** Red algae that are hardened by calcareous (containing calcium carbonate) deposits. They can be articulated (branched) or crustose (thin crusts attached to hard surfaces).
- ECOSYSTEM SERVICES** The benefits obtained by people from ecosystems, such as provisioning resources for consumption (e.g., fish), regulating systems (e.g., control of climate), supporting systems (e.g., nutrient cycling), and cultural benefits (e.g., recreation).
- EPIBIONT** An organism that lives on the surface of another organism and is generally harmless to the host.
- EPIPHYTES** A plant that grows on another plant and is not parasitic.
- FROND** The photosynthetic structure of an alga comprised of a stipe and one or more blades.
- GAMETOPHYTE** The multicellular, independently-living stage in the life cycle of an alga with alternating generations that produces gametes (haploid eggs or sperm). For kelps, this stage is often microscopic.

HOLDFAST The structure that anchors an alga to rock, sand, or other substratum. It can be rootlike or disc-shaped in appearance.

KELP Marine algae generally of the order Laminariales, although sometimes considered to include another order of large brown algae, the Fucales).

MESOCOSM An experimental setup that mimics a portion of an ecosystem to allow testing of mechanistic hypotheses.

PHYCOCOLLOID Algal colloids (chemically modified sugar molecules) in the cell walls of many seaweeds. The three major phycocolloids are alginates, agars, and carrageenans.

PNEUMATOCYSTS Gas-filled organs on algae that provide the alga with buoyancy to enable it to extend vertically through the water column.

SESSILE An organism that is fixed in one place (nonmobile), such as a barnacle.

SPOROPHYLL The specialized reproductive blades on the sporophyte stage of an alga where spores are produced.

SPOROPHYTE The multicellular, independently-living stage in the life cycle of an alga that is diploid and produces haploid spores. For kelps, this is the macroscopic that creates forests.

STIPE A thickened, stemlike structure bearing other structures such as blades. The stipe of subcanopy species is short, but stipes of surface canopy-forming species are very long.

URCHIN BARRENS An area largely devoid of fleshy red and brown algae caused by extensive grazing by sea urchins. Such areas are characterized by high cover of coralline algae.

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