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Kelp Forests
Dynamic Patterns, Processes, and Feedbacks

Robert S. Steneck and Craig R. Johnson

Kelp forests dominate shallow rocky coasts in most cold-water marine environments worldwide. Foundation species (*sensu* Dayton 1972) form the canopy of kelp forests, which is comprised of tall or medium-sized brown algae that create the largest three-dimensional biogenic habitat found in benthic marine systems. Kelp forests provide habitat for other organisms, including marine mammals, fishes, and invertebrates such as crabs, sea urchins, lobsters, and molluscs, as well as other algae, which makes them one of the most diverse, productive ecosystems in the world (Mann 1973, 2000; Dayton 1985a,b). The high productivity and biomass of kelp forests concentrate food, buffer coastlines against waves, and regulate recruitment of other coastal species. Kelp forests may have also provided ecosystem services more than 10,000 years ago for the first people to migrate to the Americas via the "kelp highway," a maritime route from Asia (Erlandson et al. 2007).

This chapter reviews key aspects of kelp forest ecology as they relate to ecosystem structure and functioning. Kelp forests exhibit unique dynamic behavior that has attracted theoretical ecologists interested in alternative stable states (e.g., Scheffer 2010). In just a few years, overgrazing by sea urchins can deforest mature kelp forests, shifting them to an alternative community state called "barrens" (Steneck et al. 2013). However, the duration of each community state depends on biogeography, community functional composition, and ecological feedbacks. The alternative barren state may persist for centuries or may rapidly switch back to a kelp-forested state in less than a decade (Steneck et al. 2002, 2008). Worldwide, kelp forests are the only ecosystems that exhibit such rapid shifts between community states and are therefore excellent systems for studying the ecological effects of large-scale changes in biogenic habitats and the feedback mechanisms that drive and maintain each state. Other sources of deforestation, which have different feedback mechanisms, give way to diminutive algal turfs that accumulate sediment and inhibit kelp recruitment (Connell et al. 2008; Moy and Christie 2012).

The dynamics between kelps and understory species can differ profoundly over space, time, and community composition (Dayton et al. 1984; Blamey et al. 2010; Blamey and Branch 2012; Strain and Johnson 2012, 2013). This chapter will explore biogeographic patterns, the processes believed to *drive* deforestation, and the ecological consequences of deforestation for organisms that are dependent on kelp beds. Beyond kelp forests, the concepts covered in this chapter, such as stability, resilience, and alternative stable states in natural communities, relate to human impacts and management, which are more thoroughly discussed in the last section of this book. To set the stage, we illustrate key convergences and divergences in kelp forest structure and function by describing the evolutionary roots of kelp forest biogeography phyletically and functionally.

The Evolution and Global Distribution of a Major Marine Biome

Kelp forests constitute a biome defined by dense stands of tall canopy-forming brown algae. They typically grow on shallow rocky reefs to depths of about 30–40 m in temperate cold-water regions. The ecological and economic importance of kelp forests is comparable to that of coral reefs in tropical waters. These communities comprise dense and productive assemblages of marine macroalgae (seaweeds), characterized by a closed or semi-closed canopy of large brown algae (phylum Ochrophyta, class Phaeophyceae), subcanopies and understory seaweeds, and associated animals. True kelps are brown algae from the order Laminariales, but here we use "k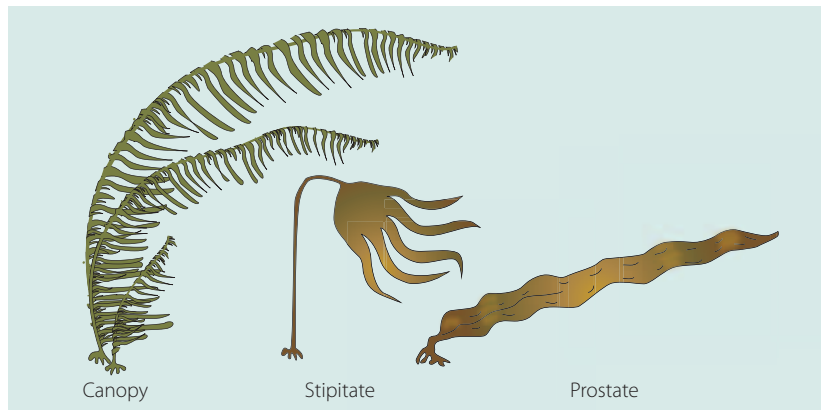elp forest" to describe any seaweed assemblage (and associated animals) that is dominated by a closed or semi-closed canopy of large brown seaweeds in temperate or cold waters. We include fucoid genera (order Fucales) such as *Durvillaea* and *Phyllospora*, as well as *Desmarestia* (order Desmarestiales), which form dense closed canopies convergent with the habitat architecture of true kelps in the shallow subtidal zone in the Southern Hemisphere (**Figure 14.1**). Nearly all canopy-forming algae are brown algae, potentially because they are the only phylum that evolved the capacity to translocate photosynthates via specialized cells called "trumpet hyphae." Collectively, these large brown seaweeds create a group of foundation species or "ecosystem engineers" (Jones et al.1994; Steneck et al. 2002) that modify the environment (e.g., Velmirov and Griffith 1979; Dayton et al. 1984; Dayton 1985a; Johnson and Mann 1988; Kennelly 1989; Melville and Connell 2001; Wernberg et al. 2005) and create habitat for other species (Christie et al. 2009). Due to their size, large brown seaweeds also effectively transport detrital macroalgal material, facilitating allochthonous trophic connectivity (Branch and Griffith 1988; Harrold et al. 1998; Krumhansl and Scheibling 2012).

Diversity, biogeography, and evolution

The taxonomic composition and evolutionary roots of kelp forest assemblages vary substantially. Laminarialian species diversity is much higher in the Northern than in the Southern Hemisphere (**Table 14.1**; Estes and Steinberg 1988), suggesting that true kelps evolved in the Northern Hemisphere (Estes and Steinberg 1988) 15–35 million years ago (Ma; Saunders and Druehl 1992), after the global cooling of the oceans at the end of the Eocene (Pearson and Palmer 2000). In contrast, kelp forests in the Southern Hemisphere often include only a single or at most two to four laminarialian species, while a much richer flora of fucoids (order Fucales) contributes to their canopies and subcanopies (see Figure 14.2; Table 14.1). In the Northern Hemisphere, fucoid species typically form dense canopies only in the intertidal zone (species of *Fucus, Pelvetia*, and *Ascophyllum*). The genus *Laminaria* is the most species-rich of the laminarialian genera, with 26 species recognized currently (Guiry and Guiry 2012). *Laminaria* species are important on all temperate rocky coastlines in the Northern Hemisphere, while

(A) Divergent morphology

Canopy   Stipitate   Prostate

(B) Convergent morphology

Laminaria digitata   *Laminaria hyperborea*

0.5 m   0.5 m

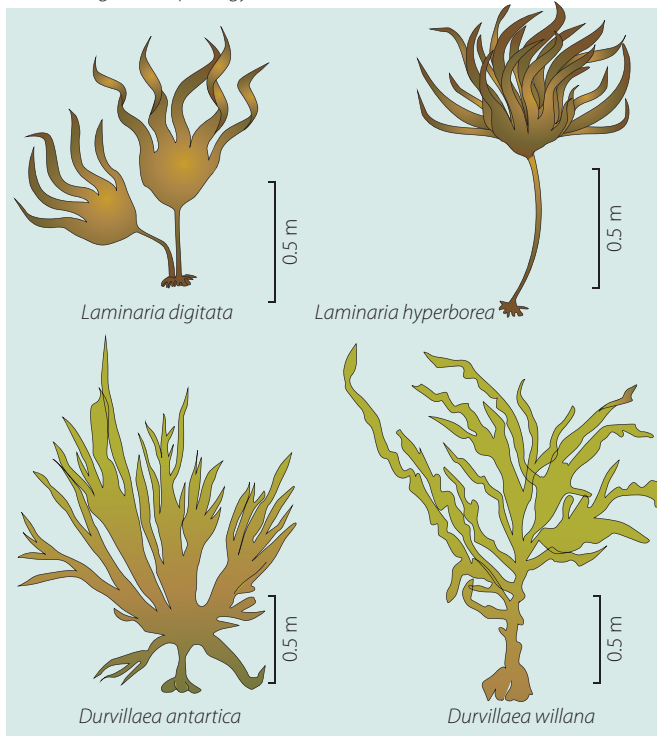*Durvillaea antartica*   *Durvillaea willana*

0.5 m   0.5 m

Figure 14.1   Kelp forest growth forms and evidence for divergent and convergent evolution. (A) Laminarian kelps can vary remarkably in their morphology. Canopy kelps extend 5 to 45 m above the substrate, stipitate kelps usually extends less than 2 m above the substrate, and prostrate kelps often drape the seafloor. (B) Unrelated laminarian and fucalean kelps can be remarkably similar in canopy height and thallus morphology. (Scale applies to all four illustrated kelps.)

TABLE 14.1   Diversity of dominant kelp forest taxa

	LAMINARIALES		DESMARESTIALES		FUCALES	
	GENERA	SPECIES	GENERA	SPECIES	GENERA	SPECIES
Northern Hemisphere						
Arctic	4	13	1	2	2	4
Western North Pacific	16	50	1	6	7	163
Eastern North Pacific	20	44	1	11	6	17
Western North Atlantic	5	13	2	3	3	10
Eastern North Atlantic	6	24	2	7	9	30
Southern Hemisphere						
South Africa	3	4	1	1	11	17
Southern Australia	4	5	2	3	17	63
New Zealand	4	7	1	2	9	29

Source: Guiry and Guiry 2012, with assistance from John Bolton and Jennifer Dalen.
Note: Laminariales is more diverse in the Northern Hemisphere, whereas Fucales is more diverse in the Southern Hemisphere. Desmarestiales includes only a few genera with modest canopy heights (~1 m).

in the Southern Hemisphere there are only two species: *L. pallida,* from southern African shores and a small number of Indian Ocean islands, and *L. abyssalis,* from deep water off tropical Brazil. Some important species of kelp may have colonized the Southern Hemisphere relatively recently. For example, genetic data suggest that the iconic giant kelp (*Macrocystis*) evolved in the Northern Hemisphere and colonized the Southern Hemisphere as recently as 10,000 years ago (Coyer et al. 2001).

Modern kelp forest biogeography reflects the centers of origin, priority effects, and timing of the two predominant taxa that create kelp forests. The orders Fucales and Laminariales probably diverged in the Early Paleocene, about 65 Ma (Fraser et al. 2010). These taxa probably remained separated in Earth's small polar regions through the relatively warm Miocene (23 Ma). Since then, however, both Fucales and Laminariales have radiated (Fraser et al. 2010; Canovas et al. 2011; Martin and Zuccarello 2012; Estes et al. 2013), resulting in distinct hemispheric phylogenies and diversities (see Table 14.1). Southern Australia's history of continental drift led to a coast with cool marine waters throughout the Cenozoic (>65 Ma), facilitating the evolution of the world's greatest macroalgal diversity (Womersley 1981; Bolton 1994, 1996), including fucoid-dominated kelp forests of *Durvillaea, Phyllospora, Hormosira, Cystophora, Seiococcus, Carpoglossum,* and *Xiphophora.* Around the same time (12–27 Ma), Northern Hemisphere laminarian genera diversified with the evolution of *Agarum, Laminaria, Alaria, Undaria, Saccharina, Nereocystis,* and *Pelagophycus* (Estes et al. 2013). The geologic background that resulted in high algal diversity and endemism in Australia carried through all dominant algal phyla (i.e. red, green, and brown algae; Norton et al. 1996). Thus species diversity among kelps and within kelp forests probably reflects evo-

lutionary rather than specific ecological histories. Some kelp forest consumers, such as carnivorous mammals and fishes, evolved more recently and so may not have followed this trend.

Global distribution of kelp forests: Setting the stage

Globally, kelp forests (but not kelp distributions) are largely confined to a mid-latitude band between the ice- and light-limiting poles (Dunton and Dayton 1995) and warm, nutrient-poor waters in the tropics (**Figure 14.2**; Bolton and Anderson 1987; Gerard 1997). This band corresponds to the global algal biomass peak found at about 45°–60° N latitude (Konar et al. 2010). Except in areas of extensive upwelling (west coasts of North and South America) or areas of local upwelling in deeper water (Graham et al. 2007), low-latitude kelps (below 40° latitude) are often diminutive, have high surface-area-to-volume ratios, and share community dominance with or competitively lose to fucoids such as *Sargassum* and other large brown algae, which become more diverse and abundant toward the tropics (Hatcher et al. 1987; Wernberg et al. 2011). Seasonality of temperature, nutrients, and light define where kelp forests and their constituent biota develop. This observation is consistent with the idea that thermogeography, or the geographic pattern of temperatures over time, corresponds with algal biogeography (Adey and Steneck 2001; Adey and Hayek 2011). As a result, high-biomass kelp forests form mid-latitude belts in shallow water on hard substrates (Adey and Hayek 2011; Krause-Jensen et al. 2012).

Exceptions to this pattern relate to cold-water ocean currents on western continental coasts (see Figure 14.2). For example, the southernmost kelp forests in the Northern Hemisphere are found on the west coast of North America extending to the Gulf of California, where they experience
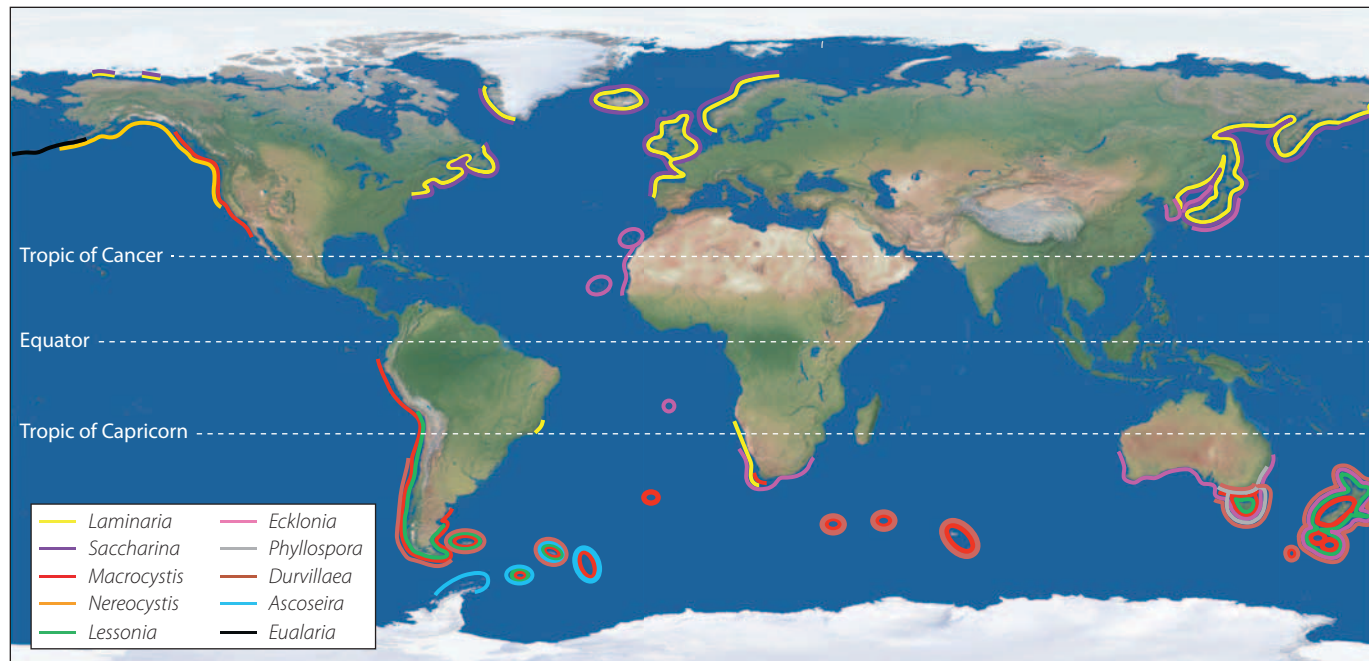
Figure 14.2 Kelp forests of the world and their dominant genera. Mid-latitude bands in both hemispheres are where kelp deforestation by sea urchins is common. Important "true kelp" (i.e., order Laminariales) genera include *Laminaria*, *Saccharina*, *Macrocystis*, *Eualaria*, *Nereocystis*, *Lessonia*, and *Ecklonia*. *Durvillaea* and *Phyllospora* (order Fucales) and *Ascoseira* (order Ascoseirales) are examples of evolutionarily distinct but convergent canopy-forming kelps. Species ranges often exceed regions where abundance warrants "kelp forest" designation. Expert sources: Neville Barrett, Russ Babcock, and Thomas Wernberg (Australia), John Bolton (South Africa), Jennifer Dalen (New Zealand), Hartvig Christie (Norway), Ken Dunton (Arctic Alaska), Jim Estes (Aleutians and Alaska), Maria Ramirez and Alejandro Buschmann (South America), and Margaret Clayton (Antarctica, subantarctic islands). References: Steneck et al. 2002 (global); Graham et al. 2007 (*Macrocystis*—global); Fraser et al. 2010 (*Durvillaea*—global); Fujita 2011 (Japan); Martin and Zuccarello 2012 (*Lessonia*—global); Ramirez and Santelices 1991 (Pacific South America); Museum of New Zealand te Papa Tongarewa website (collections.tepapa.govt. nz); Guiry and Guiry 2012 (global).

the south-flowing cold California Current. On the west coasts of Africa and South America, canopy-forming laminarialian species extend much farther north than they do on the continents' east coasts (Graham et al. 2007), largely due to north-flowing cold currents and associated upwelling of nutrient-rich water (see Figure 14.2). Conversely, the north-flowing eastern current of the Indian Ocean gyre is offshore on the west coast of Australia, so the south-flowing, warm, nutrient-poor Leeuwin Current dominates the coast. The resulting elevated temperature has a marked effect on the distribution of seaweeds on this coast (Smale et al. 2011; Wernberg et al. 2011).

Kelp forests are also rare or limited above the Arctic Circle. Their absence may be due to low temperatures, limited light and nutrients, or ice (Dunton 1985; Krause-Jensen et al. 2012). Nevertheless, laminarians are found as high as 75°–80° N (*Laminaria solidungula* in particular, but also *Saccharina latissima*: Wienke et al. 2006). Their northern boundary coincides with the limit of dense pack ice and the 1°C August isotherm (Müller et al. 2009; Chapman and Linley 1980). Strong seasonality, characteristic of the Arctic, requires significant adaptations. Successful kelps in the Arctic have high carbon or nitrogen storage capacities because light is available only in the summer, but nutrients are available primarily in the winter. On the Arctic North Slope of Alaska, *L. solidungula* stores carbon in the summer and grows during the winter (Dunton 1985). In contrast, *S. latissima* stores nitrogen during the winter and grows in the spring and early summer (Dunton 1985).

True kelps do not extend into the Antarctic Circle, despite a long geologic history of cold water (Wienke et al. 2006) and abundant seasonally ice-free substrate. However, true kelps are not far away. *Macrocystis* is abundant at Cape Horn (ca. 56° S) and in South Georgia (ca. 55° S), but absent from the Antarctic Peninsula (starting at 63° S) and in South Orkney (60° S; see Figure 14.2). While there are no true kelps in Antarctica (Moe and Silva 1977; Wienke and Clayton 2002), there are "kelp forests" created by other orders of large canopy-forming brown algae such the Desmarestiales and the endemic order Ascoseirales (Wiencke and Clayton 2002). Species in these orders look like true kelps, having evolved convergently to assume laminarian shapes and functions created by their closed canopies (Wiencke and Clayton 2002; Wiencke et al. 2006). If surface waters warm by just a few degrees, true kelps

may establish on the Antarctic Peninsula, but kelps are already *functionally* well represented.

The Southern Hemisphere fucoid genus *Durvillaea* and its Northern Hemisphere counterpart *Laminaria* are morphologically and biomechanically similar (i.e., both can grow to 15 m in length; see Figure 14.1; Harder et al. 2006). The nutrient physiology of the endemic ascoseiralian kelp *Ascoseira mirabilis* of the Antarctic Peninsula (Gomez et al. 1995) has converged with that of the Arctic kelp *Saccharina latissima* (Dunton 1985): both have evolved photosynthetic adaptations to protracted darkness. Convergences in morphology, distribution, abundance, and physiology of kelps across different orders suggest a limited number of solutions to particular oceanographic conditions. These hemispheric differences among laminarian, fucalean, and ascoseiralian kelps create excellent opportunities to explore convergent ecological patterns and processes shaping kelp forests.

Assembly and Disassembly of Kelp Forests: Global and Local Ecosystem Drivers

Kelp forests persist in a balance between ecological processes driving successional change and those maintaining stability (Dayton et al. 1984). They flourish as a result of recruitment and net productivity and decline due to biomass loss from physical and biological disturbances. Ecological interactions control kelp forest development and deforestation. The successional processes involved include spore dispersal, germination, gametogenesis, growth, and intra- and interspecific competition. Deforestation results from disturbances such as oceanographic anomalies, changes in water quality (nutrient and sediment levels), and natural and human-caused variations in predator abundance and community composition. In this section we consider how these processes interact to influence where kelps live, forests develop, and deforestation occurs.

Kelp growth and forestation

The three interacting processes controlling the development of kelp forests are recruitment, growth, and competition (North 1994). Locally, kelp forests are established and maintained by propagule recruitment and settlement. Recruitment is often seasonal, but the timing of peaks in reproductive output differs among species. Established propagules are thinned by intra- and interspecific competition (Dayton et al. 1984; Reed and Foster 1984; Chapman 1986). Settlement rates and postsettlement survival are also influenced by local conditions such as light, nutrient and sediment levels, and water movement. In complex kelp forests with multiple levels (see the canopy, stipitate, and prostrate forms in Figure 14.1), such as the California kelp forest, kelp recruitment and growth are regulated by light (Dayton et al. 1984; Reed and Foster 1984; Graham et al. 1997) and nutrient availability (Dayton et al. 1999). Canopy kelps affect light and water movement in the habitats they occupy (**Figure 14.3**), and following storms that deforest or thin kelp canopies, recruitment is usually strong. However, the kelp species that become dominant depend on nutrient conditions and reproductive timing (Dayton et al. 1984; North 1994; Tegner et al. 1997).

Kelp growth is influenced by nutrient availability, temperature, and light. Kelps can be physiologically stressed at high temperatures, particularly when nutrient availability is low (Tegner et al. 1996; Gerard 1997). In some nonup-
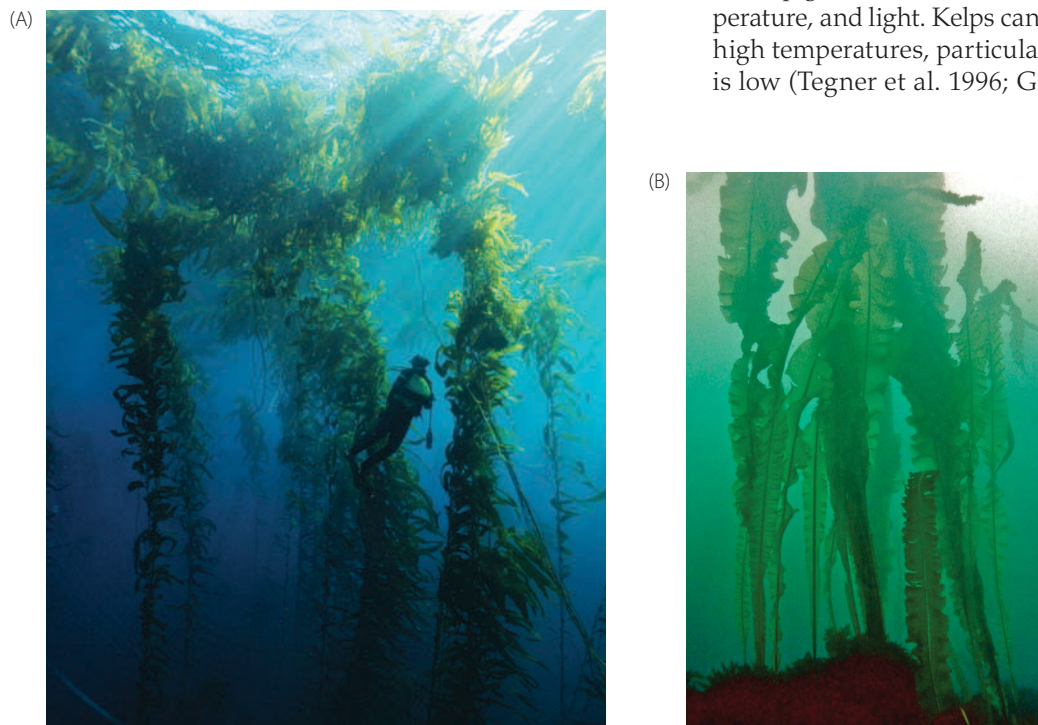
(A)

(B)

Figure 14.3 Canopy kelps. (A) *Macrocystis pyrifera*, at a study site in eastern Tasmania, 2010. (B) *Eualaria fistulosa*, Aleutian Islands, Alaska, 2008. (A courtesy of Craig Sanderson; B courtesy of Robert Steneck.)

welling regions, periods of low nutrient concentrations correspond to warm summer temperatures, when the water is stratified, and the combined effects of low nutrients and high temperatures result in higher kelp erosion than growth (Gagne et al. 1982). In kelp forests driven by nitrogen upwelling, such as those in southern California, when El Niño events disrupt that upwelling, kelps such as *Macrocystis* (Gerard 1982) can become nutrient-starved and die back (Tegner and Dayton 1991; Tegner et al. 1996). As a result, the distribution, abundance, species composition, and size of kelps decline as sea surface temperatures increase (Dayton et al. 1999). In extreme cases, deforestation can occur due to these bottom-up limitations.

Kelp deforestation: Abiotic and biotic drivers

Kelp deforestation can result from disease, herbivory, or physiological stress. At lower latitudes, periodic deforestation often results from oceanographic anomalies in temperature, salinity, or nutrients that either kill kelp directly or trigger diseases that become lethal to physiologically stressed plants. At mid-latitudes in both hemispheres, sea urchin herbivory is the most significant agent of kelp deforestation (Steneck et al. 2002). Latitudinal differences in consumer diversity and in processes shaping kelp forests have led to different dynamics among locations within the same kelp forest system. For example, sea otters are a keystone species in the Aleutian Islands due to their ability to control sea urchin populations (Estes and Palmisano 1974; Estes and Duggins 1995), but have relatively small effects in some California kelp forests (Foster 1990). Thus the geography of kelp deforestation processes is important.

Except for kelp-free patches created by climate change, deforestation due to physical factors tends to create relatively small and short-lived patches. The oldest term for algal deforestation is the Japanese word *isoyake*, which means "rock burning" (Fujita, pers. comm., 2002). The word was coined by Yendo (1902, 1903) to describe algal deforestation in central Japan, which was thought to be a result of salinity anomalies (Yendo 1903, 1914) rather than grazing (Yendo 1902). The isoyake killed all foliaceous and encrusting coralline algae before recovery occurred several years later (Yendo 1914). On Honshu Island, near the southern limit of Japanese kelp forests, anomalous incursions of the warm Tsushima Current (a warm branch of the Kuroshio Current) periodically create isoyake conditions. Such oceanographically induced kelp deforestation was originally thought to be short-lived and reversible (Yendo 1914).

As oceans warm due to climate change, warming events are expected to cause local die-offs of large canopy-forming brown algae (Valentine and Johnson 2004; Wernberg et al. 2012). Large-scale declines of kelp, potentially as a direct result of ocean warming, have already been observed on the coasts of Portugal (Isabel Pinto, pers. comm.), southern Norway (Moy and Christie 2012), and eastern Tasmania (Johnson et al. 2011). In Portugal and Norway, the kelp has been replaced by turf-forming non-kelp seaweeds. In Tasmania, in areas where extensive surface canopies of giant kelp (*Macrocystis pyrifera*) have been completely or nearly lost, giant kelp has been replaced by *Ecklonia radiata*, a small laminarialian dominant across southern Australia.

Kelp deforestation can also result from El Niño events. Strong El Niños halt coastal upwelling and cause surface waters to warm (Dayton et al. 1992). In southern California, these events cause patchy deforestation, but recovery is rapid (Tegner and Dayton 1987; Dayton et al. 1992). Such physiological stresses are probably more common toward the low-latitude range limits of kelps. Following the El Niño event of 1982–1983, the northern limits of three brown algae in northern Chile shifted south toward higher latitudes (Peters and Breeman 1993). These physiological stresses may also make kelps more susceptible to disease. Low-latitude kelps in northern New Zealand succumbed to a disease, potentially triggered by physiological stress (Cole and Babcock 1996; Cole and Syms 1999).

SEA URCHIN DEFORESTATION AND "BARREN" FORMATION At mid-latitudes, kelp development is less likely to be limited by physical processes, and deforestation is often caused by sea urchin herbivory (Leighton et al. 1966; Lawrence 1975; Himmelman 1980; Dayton 1985a,b; Duggins 1980; Estes and Duggins 1995; Mann 2000; Steneck et al. 2002, 2013; Steneck 2013). Sea urchin grazing affects kelp forests by removing the habitat and food that kelps create. Although the phyletic diversity of kelp forests is high, that of the herbivore group most capable of kelp deforestation is not.

Kelp deforestation driven by sea urchin herbivory often results in a community characterized by calcified disturbance-resistant crustose coralline algae. Crustose corallines are red encrusting algae that often dominate areas of intense grazing pressure (**Figure 14.4**; Steneck 1986). This community state is alternatively called a "barren," "coralline barren," or "sea urchin barren" (Chapman 1981). A global review of kelp forest ecosystems found that kelp forests in 18 of 19 regions worldwide, from Alaska to Argentina, were at some point transformed into coralline communities by sea urchin grazing (Steneck et al. 2002).

KELP FOREST–BARREN DYNAMICS: PATTERNS AND PROCESSES Sea urchin–kelp forest interactions often result in strong gradients in community structure. Sea urchin grazing creates coralline community patches devoid of fleshy macroalgae, while adjacent areas are dominated by erect algae and are often sea urchin free (Dayton et al. 1984; Harrold and Reed 1985; Johnson and Mann 1988; Konar and Estes 2003; Johnson et al. 2005, 2011).

There are two types of boundaries between kelp forests and coralline communities. A fairly stable boundary occurs when the shallow end of the kelp forest lies within the turbulent wave base. A more dynamic boundary is found

Figure 14.4 Phase shift between a sea urchin barren-coralline community (left) and a kelp forest (right) at Pemaquid Point, Maine. The upper photos are master shots showing the landscape; the lower shots show specific differences. (A) A ledge dominated by sea urchins and crustose coralline algae,1985. This ledge existed in this condition until 1995. (B) Close-up of a grazing chiton (ca. 2 cm length), 1975. The white circle surrounds a newly settled sea urchin living in a refuge between the branches of a coralline alga. (C) *Saccharina* sp., at the same location following the phase shift, 1995. (D) Filamentous and corticated macroalgal understory with *Chondrus crispus* in upper right corner, 2011. (Courtesy of Robert Steneck.)

Barrens
1975–1990

Kelp forest
1995–2011
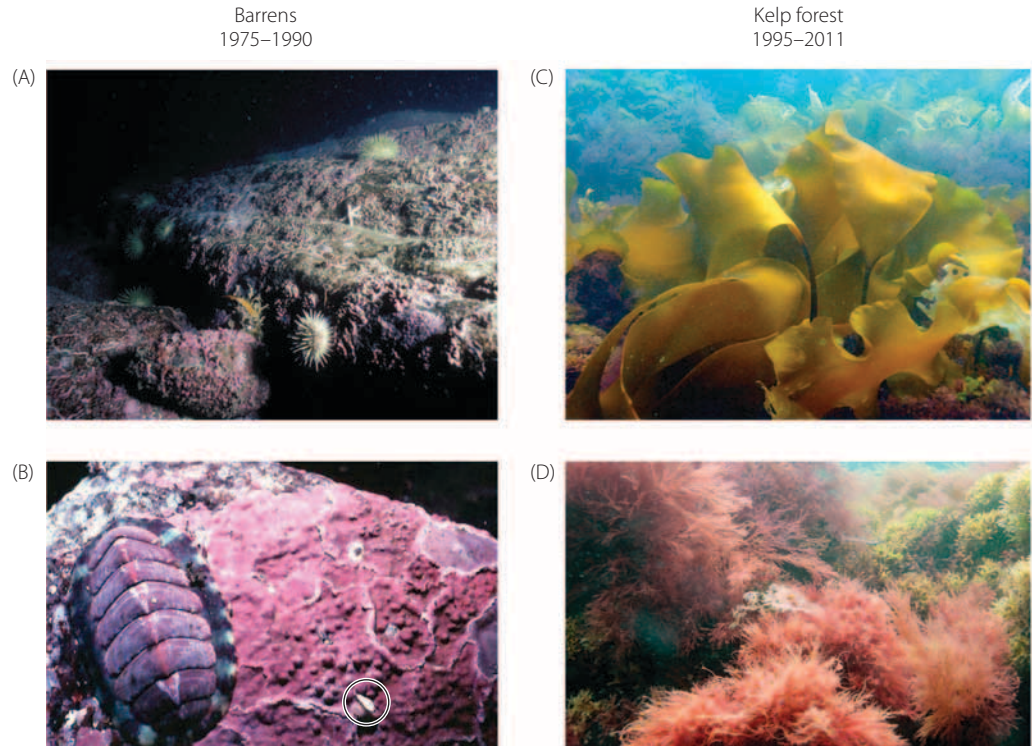
at the kelp forest extinction depth of 20–40 m (depending on water clarity; Mann 1977; Chapman 1981; Vadas and Steneck 1988; Witman and Dayton 2001; Konar and Estes 2003; Adey and Hayek 2011).

Shallow sea urchin–free turbulent zones are found globally. In Maine, nearly zero sea urchins were found at depths of less than 3 m at turbulent sites between 1975 and 1994, despite high population densities at greater depths (Steneck and Carlton 2001). Similar zonation patterns were found in New Zealand and Tasmania (Australia), where thriving kelp beds persist on wave impacted coasts at depths of 5–10 m in a zone above the upper boundary of extensive sea urchin barrens at greater depth (Choat and Schiel 1982; Johnson et al. 2005, 2011).

Sea urchins usually reach peak densities between depths of 5 and 15 m, although they may reach greater densities in deepwater areas that experience a regular food supply of macroalgae detritus (Britton-Simmons et al. 2012). On sea urchin barrens with relatively stable boundaries, sea urchins are often food limited. They are unable to migrate into food-rich kelp forests because of the abrasive sweeping motion of algal fronds (Konar and Estes 2003).

Kelp interactions involving abrasion, or "whiplash" (*sensu* Dayton 1975), exclude most understory invertebrates (Connell 2003). Water movement benefits kelp productivity by mixing the diffusion boundary layer, facilitating gas exchange and nutrient uptake (e.g., Wheeler 1988), and by reducing sea urchin grazing via whiplash (Ebert 1967; Konar and Estes 2003). Since whiplash is a result of water movement, the kelp fringe typically extends into deeper water on wave-exposed shores than on wave-protected

shores (Himmelman 1985; Adey and Hayak 2011). Although sea urchins can graze on kelp during calm periods, they are often displaced to unfavorable habitats by waves. As a result, they are often limited to zones below the turbulent wave base (Witman 1987; Siddon and Witman 2003; Lauzon-Guay and Scheibling 2007), where they are often found at high densities eating drift algae (Steneck and Carlton 2001). The ubiquity of the kelp fringe suggests that sea urchins avoid areas where sweeping fronds or dislodgement can break their spines because the metabolic cost of repairing them is high (Ebert 1967).

In turbulent environments, the capacity of sea urchin tube feet to attach and hold on to hard substrates is critical. Siddon and Witman (2003) measured the forces necessary to dislodge sea urchins and constrain their movement, thus limiting their shallow depth distribution. Sea urchin grazing shifts benthic community structure to grazing-resistant coralline algae (reviewed in Lawrence 1975; Dayton et al. 1984; Steneck and Dethier 1994), which improves the holding properties of the substrate. Feedbacks between water movement, substrate properties, and echinoid tube feet may be critical to maintaining discrete kelp-free patches.

In contrast to the stable shallow-water kelp zone, the kelp zone below the wave zone is more dynamic and experiences expansive phase shifts between kelp forests and coralline communities (see Figure 14.4; Steneck et al. 2002). Over the past few decades, several studies have shown transformations of kelp forests into coralline communities (Estes et al. 1998; Hagen 1983). In Maine, the loss of predatory fishes allowed mobile benthic invertebrates
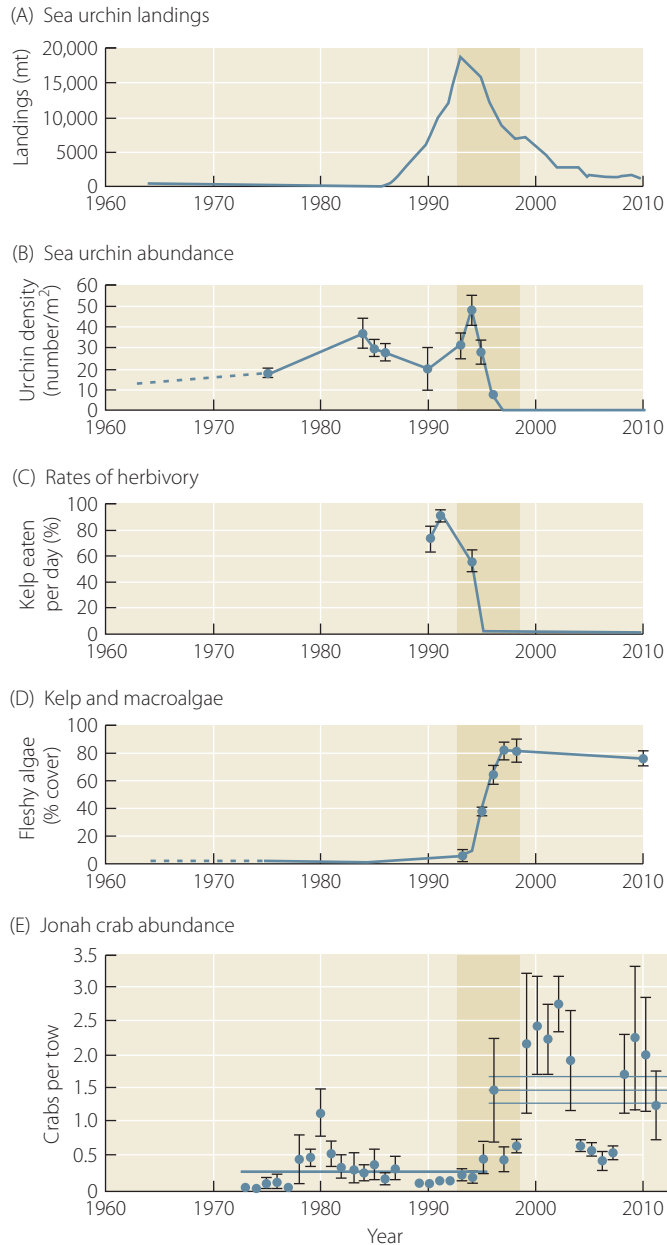
(A) Sea urchin landings

(B) Sea urchin abundance

(C) Rates of herbivory

(D) Kelp and macroalgae

(E) Jonah crab abundance

Figure 14.5 Fifty-year trends in sea urchin landings, abundance, rates of herbivory, fleshy algal cover, and crab abundance in mid-coast Maine. The dark vertical bar indicates the phase shift to kelp forest coinciding with maximum harvest of sea urchins (±SE). Dashed lines in B and D were derived from published studies conducted in the same region in the 1960s (Adey 1964, 1965). Horizontal lines in E illustrate the average (±SE) before and after the 1995 algal phase shift. (After Steneck et al. 2013.)

of sea urchins to coexist with kelp (Harrold and Reed 1985; Ebeling et al.1985). In Alaska, unusual influxes of salps sufficiently feed the omnivorous sea urchins, halting kelp herbivory (Duggins 1981). When sea urchins become food limited, however, they can form aggregations, or "fronts" (Dean et al. 1984; Lauzon-Guay and Scheibling 2007), that overgraze kelp forests, creating barrens (Lawrence 1975). These fronts remove all erect foliose algae in their path.

The iterative flipping between kelp forests and barrens along Nova Scotia's eastern shore is a striking example of rapid dynamic changes following the loss of coastal predators such as Atlantic cod (**Figure 14.6**). High-density populations of sea urchins have been periodically infected by a warm temperature–dependent pathogen that kills most sea urchins at depths of less than 30 m (Scheibling and Hennigar 1997). Each time, kelp has increased, but urchins have recovered quickly (Scheibling 1986) because the pathogen cannot survive over winter, and surviving deepwater urchins rapidly recolonize shallow water areas and restore the barrens. This cycle has occurred three times since 1965 (reviewed in Steneck et al. 2002). Similar pathogen-induced sea urchin mortality has been seen in Californian kelp forests (Lafferty 2004).

GLOBAL FISHING OF SEA URCHIN PREDATORS AND EX-PANDING SEA URCHIN BARRENS   The stability of kelp forests prior to human impacts is unknown, but it has been suggested that kelp once dominated "pristine" cold-water rocky shores (Jackson et al. 2001). Carbon and nitrogen isotope studies of fish bones collected from Indian middens also indicate that macroalgae were the dominant primary producers in Maine's coastal zones 4500–500 years ago (Bourque et al. 2008). Historical records of kelp deforestation reveal iterative but asynchronous trends in increasing sea urchin abundances.

Historically, sea urchins may have been rare in the western North Atlantic. In Maine, both the earliest written accounts (Steneck et al. 2002) and the first scientific study (Johnson and Skutch 1928) describe the shallow subtidal coastal zones as kelp-dominated. By the 1960s, however, the coast had become a mosaic of kelp forests with widely spaced barren patches (Lamb and Zimmerman 1964; Adey 1965). Over the next two decades, sea urchin abundance and coralline communities expanded throughout the Gulf of Maine (Sebens 1985; Witman 1985; Steneck et al. 2013). In the 1950s, Nova Scotia was also described as kelp-

such as crabs and sea urchins to increase in abundance (Steneck et al.2013). However, the recent sea urchin fishery acted as a large-scale herbivore removal experiment (**Figure 14.5A,B**; Steneck et al. 2013). Herbivory rates declined, and kelp and other algae increased (**Figure 14.5C,D**). Over a few years, these changes occurred along some 500 km of Maine coast (Steneck et al. 2013). North and central coasts of Norway also reverted back to kelp forests following declines in sea urchins (Christie et al. 1995). These systems phase-shifted rapidly from coralline communities to kelp forests with herbivore removal and remained in the alternative state for decades.

Food availability can both trigger and prevent kelp deforestation. In some highly productive Californian kelp beds, steady inputs of algal detritus allow high densities

Figure 14.6 Temporal trends in kelp forest and sea urchin-barrens in Nova Scotia. Arrows indicate the timing and magnitude of major community-altering forcing functions. Widths of arrowheads indicate the magnitude of the forcing function's impact. Strong fluctuations in Nova Scotia's sea urchin populations result from periodic disease-induced mass mortalities, and kelp abundance fluctuates inversely with that of sea urchins. (After Steneck et al. 2002; Scheibling et al. 1999).
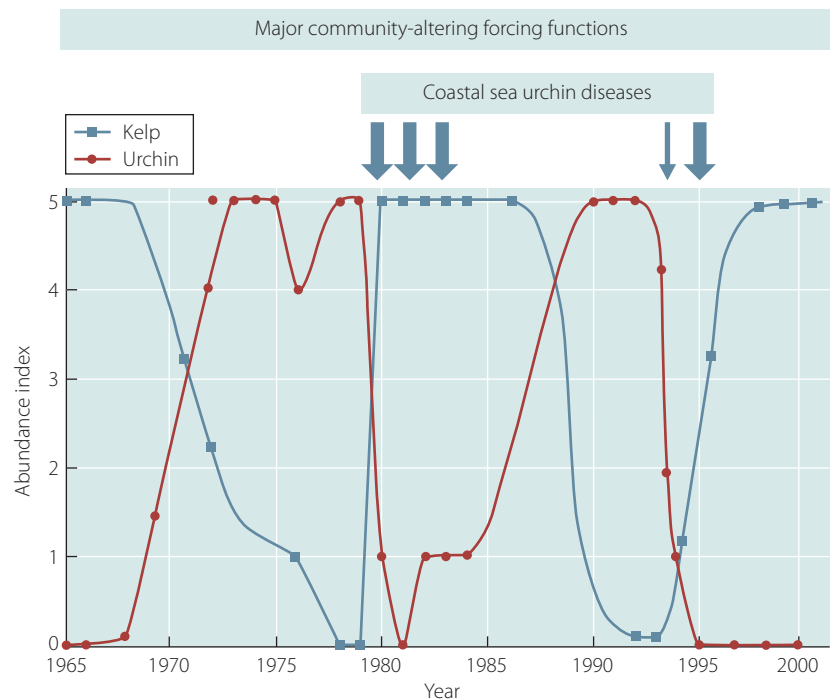

dominated (MacFarlane 1952). A decade later, the first phase shift to coralline barren patches occurred. These patches became widespread barrens (Breen and Mann 1976), which were thought to be stable (Mann 1977) until high sea urchin population densities led to outbreaks of disease (see Figure 14.6; Miller and Colodey 1983). By the 1980s, sea urchin barrens were widespread from Massachusetts to Labrador (Pringle et al. 1980; Steneck et al. 2002, 2013). Prior to this time, there is no evidence of widespread sea urchin barrens.

These patterns hold true in the eastern North Atlantic as well. During the 1970s, sea urchin densities increased along the Norwegian coast in sheltered to moderately wave-exposed areas, while kelp forests persisted in the outer wave-exposed areas (Sivertsen 1997). By the 1980s, extensive coralline communities were found along the coast (Hagen 1983; Sivertsen 1997, 2006). Although sea urchin densities have declined in southern Norway (Christie et al. 1995), dense populations of sea urchins remain in northern regions (Christie, pers. comm.). Meanwhile, in the South Pacific, high densities of sea urchins in New Zealand (Choat and Schiel 1982; Andrew 1993) and in New South Wales, in eastern Australia (Andrew 1993), have resulted in patches of coralline communities. By the late 1990s in New South Wales, more than 50% of rocky shores were composed of sea urchin barrens (Andrew and O'Neil 2000).

Globally, this temporal trend was a phase shift from apparently stable kelp forests with few sea urchins to patches with sea urchins at high densities, and often extensive coralline communities, that expanded over time. Why did so many disparate kelp forests shift to sea urchin-dominated coralline communities? The key change in many of these systems is thought to be the fisheries-induced decline of sea urchin predators. Thus the hypothesis that predators limit sea urchins in kelp forests warrants further attention.

Predation: Indirect effects on kelp forests

Predation is believed to exert top-down control on a large range of sea urchin species in kelp forest ecosystems (Jackson et al. 2001). This conclusion is supported by several archaeological studies of prehistoric encampments, which found that sea urchins were initially rare in midden strata, but increased after human fishing pressure reduced predator abundances (Simensted et al. 1978; Erlandson et al. 1996, 2009; Bourque et al. 2008). For example, although Japan has a long history of fishing and locally caught finfish have been depicted in archaeological artifacts dating to AD 400 (Sansom 1952), sea urchins were relatively rare until the early twentieth century (Yendo 1902). In this historically agrarian culture, fishing was modest until 1914, when shipbuilding accelerated coastal fishing pressure (Allen 2003). Although sea urchins were first recorded as food in the 800s and were fished in the 1800s, it was not until the 1930s that widespread sea urchin harvesting began. Harvesting of sea urchins began as a way to limit grazing on the kelp *Laminaria ochotensis*, a valued food. However, a directed fishery quickly developed for sea urchin roe (Andrew et al. 2002).

Predation across all life history stages can limit sea urchin distribution and abundance. While the chronologies of predator decline differ among regions, all exhibit a decline in predator diversity, abundance, or size. A global review found that 14 of 18 kelp forest ecosystems were described as predator limited (Steneck et al. 2002). Predation, however, is a complex ecological process because the habitats, species composition, body sizes, and feeding capabilities of predators can change significantly over time and space. Many studies have sought to examine the relationship between sea urchins and their predators. Here we review a few examples and discuss their theoretical and ecosystem implications.

Predation is often size-specific, such that prey vulnerability is inversely related to body size. One of the largest kelp-dwelling sea urchins, the red sea urchin (*Strongylocentrotus franciscanus*), is often found with the purple sea urchin (*Strongylocentrotus purpuratus*) in southern California. Aquarium studies determined that the spiny lobster (*Panulirus interruptus*) is an important predator of intermediate and smaller sizes of both sea urchins (Tegner and Levin 1983). The spine canopy of the large red sea urchins acts as nursery habitat for newly settled sea urchins (Tegner and Levin 1983). This relationship leads to a bimodal size distribution of sea urchins, in which large, predator-immune red sea urchins and small, newly recruited sea urchins are most abundant.

In the western North Atlantic, two interrelated patterns are consistent with the hypothesis that predators limit sea urchin populations. First is the inverse temporal correlation between predatory finfish and sea urchins. In the 1920s, kelp forests (Johnson and Skutch 1928) and large predators such as Atlantic cod were abundant in the subtidal zones of coastal Maine (Rich 1929). However, the rapid escalation of fishing pressure in the 1930s extirpated coastal groundfish, and their abundance has yet to fully recover (Steneck and Carlton 2001; Steneck et al. 2013). This happened throughout the western North Atlantic including eastern Nova Scotia. Second, predator-induced bimodal size frequency distributions have been described for the green sea urchin (*Strongylocentrotus droebachiensis*) in the western North Atlantic (Himmelman et al. 1983; Keats et al. 1986; Himmelman 1986; Scheibling 1986; Scheibling and Hamm 1991; Ojeda and Dearborn 1991). As in the case of the red and purple sea urchins of southern California, small spaces protect newly settled sea urchins (e.g., see white circle in Figure 14.4B). Once they grow out of such refuges, they become vulnerable to predators. Only when they reach large sizes do they become immune to local, relatively small, predators. This bimodal pattern holds well in areas where small predators dominate the ecosystem, but in areas where shell-crushing predatory fishes occur, they feed on even the largest sea urchins (Keats et al. 1986; Witman and Sebens 1992; Vadas and Steneck 1995). However, predation patterns can also vary across habitat and region. For example, the medium-sized sea urchin species *S. droebachiensis* is more susceptible to predation by invertebrates in sea urchin barrens than in mussel beds because crabs preferentially feed on mussels (Siddon and Witman 2004).

In New Zealand, grazing by the common endemic echinoid *E. chloroticus* suppresses large brown algae (Andrew 1988) except in the presence of the predatory rock lobster (*Jasus edwardsii*). When present, this predator reduces herbivory by preying on and restricting the sea urchin's grazing range (Barker 2007).

Circumstances in which abundances of both sea urchins and their predators are low imply that other mechanisms may limit sea urchin numbers (Connell and Irving 2008).

In some cases, shifts in sea urchin grazing pressure arise because of switches in sea urchin behavior in response to the availability of drift algae. When drift material is available to graze on, some sea urchins will remain in cryptic microhabitat (Harrold and Reed 1985), but will emerge in dense aggregations, or "fronts," to graze attached algae when drift is scarce. Thus, without any change in sea urchin density, reduced kelp productivity that decreases drift algae can result in an emergence of sea urchins and overgrazing on attached algae (Ebeling et al. 1985). In some sea urchin species, however, there is no evidence for these behavioral shifts; for these species, the extent of kelp destruction is related only to their density (Flukes et al. 2012).

Nonetheless, predators appear to have cascading effects on kelp forest structure via sea urchin grazing in many situations. This observation has contributed significantly to the general ecological theory of trophic cascades.

Trophic cascades: General ecological theory illustrated by kelp forest dynamics

In their simplest form, trophic cascades show the indirect effects of consumption at three or more trophic levels, so carnivores that limit sea urchin abundance or grazing indirectly increase plant biomass (Estes et al. 2010). This pattern was first described in rocky intertidal habitats (Paine 1980), but is perhaps best illustrated in the kelp forests of Alaska's Aleutian Islands (**Figure 14.7**). There, sea otter (*Enhydra lutris*) predation functionally eliminates the sea urchin *S. polyacanthus*, releasing kelp from herbivory (Estes and Palmisano 1974; Estes and Duggins 1995; Estes et al. 1989, 2010).

In Aleutian kelp forests, sea urchins are the only ecologically important consumer of kelp, and sea otters are the most important predator of sea urchins. Due to their low consumer diversity, these ecosystems have a relatively simplified food web with strong interactions. Thus we have been able to examine how shifts between kelp forests and urchin barrens are driven by carnivore-mediated sea urchin herbivory.

Sea otter pelts are remarkably warm, and consequently the animals were hunted quickly after their discovery by Europeans in 1741 (Estes et al. 1989). By the 1800s, fur traders had hunted sea otters to the brink of extinction, releasing sea urchins from predator control, which caused their populations to proliferate and resulted in the collapse of kelp forests (reviewed in Steneck et al. 2002). Widespread sea urchin barrens persisted from 1910 to the 1970s, when otter populations returned to functional abundance with human intervention. From the 1970s to the 1990s, sea otters were abundant, sea urchins were rare, and kelp forests flourished (Estes et al. 1998). In the 1990s, however, sea otter populations crashed, possibly because they had fallen under predator control by killer whales (Estes et al. 1998). A parallel case exists in the North Atlantic, where predatory fish function as sea otters do in the North Pacific (Estes et al. 2013; Steneck et al. 2013).
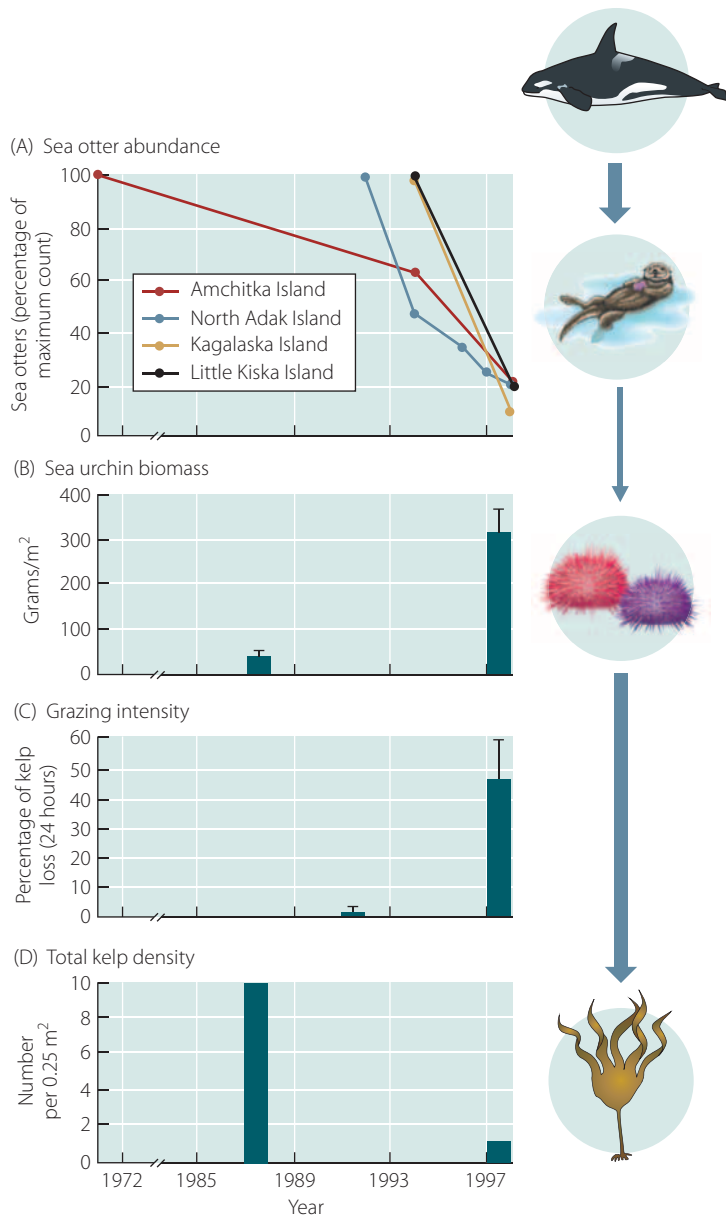
(A) Sea otter abundance

Legend:
- Amchitka Island
- North Adak Island
- Kagalaska Island
- Little Kiska Island

(B) Sea urchin biomass

(C) Grazing intensity

(D) Total kelp density

Figure 14.7   Chronology of sea otter predators and sea urchin prey in the Aleutian Islands. Sea otters control sea urchin abundance, which in turn controls kelp abundance in the region (relative influence of trophic control is indicated by differing weights of vertical arrows). Recent declines in sea otters are thought to result from elevated predation by killer whales. (After Estes et al. 1998.)

Farther south along the west coast of North America, kelp forest ecosystems have higher species diversity and rarely experience shifts to barrens (**Figure 14.8**). Diversity peaks in southern California, where kelp forests have seven important genera of kelp, compared with one in the Aleutians. Southern California also has three important sea urchin species (*L. pictus, S. purpuratus,* and *S. franciscanus*), three abalone species (genus *Haliotis*), three other species of herbivorous gastropods (genus *Tegula*), and several species of herbivorous fishes. All of these herbivores are controlled by a variety of predators, including sea otters, several fish species, including sheephead (*Semicossyphus pulcher*; Cowen 1983), spiny lobsters, and octopuses. Although sea otter extirpation also occurred along the coast of California, high functional diversity among consumers probably diluted species interaction strengths, making the resulting trophic cascades less conspicuous. Subsequent experiments demonstrated that high predator diversity reduces the abundance and function of a variety of herbivores, resulting in a cascading increase in kelp biomass (Byrnes et al. 2006).

Alternative Stable States: Ecosystem Flips, Locks, and Feedbacks

Kelp forests are dynamic and are capable of oscillating rapidly between canopies with many associated organisms to featureless barrens (see Figures 14.5 and 14.6). However, unlike Nova Scotia's kelp forests, which oscillate between states depending on the incidence of sea urchin disease (Scheibling and Lauzon-Guay 2010), many kelp forests can persist in one state or the other for decades or centuries. Long durations in a single state occur because kelp forest systems can exhibit
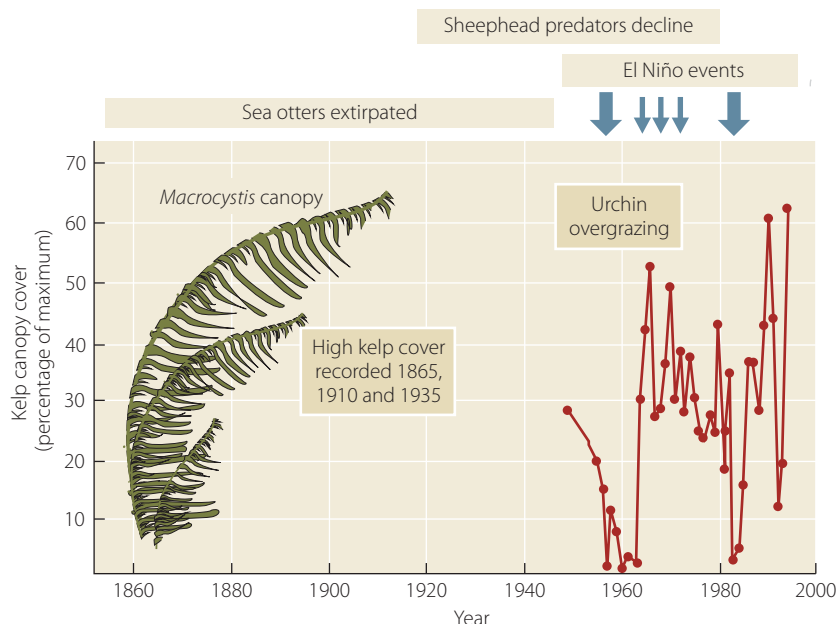

Figure 14.8   Temporal trends in the kelp forests of Point Loma, California. Width of arrowheads reflects the magnitude of community-altering forcing functions due to El Niño events. Kelp forest declines result from El Niño events and short-lived outbreaks of sea urchins. (After Steneck et al. 2002.)

BOX 14.1   Phase Shifts, Alternative Stable States, and Hysteresis

Phase shifts are large changes in community structure from one state to another in ecological time. Shifts from kelp forests to sea urchin barrens or to turf algae, and shifts back to kelp, are examples of phase shifts. (i) Trajectories of phase shifts. The community state might be kelp biomass, while the environmental conditions might represent abiotic (e.g., water temperature) or biotic (e.g., sea urchin biomass) conditions. When the community state is kelp biomass, State A is a kelp forest, while State B is a degraded state, such as a sea urchin barren. Phase shifts can be linear or nonlinear continuous shifts, in which systems move back and forth on similar trajectories as environmental conditions change (dashed blue lines). Alternatively, they can be discontinuous shifts (dashed red lines), in which the trajectory of the shift from State A to State B differs from the shift from State B to State A. With *continuous shifts*, systems exist in one state for a given environmental condition, while with *discontinuous shifts*, the system can have alternative states for a given environmental condition. (ii) Dynamics of a discontinuous phase shift. The blue line represents system equilibria; solid sections are stable and dashed sections are unstable. Gray arrows show how the system moves when away from equilibrium. If a system in State A (a kelp forest) is forced to the tipping point, it flips to the degraded State B (red arrows

and red dashed line). If forcing is then relaxed, the system will remain in the degraded state while conditions are to the right of the recovery point, despite returning to environmental conditions that initially supported the kelp forest state. This separation of tipping and recovery points defines the hysteresis, and its magnitude is the distance between degradation and recovery trajectories (vertical dotted lines). Between these trajectories, the system can exist in either state (solid blue lines) under identical conditions.
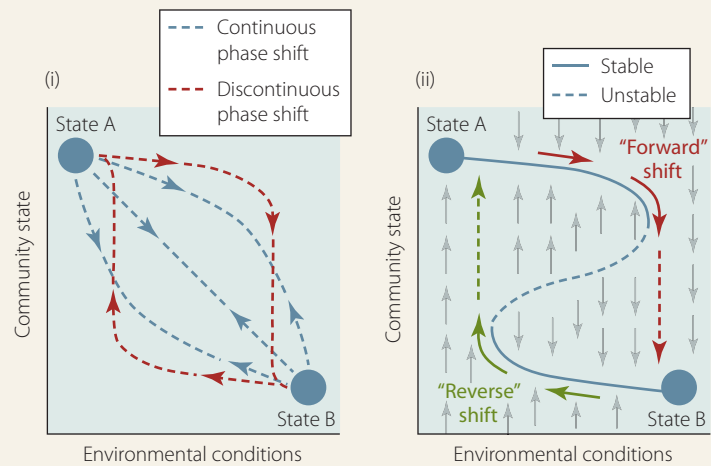

alternative stable states with ecological "hysteresis" (*sensu* Scheffer et al. 2001). Hysteresis reflects the fact that once a system "flips" from one state to another, it can be difficult for that system to return to its original state (**Box 14.1**). In a kelp forest, once a sea urchin barren has formed, if kelp is to recover, then sea urchin biomass must be reduced to a level much lower than what originally caused kelp deforestation. For example, in Nova Scotia, the "tipping point" necessary to convert kelp beds to sea urchin barrens is a sea urchin biomass of about 2 kg/m^2, while established barrens must have a sea urchin biomass of 0.2 kg/m^2 or less (the recovery point) to allow kelp regrowth (Breen and Mann 1976; Scheibling et al. 1999; Lauzon-Guay and Scheibling 2007). A remarkably similar ratio of sea urchin abundances at the tipping and recovery points occurs in Tasmania, where approximately 2/m^2 densities of the sea urchin *Centrostephanus rodgersii* are sufficient to create barrens, but within barrens, sea urchin densities need to be 0.2/m^2 or less for kelp to recover (Johnson et al. 2011; Marzloff et al. 2013). This means that it takes fewer sea urchins to maintain a barren than to create one.

How alternative stable states should be defined and what constitutes proof of their existence has elicited some controversy (Petraitis and Latham 1999; Petraitis and Dudgeon 2004). Three primary criteria are necessary for documenting alternative stable ecosystem states. First,

transitions between states must occur quickly relative to the potential longevity of each state in the same physical habitat. Second, shifts must result from a pulse (temporary) perturbation rather than a press (chronic) perturbation, and when environmental conditions return to their initial state, the system must not return to its original state. Finally, the study must be long enough that the alternative state is self-sustaining beyond the turnover time of its dominant constituents (Petraitis and Latham 1999; Petraitis and Dudgeon 2004). Although these criteria document alternative stable states, they do not explain *why* ecosystems switch between these states. The controversy among researchers in this field revolves around whether alternative stable states are the result of stochastic (largely unpredictable) or deterministic events (Bertness et al. 2002). We suggest that understanding *why* an ecosystem locks into an alternative state requires an understanding of the feedback mechanisms (Petraitis and Latham 1999; Marzloff et al. 2011) that prevent or slow its return to its original state.

Maine's kelp forest–coralline community ecosystem is an example of an ecosystem with alternative stable states (see Figures 14.4 and 14.5). In this case, the sea urchin fishery was a widespread pulse perturbation (resulting in large-scale herbivore removal: see Figure 14.5A) over a relatively short time. After this perturbation, ecosystem

Figure 14.9 Conceptual model of processes that flip, lock, and reinforce alternative stable state feedbacks on the Maine coast. Asterisks identify key driving processes discussed in the text. Note that crab abundance is a proxy for crab predation. (A) Elevated herbivory due to increased sea urchin abundance leads to kelp deforestation and reduced macroalgal habitat architecture. (B) Fishing pressure on sea urchins reduces their herbivory, increases macroalgae, and thereby increases nursery habitat for settling crabs and other micropredators on sea urchins. The increase in predation by adult crabs further reduces adult sea urchin populations. (After Steneck et al. 2013.)
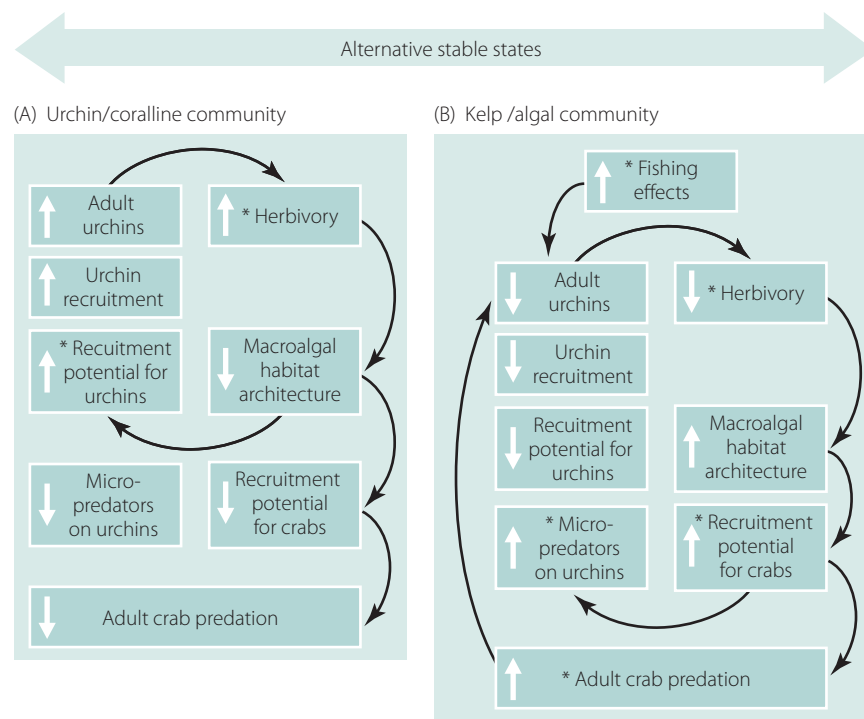
function changed fundamentally, and the change persisted long enough to meet the strict definitions of persistence stability (Connell and Sousa 1983; see Figure 14.5B,D). Evidence suggests that fisheries-induced changes in the ecological process of herbivory have directly or indirectly flipped this ecosystem and locked it into an alternative state (**Figure 14.9**; see also Figure 14.5; Steneck et al. 2013). Between 1996 and 2002, despite high abundances of newly settled sea urchins, virtually no sea urchins survived to adulthood because algal succession to densely branched morphologies created nursery habitat for settling crabs that preyed on newly settled sea urchins. Experiments intended to restore herbivory to prefishing levels, in which more than 50,000 adult sea urchins were translocated to multiple sites over 2 years, resulted in complete sea urchin mortality in both years due to predation by large Jonah crabs (*Cancer borealis*). Jonah crab densities increased five-fold coast-wide soon after the phase shift (**Figure 14.5E**). The fisheries-induced extirpation of sea urchins in Maine allowed algal community recovery and increased the recruitment of sea urchin predators. Once these predators were established, sea urchins could not recover, even in no-take areas or when adult sea urchins were reintroduced (Steneck et al. 2013). Cascading sequential processes of herbivory, recruitment, and predation created reinforcing feedback, locking this ecosystem into the kelp forest state (see Figure 14.9; Steneck et al. 2013). Crab removal and high sea urchin recruitment would be required to shift the system back to a coralline community.

There is a clear pattern in the rapid shift of Maine's stable coralline barren to an alternative stable kelp forest state (see Figure 14.5). Changes in habitat architecture (see Figures 14.4D and 14.5D) increased crab recruitment (see Figure 14.5E; Steneck et al. 2013), changing ecological

processes and creating a hostile environment for settling and adult sea urchins. This change effectively "locked" the ecosystem into its alternative state. In contrast, these ecological processes differed in Nova Scotia (see Figure 14.6), even though species composition in both alternative phases was the same as in Maine. The difference between these ecosystems is that in Nova Scotia, there was always a deepwater refuge from the sea urchin disease, which allowed some sea urchins to survive, promoting rapid recovery to the coralline community state. Without sufficient time for algal succession to habitats crabs prefer, this system does not create a habitat hostile to sea urchins. Thus, although the potential exists, there is no evidence yet to suggest that the shift between kelp forests and coralline communities in Nova Scotia represents alternative *stable* states.

Multiplicative effects of climate change and fishing

Recent experiments in Tasmania have revealed the existence of alternative stable states in other kelp bed communities. The waters off eastern Tasmania are recognized as a "global hot spot," where between 1940 and 2010 the mean ocean temperature increased about 2°C (Hill et al. 2011; Johnson et al. 2011), at a rate about four times the global average (**Figure 14.10A**). Therefore, communities in eastern Tasmania are likely to presage the future of other temperate regions anticipating ocean warming. In southeastern Australia, ocean warming is a result of shifts in oceanography, which increase the flow and southward penetration of the East Australian Current (EAC; Ridgway 2007a; Johnson et al. 2011). The EAC is the western boundary current of the South Pacific gyre, and its intensification
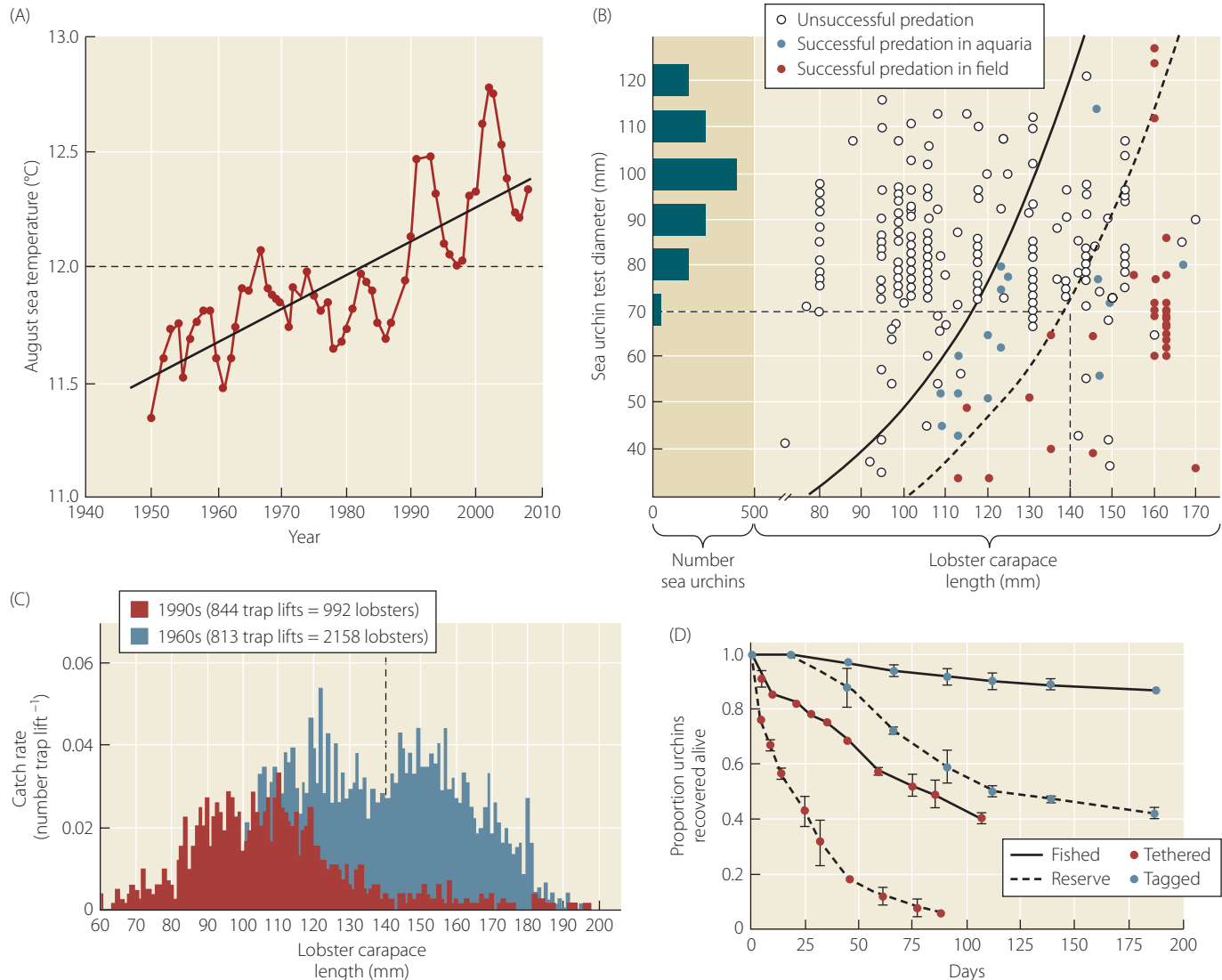
(A)

(B)

(C)

(D)

Figure 14.10 The formation of *Centrostephanus rodgersii* barrens in eastern Tasmania is the result of interaction between climate change and ecological overfishing of lobsters. (A) Four-year running averages of winter water temperatures show that warming has increased the frequency of years in which winter temperature exceeds the 12°C threshold for larval development of *C. rodgersii* (horizontal dashed line). (B) Predation on sea urchins is size-specific, with only large lobsters (>140 mm carapace length) preying successfully on emergent sea urchins. Each point represents a lobster–sea urchin encounter. Open circles = unsuccessful predation; solid gray circles = successful predation in aquaria after a hole was made in the sea urchin test to induce attack; solid red circles = successful field predation captured by remote video. Solid curve = minimum lobster size

to wrap first pair of walking legs around a sea urchin to remove it from the substrate; dashed curve = same relationship shifted to the right to coincide with solid red circles. (C) Extent to which fishing has depleted large (>140 mm) lobsters. The dashed line indicates the minimum size of lobster necessary to prey on emergent sea urchins. The change in the distribution of sizes to the right of this point (i.e., 140 mm and larger) from the 1960s to the 1990s is obvious. By the 1990s, large lobsters were functionally absent from inshore reefs. (D). Mortality curves of tagged and tethered sea urchins, showing that predation potential (tethered sea urchins) and actual predation rates (tagged sea urchins) are greater in unfished reserves, where large lobsters occur, than in fished areas, where large lobsters are rare. (After Ling et al. 2009a; Johnson et al. 2011; Ling and Johnson 2012.)

stems from a gyre "spin up" as a result of increased wind stress in the Southern Ocean. The phenomenon may have been initiated by depleted ozone in the Antarctic region before climate change contributed to the increased wind stress (Cai et al. 2005; Cai 2006; Hill et al. 2008; Johnson et al. 2011). Irrespective of the cause, the warming trend is expected to continue (Ridgway and Hill 2009).

The EAC also transports larvae and adults of numerous species, many of which are newly established in Tasmania, so the shift in the current has resulted in marked changes in the biogeography of benthic and pelagic species (Johnson et al. 2011). Foremost is the introduction of the sea urchin *Centrostephanus rodgersii*, a large and voracious herbivore that, until recently, was known only from New

South Wales, much farther to the north. In Tasmania, kelp forests on exposed coasts were thought to be stable until the southward migration *C. rodgersii* via islands in the Bass Strait, the body of water separating Tasmania from the Australian mainland. This sea urchin was first observed in northeastern Tasmanian waters in the late 1960s (Johnson et al. 2005, 2011), while the first individual on the Tasmanian coast was recorded in 1978 (Edgar 1997). By 2000, there were extensive urchin barrens across northeastern Tasmania, and sea urchin populations had spread along the east coast (**Figure 14.11**; Johnson et al. 2005, 2011; Ling 2008; Ling et al. 2009b).
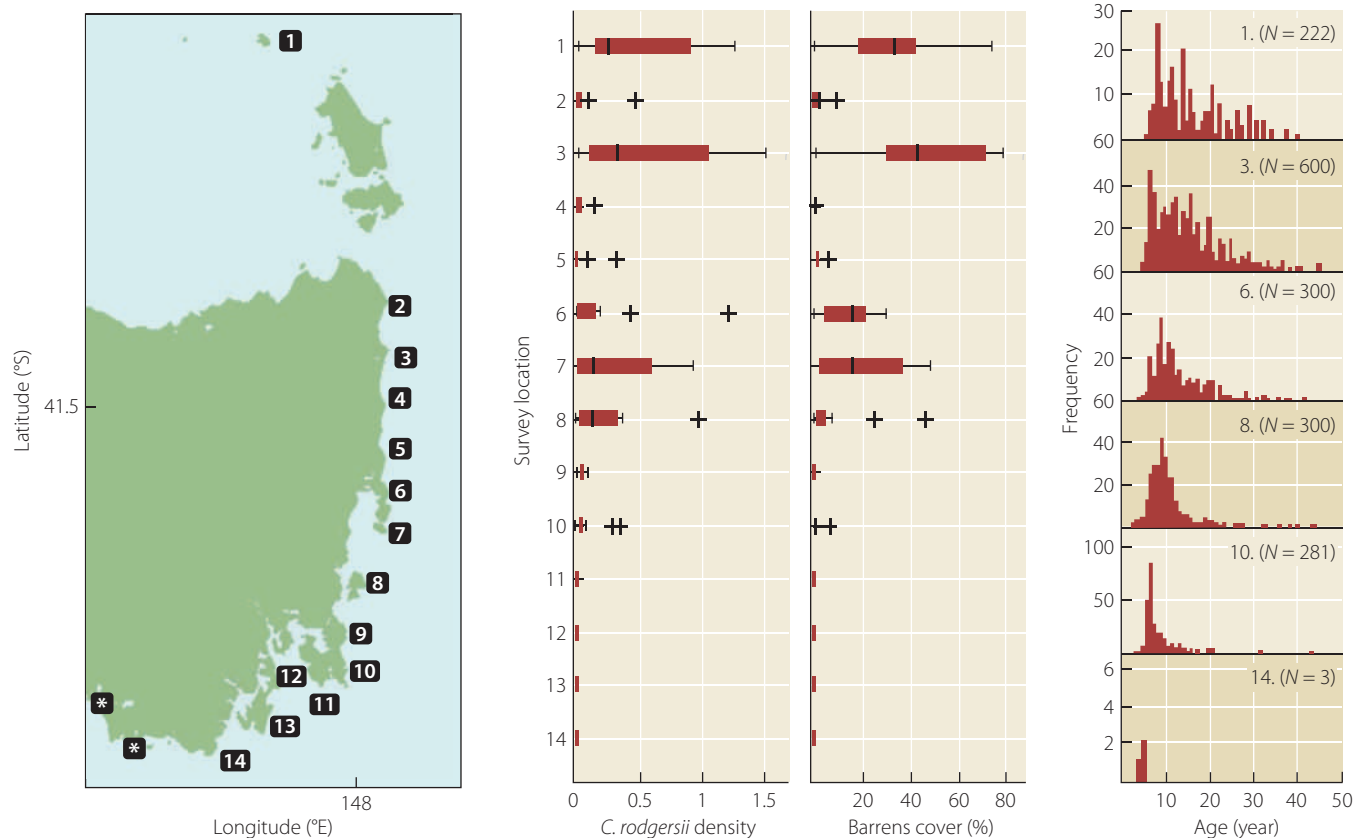
The larval phase of *C. rodgersii* lasts 3 months or more (Huggett et al. 2005; Swanson et al. 2012), providing ample time for transport to Tasmanian waters. Genetic data confirm major and prolonged transport to Tasmania, rather than arrival by chance events (Banks et al. 2010; Johnson et al. 2011). However, *C. rodgersii* is a winter-spawning species and requires a water temperature above 12°C for normal larval development (see Figure 14.10A; Ling et al. 2008). Therefore, the warming of Tasmanian waters, which allows normal gonad development and seasonal spawning in its new range (Ling et al. 2008, 2009b) ensures that the supply of *C. rodgersii* larvae to Tasmanian reefs no longer depends on the EAC.
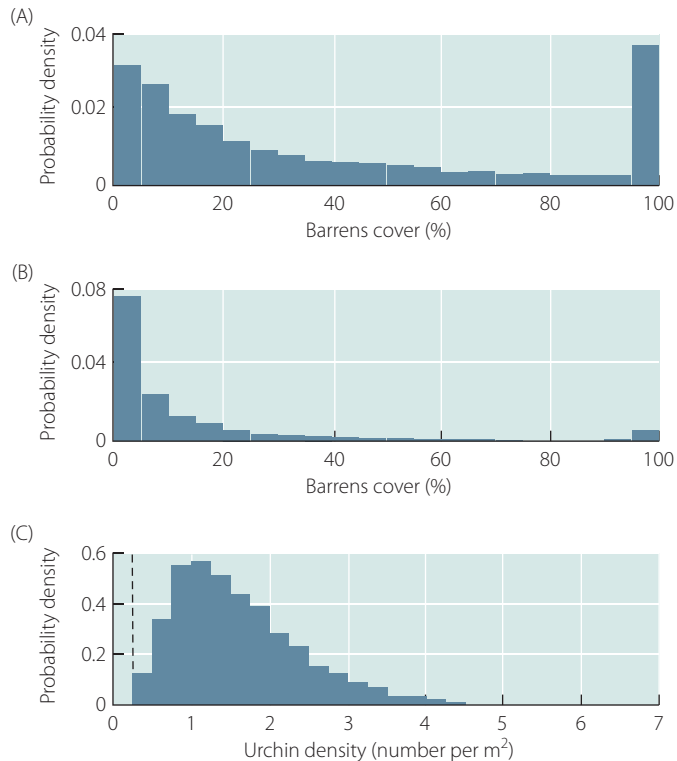
The climate-driven incursion of *C. rodgersii* into Tasmania is problematic because, unlike the smaller native sea urchin (*Heliocidaris erythrogramma*) that forms small, local-ized barrens in sheltered waters, *C. rodgersii* can form extensive barrens along the open coast (Johnson et al. 2005, 2011; Ling et al. 2009b). On extensive barrens in Tasmania, at least 150 species of seaweeds and benthic invertebrates have been lost (Ling 2008), and barren formation can result in the local collapse of abalone (*Haliotis rubra*) and rock lobster (*Jasus edwardsii*) fisheries (Johnson et al. 2005; 2011). Even in intact kelp beds, *C. rodgersii* negatively affects abalone fisheries by inducing cryptic behavior in abalone, making them less visible to the fishery (E. Strain, in press), and by decreasing abalone growth and survival (Strain and Johnson 2009, in press).

Destructive overgrazing of kelp beds and formation of sea urchin barrens by *C. rodgersii* is the largest threat to rocky reef systems in eastern Tasmania. Climate change is responsible for the southward migration of *C. rodgersii*, but it is not the sole driver of this threat. Overfishing of the lobster *Jasus edwardsii*, a key predator of sea urchins at large body sizes (Ling et al. 2009a; Ling and Johnson 2012), is what allowed the growth of large sea urchin populations capable of extensive destructive grazing (**Figure 14.10B–D**).

Figure 14.11   Establishment of *C. rodgersii* and barrens formation in eastern Tasmania began in the northeast and, over the course of approximately 2 decades, spread south with the increasing influence of the warm East Australian Current. Data from 2000–2002. Asterisks indicate sites where *C. rodgersii* was found in 2005 and show how far around the coastline the species has spread. (After Johnson et al. 2011.)

(A)

(B)

(C)

Figure 14.12 Modeling showing hysteresis in kelp bed–urchin barren dynamics in Tasmania. (A) The probability of barren cover in 2032 across sites in eastern Tasmania that currently support kelp beds if management restrictions in the lobster fishery are maintained at 2012 settings. (B) The same projection based on a reduced allowable lobster catch, which predicts that relatively few sites will develop into barrens if a higher lobster density is maintained. (C) Projection to 2032 for the effect of the same level of reduced lobster catch on sea urchin density on extensive barrens. The vertical dashed line indicates the sea urchin density threshold below which kelp will recover. Hysteresis is evident in that the same management scenario (reduced lobster density) yields a much reduced risk of extensive barrens forming, but virtually no likelihood of kelp recovery on existing barrens (C. Johnson, unpub. data).

The predation interaction of lobsters with both *H. erythrogramma* (Pederson and Johnson 2006) and *C. rodgersii* is strongly size-specific. Given the large adult body size of *C. rodgersii* (~70 mm test diameter, 225 mm spine canopy diameter on emergence from the reef matrix: Ling and Johnson 2009; Ling et al. 2009a), only lobsters that are much larger (140+ mm carapace length) than the minimum legal size of 105 mm CL, are capable of preying on them (see Figure 14.10B). This example illustrates that the functional attributes of food webs can be affected by fisheries-induced changes in predator body size. Moreover, heavy fishing, combined with rapid climate-related changes in regional oceanography, can have a profound influence on coastal communities in general and on the formation of extensive sea urchin barrens in particular (Johnson et al. 2005, 2011; Ling et al. 2009a).

In Tasmania, the shift from kelp beds to *C. rodgersii* barrens represents a discontinuous phase shift (see Box 14.1) and thus presents particular management challenges. Kelp beds and sea urchin barrens represent alternative stable states because the system can exist in either state at the same intermediate density of sea urchins (Andrew and Underwood 1993; Johnson et al. 2005; Marzloff et al. 2011, 2013) and because there are reinforcing feedbacks maintaining each state once it occurs (Marzloff et al. 2011). The extent of the hysteresis is also evident in management. Modeling based on the empirical data shows that imposing a reduced lobster catch on Tasmania's east coast will dramatically reduce the likelihood of present kelp beds phase shifting to sea urchin barrens over a 20-year period,

but will have virtually no effect on phase-shifting existing extensive barrens to kelp beds (**Figure 14.12**). This finding emphasizes that "an ounce of prevention is worth a pound of cure" and will apply to other kinds of discontinuous phase shifts in kelp beds.

Other phase shifts from kelp forest: Interactions of local stressors with climate change

Switches between kelp forests and sea urchin barrens are only one of the phase shifts that occur in kelp forest systems. As a result of climate change, or multiplicative interactions between climate change and local stressors such as reduced water quality, there are increasing reports of transitions between species of kelp (Tegner et al. 1996; Steneck et al. 2002; Johnson et al. 2011), or from kelp beds to communities of small turf species (Valentine and Johnson 2005a,b; Connell and Russell 2010; Moy and Christie 2012). These shifts may be continuous or discontinuous (see Box 14.1).

In eastern Tasmania, another change associated with warming is a decline in kelp forests dominated by the giant kelp *Macrocystis pyrifera* (Johnson et al. 2011). Across seven sites in eastern Tasmania, *M. pyrifera* canopy cover declined by about 91% between 1946 and 2008, with several sites showing 95–98% declines (**Figure 14.13**). It is not clear whether the decline is driven by warming alone because the EAC also has very low nitrate levels and *M. pyrifera* has poor nitrogen storage capacity (Gerard 1982). Most areas previously dominated by *M. pyrifera* are now covered by the smaller subsurface kelp *Ecklonia radiata*. While *M. pyrifera* is a boom-and-bust species (Dayton et al. 1984; Graham et al. 2007), and there has been some *M. pyrifera* recovery at southern sites influenced by cool nutrient-rich subantarctic water (Ridgway 2007b), the decline of *M. pyrifera* kelp forests in eastern Tasmania is clear. From the late 1950s to the early 1970s, *M. pyrifera* supported a giant kelp harvesting industry (Sanderson 1987). Dramatic declines in canopy extent began in the 1980s, and in 2012 the Australian federal government listed giant kelp forests in southeastern Australia as an
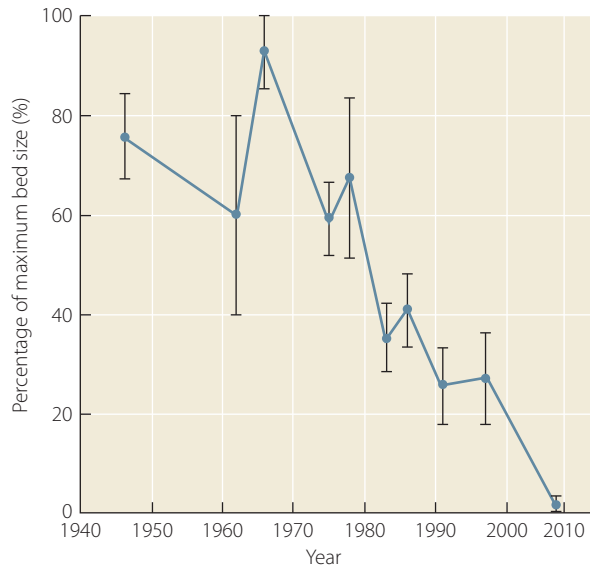
Figure 14.13   Mean extent (±SE, estimated from aerial photographs) of giant kelp (*Macrocystis pyrifera*) canopy cover at seven eastern Tasmanian sites expressed as a percentage of the maximum area of beds at each site over the period 1946–2007.

endangered ecological community. This is the first official endangered listing of a kelp forest community as a direct result of climate change. The decline in *M. pyrifera* is probably a continuous phase shift, in which a return of colder, relatively nutrient-rich waters would facilitate recovery of these kelp forests.

Phase shifts to a matrix of turf algae and sediment involve a different mechanism. In South Australia, kelps and turfs compete for space: dense turfs and the sediment they accumulate inhibit kelp recruitment (Connell and Russell 2010), and closed canopies of kelp inhibit turf development (Falkenberg et al. 2012). While both turfs (Gorgula and Connell 2004; Falkenberg et al. 2013) and kelps (Falkenberg et al. 2013) respond positively to increases in nutrients, eutrophication tips the competitive balance: where water quality is reduced, colonization by turfs is favored (Melville and Connell 2001). Turfs dominate in eutrophic urban waters, while kelp forests prevail in adjacent areas not affected by eutrophication (Connell et al. 2008). In the context of climate change, turf abundance is unaffected by increases in acidification alone, but when acidification is coupled with an increase in water temperature (by 3°C), there are disproportionately large increases in turf biomass and cover (Connell and Russell 2010). Similarly, there is a synergistic response by turfs to simultaneous increases in nutrients and acidification (Falkenberg et al. 2012, 2013). These observations suggest that kelp deforestation and the replacement of kelp beds by turf communities associated with eutrophication and sedimentation (Connell et al. 2008; Eriksson et al. 2002; Moy and Christie 2012) will be exacerbated by climate change.

Sediment-trapping turfs can create lethal environments by forming anoxic layers and preventing small rock-dwelling organisms from attaching (reviewed for coral reefs by Birrell et al. 2005). Extensive losses of kelp and its replacement by turf algae that trap sediments and inhibit kelp recruitment are also associated with anthropogenic ocean warming and reduced water quality in southern Norway (Moy and Christie 2012) and Portugal (Isabel Pinto, pers. comm.). The positive message is that the effects of climate change on kelp forests can be ameliorated by management to diminish stressors such as high levels of nutrients or sediment.

Kelp forest deforestation and shifts to turf communities may well be discontinuous phase shifts, but the critical experiments—requiring a return to the baseline nutrient levels and temperatures that existed when kelps dominated—have yet to be conducted. There is nonetheless evidence that the shift is discontinuous and that nonconsumptive feedbacks maintain alternative stable states because once a matrix of turf and sediment forms, it persists and inhibits kelp recruitment (Connell and Russell 2010; Valentine and Johnson 2005a,b). Even with an enhanced inoculum of spores, Valentine and Johnson (2005a) saw no meaningful recruitment of canopy-forming species on the filamentous algae–sediment matrix over 2.5 years of an experiment on reef that historically supported native kelp. Similarly, in South Australia, the turf–sediment matrix that developed in areas of experimental kelp clearing persisted 7–8 years after kelp removal, even in areas unaffected by anthropogenic nutrient input (Sean Connell, pers. comm.).

CONCLUSIONS

Kelp forests create the largest biogenic structures in the sea. These diverse and dynamic high-canopy algal-dominated ecosystems are found worldwide on shallow hard substrates in cool temperate waters. Globally, kelp forests are physically limited by ice and light toward the poles and by low-nutrient warm waters toward the equator. Between those physical limits, herbivorous sea urchins often limit kelp forest distribution and abundance, replacing kelp forests with communities of herbivore-resistant calcareous crustose coralline algae or occasionally bare rock as in eastern Tasmania. Sea urchins themselves are or were globally limited by predators, but the global decline of large predators due to fishing has resulted in sea urchin population explosions, triggering another global fishery and resulting in the depletion of sea urchins in many regions worldwide. In some cases, the fisheries-induced decline in sea urchins has resulted in an alternative sea urchin–free stable state. In other parts of the world, deforested kelps have been replaced by algal turfs; this process is mediated by interactions between eutrophication, sedimentation, and climate change. The effects of climate change, predation, and herbivory contribute to kelp forests being one of the most dynamic ecosystems worldwide.

ACKNOWLEDGMENTS

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