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INTRODUCTION TO GIANT KELP FORESTS WORLDWIDE

> After a very attentive examination of many hundreds of specimens, we have arrived at the conclusion that all the described species of this genus which have come under our notice may safely be referred to as *Macrocystis pyrifera*.
>
> —Hooker (1847)

> Numerous recent studies on *Macrocystis* interfertility, genetic relatedness, and morphological plasticity all suggest that the genus is monospecific. We propose that the genus be collapsed back into a single species, with nomenclatural priority given to *M. pyrifera*.
>
> —Demes et al. (2009)

TAXONOMIC CLASSIFICATION

Macrocystis, commonly called giant kelp but also known as giant bladder kelp, string kelp (Australia), huiro (Chile), and sargasso gigante (Mexico), is a genus of brown algae, a group characterized by containing the accessory photosynthetic pigment fucoxanthin that gives them their characteristic color. Historically, brown algae were classified as plants in the Domain Eukaryota, Kingdom Plantae, and Phylum (Division) Phaeophyta. The Plantae contained most terrestrial plants and also included two other common algal phyla with multicellular species, the green (Chlorophyta) and red algae (Rhodophyta). Collectively, the large marine species in these three phyla are commonly called "seaweeds." It is now recognized through modern techniques, however, that brown and red seaweeds have characteristics so distinct that they are separate from true "plants." High-resolution microscopy has revealed striking differences in plastid and flagella morphology among many of the traditional plant phyla, or groups within them, as well as similarities in flagella morphology and other characteristics to some colorless flagellates. These more fundamental relationships have generally been supported by analyses of genetic similarities and a better understanding of the role of endosymbiosis in shaping the photosynthetic apparatus. This flood of new information and interpretation has led to fundamental taxonomic rearrangements and the creation of new kingdoms, but there is still debate about appropriate classification (e.g., Parfrey et al. 2006). Revisions will no doubt continue, but the basic classification scheme of Cavalier-Smith (2010) is currently accepted by most phycologists (e.g., Graham et al. 2009, Guiry and Guiry 2012). This scheme places the former Phaeophyta within the Kingdom Chromista, Phylum Ochrophyta, Class Phaeophyceae, with "kelp" being the term used to refer to members in the order Laminariales (figure 1.1). Diatoms are the other major group in the Ochrophyta. The kingdom name Heterokontophyta is preferred by some researchers, others use Stramenopila (discussion in Graham et al. 2009), while some prefer the supergroup designation Chromaveolata (e.g., Adl et al. 2005, Cock et al. 2010).

Within the order Laminariales, giant kelp is now usually placed in the family Laminariaceae (Lane et al. 2006, Guiry and Guiry 2012). Based on genetic similarities, Yoon et al. (2001) placed *Macrocystis* within the family Lessoniaceae but Lane et al. (2006) argued this lacked bootstrap support. Genetic analyses in both studies indicate that the kelp genera *Pelagophycus, Nereocystis,* and *Postelsia* are most closely related to *Macrocystis,* forming a clade or two closely related clades within the family (figure 1.1). There has been considerable taxonomic work on *Macrocystis* and the genus is now considered to be monospecific, the sole species worldwide being *Macrocystis pyrifera* (discussed below). *Pelagophycus, Nereocystis,* and *Postelsia* are also considered to be monospecific (Guiry and Guiry 2012) and are endemic to the Northeast Pacific. All but *Postelsia* form subtidal kelp forests (Abbott and Hollenberg 1976).

"Kelp" originally referred to the calcined ashes resulting from burning large brown algae. It is sometimes used as the common name for all large brown algae, but particularly species in the order Laminariales. In this book, we use "kelp" to mean only species in this order. Some argue that kelps should be called chromistans, ocrophytes, phaeophyceans, etc., and not plants, because they are no longer in the kingdom Plantae. Although taxonomically correct, these names are awkward in usage, so we will refer to kelps and other algae as seaweeds, algae, or plants.

Macrocystis and its putative species have undergone considerable taxonomic revision since originally described in 1771 by Linnaeus, who included it with other brown algae under the name *Fucus pyriferus* (reviews in Womersley 1954, Neushul 1971a, Coyer et al. 2001, Demes et al. 2009). Agardh (1820) placed *F. pyriferus* into a separate genus, *Macrocystis,* and described three species based on differences in blade and float (pneumatocyst) morphology. The number of species based on these characters increased to 10 by the mid-1800s. Hooker's (1847) extensive field observations indicated these characters were highly variable and he argued there was only one species, *M. pyrifera*. Recognition of variability in these characteristics led to species revisions based primarily on holdfast morphology. This character was not considered by early investigators because they relied on specimens collected by others, specimens that generally did not include holdfasts (Womersley 1954). More recent investigators examined plants as they grew in the field, and used holdfast morphology as the primary character to distinguish species. This resulted in three commonly recognized species in both hemispheres: *M.*

Kingdom Chromista (“colored”)
Members have a plastid bounded by four membranes and containing chlorophyll *a* and *c* and various xanthophylls. Also includes organisms that have lost these characteristics but are closely related, based on multigene trees.

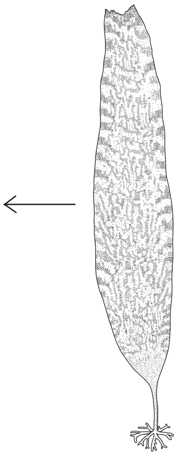
Phylum Ochrophyta (“golden-brown”)
Chromists with two flagella, one smooth and one with tripartite tubular hairs, or with modified versions of this structure.

Class Phaeophyceae (“dusky seaweed”)
Brown algae. Ochrophytes with chromistan plastids, ochrophycean flagella (on spores and/or gametes) and multicellular thalli with alginate in the cell wall. Parenchymatous members have pores or plasmodesmata between cells.

Order Laminariales (“flat blade”)
Kelps. Phaeophyceans that have an alternation of generations: gametophytes (haploid) are small, free-living, and filamentous with apical growth; sporophytes (diploid) are large, free-living, and parenchymatous with intercalary growth.

Family Laminariaceae
Members are currently based on genetic affinities. There are no common morphological features distinct from other families in this order.

Clade with *Macrocystis* and its closest relatives
(Illustrated below). The three kelps to the left can reach lengths of 10s of meters.



Laminaria farlowii illustrating a typical species of the type genus of the order

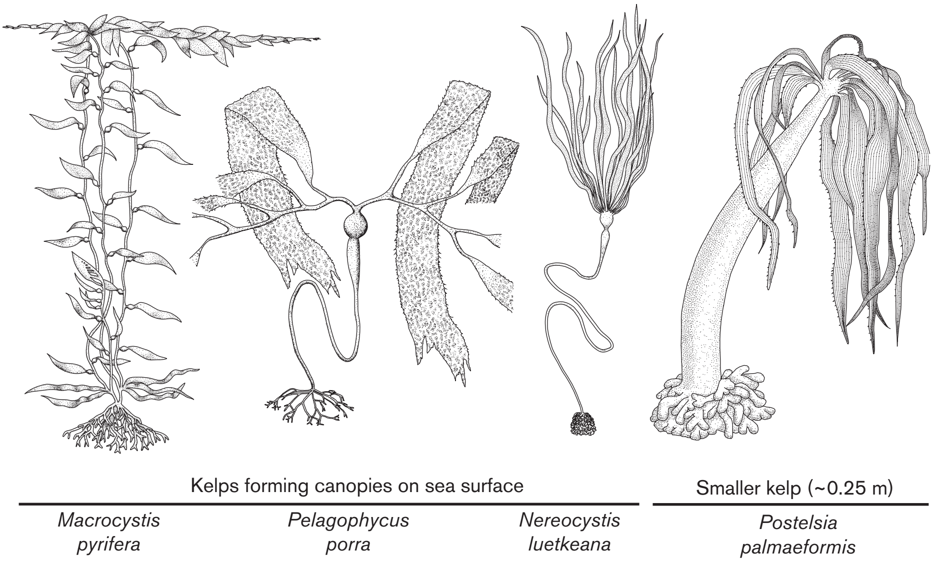


FIGURE 1.1

Macrocystis classification based on genetic and morphological characteristics, the primary ones of which are listed. See Chapter 1 text for references.

pyrifera, M. integrifolia, and *M. angustifolia* (Womersley 1954, Neushul 1971a). Hay (1986) described a fourth species, *M. laevis*, from the subantarctic Marion Islands based on its unusually smooth blades (compared to rugose / corrugated blades in other recognized giant kelp species). Morphometric measurements and transplant experiments by Brostoff (1988) showed that the holdfast morphology of *M. angustifolia* populations described by Neushul (1971a) in California intergraded with that of *M. pyrifera. M. angustifolia* was subsequently considered to occur only in the southern hemisphere (e.g., Macaya and Zuccarello 2010a).

Holdfast morphology did not stand up to scrutiny as a species indicator, however, as more research was done. Field observations and transplant experiments have shown that holdfast morphology varies with environment and that blade smoothness also does not distinguish species well (review in Demes et al. 2009; figure 1.2). Genetic and molecular studies confirm that external morphological characters are not good discriminators of species. Lewis and Neushul (1994) showed that the three "species" (*M. 'pyrifera'* and *M. 'integrifolia'* from the Northeast Pacific, and *M. 'angustifolia'* from Australia) distinguished by differences in holdfast morphology could hybridize and produce normal sporophytes, and Westermeier et al. (2007) produced hybrids with normal sporophytes in crosses of *M. 'pyrifera'* and *M. 'integrifolia'* from Chile. Molecular taxonomic work comparing the similarity of noncoding rDNA internal transcribed spacer regions (ITS1 and ITS2) by Coyer et al. (2001), and DNA barcoding (Macaya and Zuccarello 2010a) of all four "species" in the southern hemisphere and *M. pyrifera* and *M. integrifolia* in the northern hemisphere indicate that *Macrocystis* is a monospecific genus, and this was confirmed by Astorga et al. (2012). All these findings indicate there is only one species of giant kelp, *M. pyrifera* (Linnaeus) C. Agardh, and this is currently accepted (Guiry and Guiry 2012). Unless otherwise noted, therefore, we refer to this species in the text as giant kelp or *Macrocystis*. However, when referring to the literature on *Macrocystis* it can be advantageous for clarity to refer to the former species names. Where necessary we designate these, including *M. 'pyrifera,'* as ecomorphs by enclosing the ecomorph name in quotes.

EVOLUTION

The timing of origins of kelp and their relatives is problematic and not completely resolved, but significant progress has been made in the past 20 years. A variety of morphological, biochemical, and, most recently, genetic evidence indicates that species in the kingdom Chromista, as well as other photosynthetic eukaryotes, obtained their plastids via endosymbiosis with other organisms that took up residence inside cells (reviews in Yoon et al. 2004, Graham et al. 2009) early in the evolution of eukaryotic organisms. Primary endosymbiosis between prokaryotic cyanobacteria (blue-green algae) and eukaryotic protists resulted in the red and green algae (with green algae being the progenitor of "higher plants"). A secondary endosymbiosis between a uni-

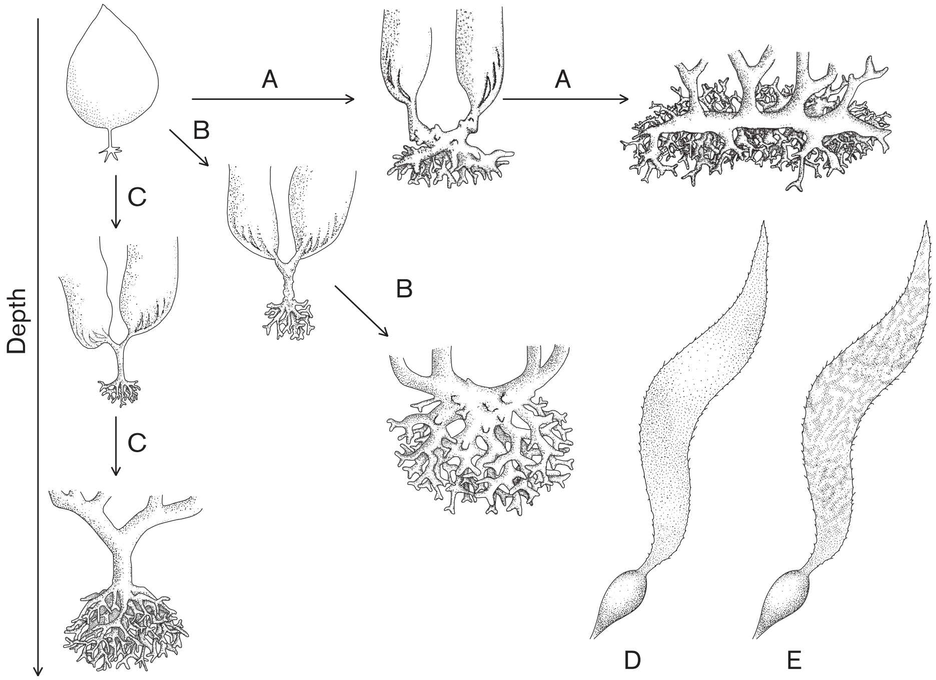


FIGURE 1.2
The development and holdfast morphology of *Macrocystis* ecomorphs, beginning as a small sporophyte (top left). (A) *M. 'integrifolia,'* (B) *M. 'augustifolia,'* and (C) *M. 'pyrifera.'* (D) The smooth blade morphology of *M. 'laevis'* compared to (E) more typical corrugated *Macrocystis* blades. 'Depth' indicates the relative depth distribution, from shallow to deep, of the holdfast ecomorphs.
SOURCE: Modified from Demes et al. (2009), reprinted with permission from Wiley Publishing.

cellular red alga and another eukaryotic protist resulted in the golden-brown algae, a lineage of which was the progenitor of kelps. Given the number of green chloroplast genes in the genome of the filamentous brown alga *Ectocarpus siliculosus*, the protist in the partnership that produced the brown algae may have been previously inhabited by a green chloroplast (Cock et al. 2010). Molecular clock methods indicate that red and green algae arose around 1500 Ma (Ma = SI unit for mega-annum or million years ago), and the secondary symbiosis that eventually led to the chromists occurred around 1300 Ma (Yoon et al. 2004) during the late Mesoproterzoic era, after the earth's transition to a more highly oxygenated atmosphere with an ozone screen (Cloud 1976). Fossil evidence (Cloud 1976) is consistent with these gene-based estimates. Medlin et al. (1997) suggested the chromists originated between 275 and 175 Ma (in the Permian–Jurassic period), but Yoon et al. (2004) suggested a much earlier origin at about 1000 Ma at the Mesoproterozoic–Neoproterozoic boundary, with the Ochrophyta arising soon afterward. An earlier study by Saunders and Druehl (1992) analyzed 5S rRNA similarities and concluded that the Phaeophyceae originated "within 200 Ma." Medlin et al. (1997)

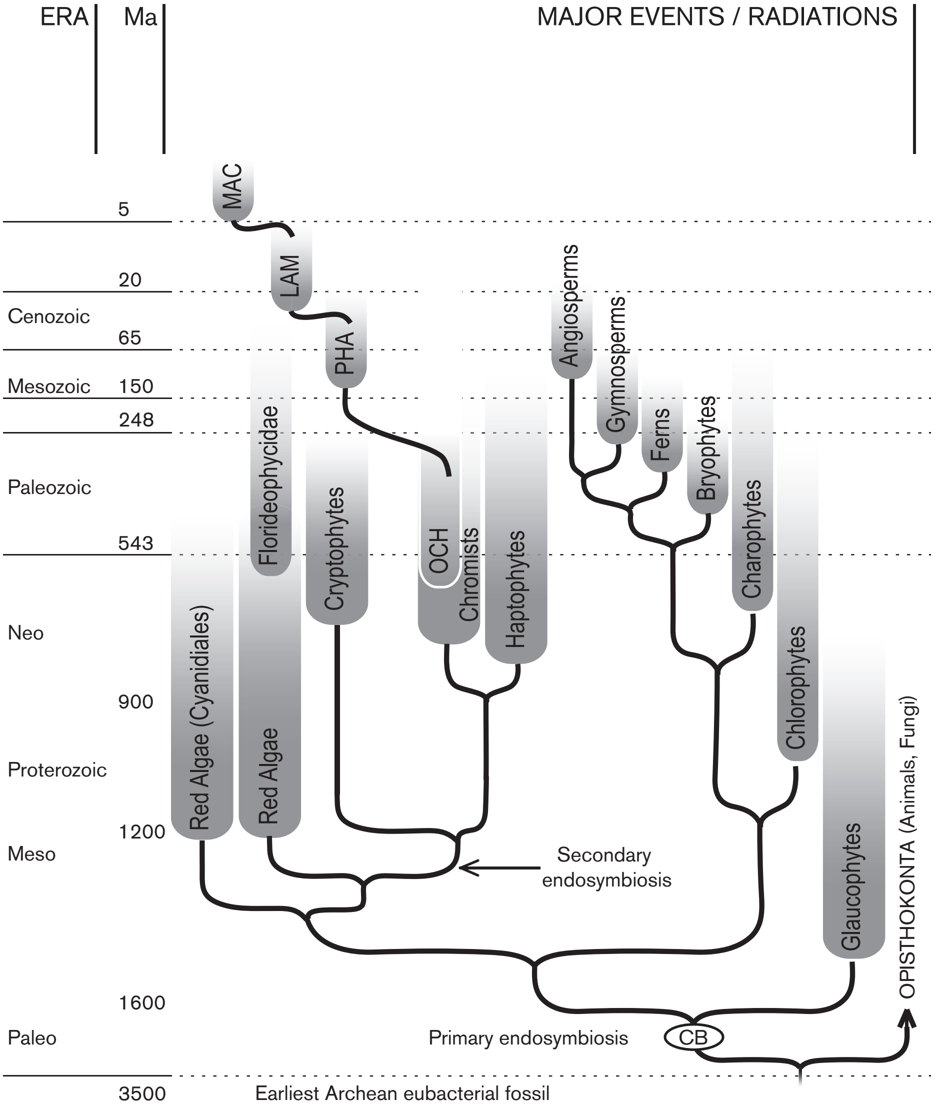


FIGURE 1.3

Evolutionary timing and relationships leading to *Macrocystis*.

Ma = millions of years ago; CB = cyanobacteria; OCH = Ochrophytes; PHA = Phaeophytes; LAM = Laminariales; MAC = *Macrocystis*.

SOURCE: Modified from Yoon et al. (2004), reprinted with permission from Oxford University Press.

estimated this origin at 150–90 Ma (in the Jurassic–Cretaceous period) from a molecular clock analysis based on 18S rRNAs (figure 1.3).

The fossil record has not shed much light on the origins and radiation of kelp and other brown algae because, with the exception of a few lightly calcified species, they lack hard parts and do not fossilize well. There are no calcified Laminariales and the only

FIGURE 1.4
Julescraneia grandicornis from the upper Miocene of California. The fossil and inset reconstruction (with the fossil location indicated by the rectangle), pneumatocyst (P) is about 16 cm in diameter.
SOURCE: From Parker and Dawson (1965), reprinted with permission from Schweizerbart Science Publishing (www.schweizerbart.de).

fossil found so far that is generally accepted as a kelp is the extinct species *Julescraneia grandicornis* from the Miocene Monterey formation in southern California (Parker and Dawson 1965). This fossil consists of impressions on two rock fragments, one with a portion of a blade and another with "antler-like branches from a large pneumatocyst" (figure 1.4). Parker and Dawson (1965) interpreted *J. grandicornis* as having characteristics of modern *Pelagophycus* and *Nereocystis*, which are close relatives of *Macrocystis* (cf. figure 1.1). The deposit was dated at 13.5–7.5 Ma (upper Miocene). The molecular clock analyses of Saunders and Druehl (1992) and their review of similar analyses by others indicate kelps diverged from other brown algae 30–16 Ma (Oligocene–Miocene), and that morphologically similar kelp taxa radiated 3 – 6 Ma. These periods roughly correspond to those suggested by Lüning and Dieck (1990) based on temperature tolerances and paleo-oceanographic conditions (figure 1.3). Saunders and Druehl (1992) pointed out that "The extensive morphological variation observed among the kelp comes from genotypically similar plants." They reference other studies supporting these dates, including the fossil record of kelp-associated limpets, the number of monospecific kelp taxa, biogeographic distributions, and hybridization among kelps.

Various selective processes may have stimulated the radiation of kelp genera and species within the times discussed above. Evolutionary attention has been focused on processes in the North Pacific region because it contains the greatest diversity of kelps (review in Lane et al. 2006) and is therefore considered to be the likely area of origin and high diversification. Various processes have been hypothesized as being primary drivers of kelp evolution. Modern kelps occur in generally cool temperate waters and so the primary evolutionary processes are likely to be related to paleoenvironmental changes that caused North Pacific waters to cool. A series of ice ages between 23.7 and 5.3 Ma (Miocene) cooled the North Pacific, as did the growth of the Isthmus of Panama, both of which generally coincided with the appearance of kelps (review in Stanley 2009). Some argue that trophic dynamics were a factor. For example, Estes and Steinberg (1988) wrote that kelp evolution in the region from Canada to northern Japan was facilitated by predatory marine mammals like sea otters that primarily foraged at depths shallower than 30 m, a depth range that coincided with the high-light zone that most kelps occupy. Their proposed mechanism was that by eating sea urchins, which can be extensive grazers of kelp, these mammals removed a potential impediment to kelp evolution. Domning (1989), a noted marine mammal biologist, countered their argument by pointing out that Stellar's sea cows (*Hydrodamalis gigas*, large, surface-dwelling, herbivorous marine mammals related to dugongs and manatees, which were hunted to extinction around 1770) and their relatives were also present, and grazing by these mammals may have affected kelp evolution. He questioned the assumption that the strength of the modern sea otter / sea urchin / kelp interaction applies to the past, given that the dynamics of kelp stands may have been quite different then. He further postulated that kelp diversification may have occurred in habitats, including those in deep water, that were inaccessible to predatory and grazing mammals.

The degree to which the various processes affected kelp evolution remains unresolved, but there is some intriguing recent evidence that past notions of the causes of shallow-water diversification as well as modern distributions may have to be altered if kelp radiation occurred in deep water. Hypotheses about diversification are commonly based on attempted reconstructions of past physical and ecological processes operating in shallow, cold, surface waters (<30 m) where modern kelps are most abundant. However, the increasing use of deep SCUBA diving, remotely operated vehicles (ROVs), and remote sensing technologies has shown that kelp can be abundant in deep temperate waters (>30 m) if they are clear and transmit light to the depths (review in Spalding et al. 2003). For example, non-float-bearing kelps can be found to 45 m deep in central California (Spalding et al. 2003) and to 130 m in southern California (Lissner and Dorsey 1986). Perissinotto and McQuaid (1992) discovered stands of *Macrocystis* nearly 70 m deep at Prince Edward Island in the Southern Ocean (the fronds of this population did not reach the sea surface). Graham, Kinlan, et al. (2007) developed a model to predict kelp distribution in tropical waters using the photosynthetic compensation depth of kelp and the depth of the mixed layer below which nutrients are sufficient for kelp growth. The model predicted both the known distribution of kelp in the tropics and that kelp populations could occur to depths of 200 m on hard substrata when light, temperature, and nutrients are suitable. The recognition that kelps are common in clear, deep waters, including those in the tropics, should lead to a reevaluation of the causes of kelp diversification and distribution.

Other hypotheses about processes shaping kelp evolution emphasize potential selection by the abiotic environment leading to the occupation of new habitats. For example, moving from the sea bottom to sea surface in the subtidal zone traverses diverse hydrodynamic conditions, from a benthic boundary layer to a surge zone to mid-water mixing, with orbital motion in breaking surf at the surface. Neushul (1972) argued that many developmental and morphological features of kelps may reflect the consequences of these changes because they affect phenomena such as nutrient availability and the ability of kelp to remain attached to the substratum. All kelp sporophytes have a similar morphology as juveniles, consisting of a small holdfast and a short stipe bearing a single blade (figure 1.1). It may be that this universal morphology, which involves juvenile kelp quickly getting blades elevated above the substratum on a stipe, is an adaptation that makes it more difficult for benthic grazers to remove the blade, the primary site of photosynthesis. Selection in response to abiotic factors such as water motion and gradients of light intensity and spectral composition between the surface and the bottom may have affected the morphology of float-bearing kelps like *Macrocystis* that occupy the full water column. These and numerous other habitat–kelp relationships indicate that the diversification of genera and species within the Laminariales inhabiting communities from deep water to the wave-swept rocky intertidal zone was most likely influenced by myriad biotic and abiotic variables. Sorting out these relationships and their relative influences is difficult in the present, let alone trying to reconstruct the past. Although the present often holds the key to the past, there are many possible keys that probably turned together. New molecular tools will clarify phylogenetic relationships, but the thorny problem of understanding the underpinning evolutionary forces that produced kelp diversification will most likely remain in the realm of plausible "just so" stories and speculation without a better fossil record and more detailed paleo-oceanographic information.

BIOGEOGRAPHY

Assuming that *Macrocystis* evolved a few million years ago, what may have influenced its biogeographic distribution and differences among populations? Giant kelp occurs along the west coast of North America, but it is most widely distributed in the southern hemisphere where there are populations along the east and west coasts of South America, off southern South Africa, Tasmania and south Australia, central and southern New Zealand and its offshore islands, and the subantarctic islands. Recent work by Macaya and Zuccarello (2010b) clarifies the geographic occurrence of *Macrocystis* (figure 1.5) and highlights the broad distributional pattern of the species and ecomorphs. In the southern hemisphere, giant kelp occurs from as far north as Peru, at around 6° S latitude, and as far south as the subantarctic islands, at around 57° S. These latitudes span water temperatures that reach as low as a few degrees Celsius during parts of the year to as high as around 25°C in subtropical areas of the north. In the northern hemisphere, the latitudinal range was thought to be from around 27° N latitude in Baja California, Mexico, to around Sitka, Alaska, at 57° N (Druehl 1970, 1981), but the northern limit was recently extended as a few small stands were found in Alaska to 60° N at Icy Bay and southwest to Kodiak Island (Saupe 2011). Chapter 5 provides more detailed distributional information as well as descriptions of forests across biogeographic regions.

As for other species with anti-tropical distributions, it is generally thought that temperature is the chief barrier to geographic expansion into warmer waters (Hedgpeth 1957). However, despite the generalization that temperature can be a major factor limiting the distribution of seaweeds, acting on various life history stages (van den Hoek 1982), it seems clear that water temperature alone poses few biogeographic limits on giant kelp. For example, the general inverse relationship between temperature and nutrients in central and southern California, and Baja California, Mexico (Jackson 1977, Edwards and Estes 2006, Lucas et al. 2011), indicates that nutrients can affect expansion and distribution, and this has been shown by Graham et al. "Global ecology" (2007) to affect kelp distribution in the tropics. Biogeographically, the southern latitudinal limit of giant kelp in the southern hemisphere coincides with the furthest landmasses in the cold temperate zone between the southern continents and Antarctica. On a wider geographic scale, wave force may well be a primary influence on the distribution of giant kelp. Our own personal observations, those of Hooker (1847), more recent algal studies (e.g., Smith and Smith 1998), and oceanographic studies all highlight the severe wave climate of the Southern Ocean. This region has consistently high wind speeds, little variation in wind direction, and no continental land barriers to impede wind and waves forces (Tomczak and Godfrey 2003). Nevertheless, the subantarctic islands have extensive giant kelp forests, but almost exclusively along lee shores and in protected inlets, despite being surrounded by some of the most tumultuous seas in the world.

It may well be the case that a combination of cold water and low light acting on the various life history stages of giant kelp prevents range expansion toward the poles (cf. van den Hoek 1982, Jackson 1987). However, Gaines and Lubchenco (1982) suggested that because herbivory increases inversely with latitude, the spread of kelp into warmer waters may also be limited by grazing. Their model, like some others for kelp diversification (see Evolution section above), is based on modern grazing interactions in shallow water. Whether these interactions are similar in deep water now or were in the past is unknown.

Early hypotheses about the origin and spread of *Macrocystis* were based primarily on its present distribution, the number of species in the genus thought to be present in the two hemispheres at the time, fossil evidence, and the distribution of other kelp species and genera (review in Coyer et al. 2001). Parker and Dawson (1965) and North (1971a) concluded, based on the more widespread distribution of the genus in the southern hemisphere, that there was a southern hemisphere origin of giant kelp with an expansion to the north (figure 1.5). They argued that a longer residence time in the southern hemisphere, indicated by the greater number of giant kelp species described there (at the time), also supported this hypothesis. Nicholson (1979) favored a northern hemisphere

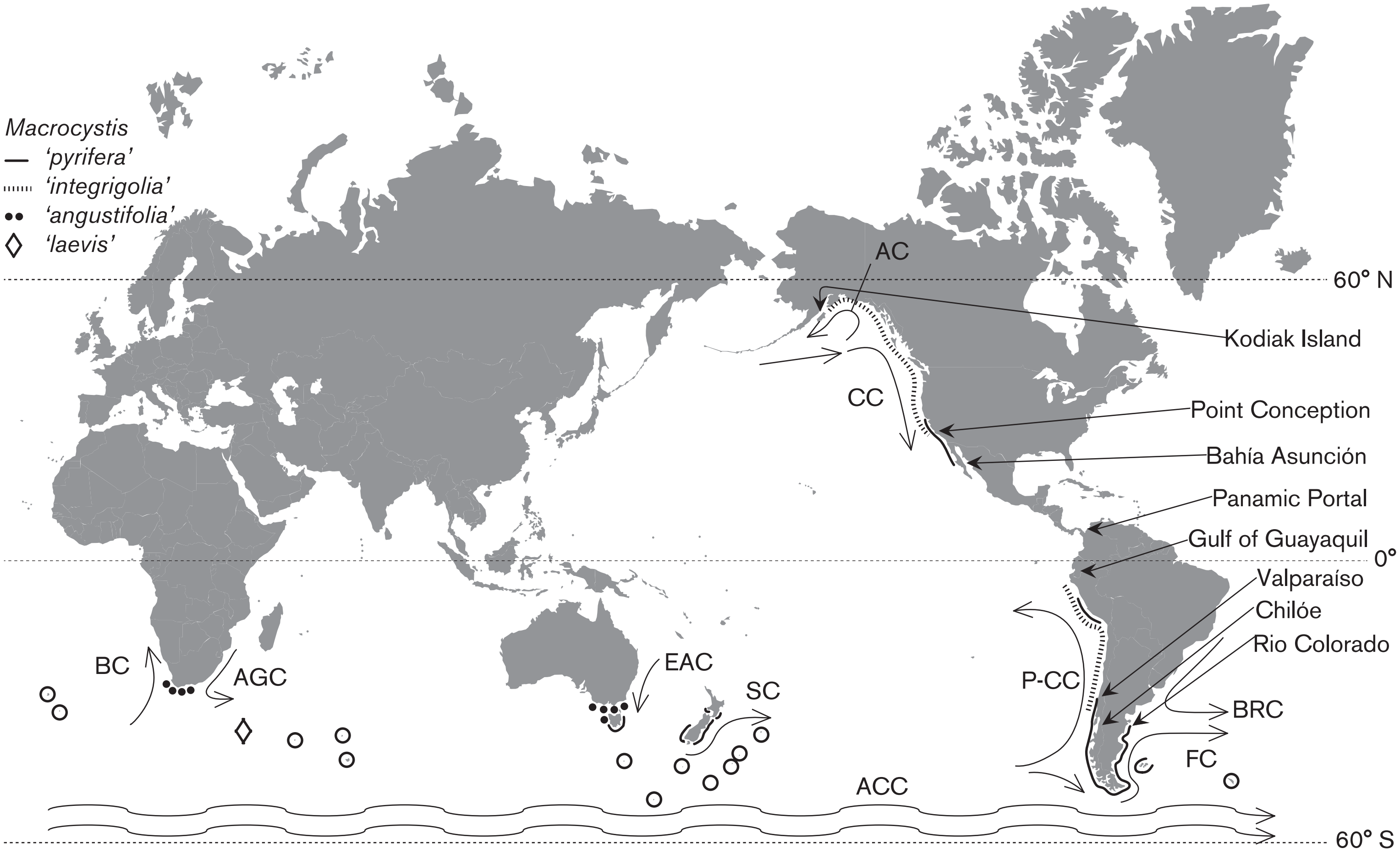


FIGURE 1.5

Worldwide distribution of *Macrocystis* and its ecomorphs, important biogeographic locations, and relationships to major currents.

Currents: AC = Alaskan; ACC = Antarctic Circumpolar also known as the West Wind Drift; AGC = Agulhas; BC = Bengula; BRC = Brazil; CC = California; EAC = East Australian, FC = Falkland; P-CC = Peru-Chile; SC = Southland.

NOTES: Open circles in the Southern Hemisphere indicate *Macrocystis 'pyrifera'* around subantarctic islands, as does the diamond for *M. 'laevis'*.

SOURCE: Reprinted from Macaya and Zuccarello (2010a), with permission from Wiley Publishing.

origin with spread to the south because more related kelp genera occur in the north and the fossil *Julescraneia* was found there. Chin et al. (1991) suggested a vicariant origin with *Macrocystis* evolving where it occurs now from a widespread ancestral complex. This hypothesis is not supported by the genetic analyses discussed below. The former hypotheses require explaining how, assuming conditions were somewhat similar to the present, a cold water species like *Macrocystis* crossed the equator, and how it moved north against the southward-flowing California Current or south against the northward-flowing Peru–Chile Current. Parker and Dawson (1965) suggested crossing the equator may have occurred during a period like the late Pliocene–Pleistocene (2–0.1 Ma) when temperatures were lower. Spread counter to the flow of major currents may have been via the transport of drifting reproductive plants in countercurrents and eddies (Nicholson 1979). Spread within the southern hemisphere could have been relatively rapid due to the cold, circular, west to east flow of the Antarctic Circumpolar Current (figure 1.5) where, as observed by Hooker (1847) and many others, vast amounts of drift *Macrocystis* can occur. With speeds up to 1.8 km hour^{-1} (Fyfe and Saenko 2005), this current could disperse drifting *Macrocystis* as well as attached animals, such as the brooding pelecypod *Gaimardia trapesina*, between suitable habitats (Helmuth et al. 1994).

Early evidence and speculation about the origins of *Macrocystis* have been superseded to some extent by recent studies. A better understanding of genetic structure and relatedness, morphological plasticity, dispersal via surface drift, and depth distribution now point strongly to *Macrocystis* having originated in the northern hemisphere and then spreading south, with *Macrocystis 'pyrifera'* the likely northern source (Astorga et al. 2012). As discussed earlier (see the "Taxonomic Classification" section) genetic and morphological data indicate that *Macrocystis* is one species with several ecomorphs, eliminating the argument for a southern hemisphere origin based on having more species there. Moreover, genetic analyses by Coyer et al. (2001) of relationships between and within ecomorphs and within and between hemispheres show that populations in the southern hemisphere are more similar to each other than those in the northern hemisphere. This evidence combined with the greater diversity of the genetic sequences in individuals from the north are indications that *Macrocystis* has existed longer in the northern than in the southern hemisphere (Coyer et al. 2001), and therefore is of northern origin. High genetic similarity among southern hemisphere populations indicates either high gene flow or very recent dispersal (Coyer et al. 2001, Macaya and Zuccarello 2010b), most likely from western South America where the landmass is continuous south of the distribution of *Macrocystis* along the west coast of North America. Coyer et al. (2001) speculated that there were probably multiple crossings between 3.1 Ma and as recent as 0.01 Ma.

The argument that giant kelp spread across the equator has become less problematic with improved knowledge of opportunities and mechanisms. Lindberg (1991) reviewed the biological and paleo-oceanographic evidence for interchange across the equator and concluded there were two main periods when this occurred. One was during the Pliocene (5.3–1.6 Ma) when northern species moved south as cooling occurred because of the closure of the Panamic Portal and the other was in the early Pleistocene (about 1 Ma) when species moved in both directions as a result of glacial cooling and increased upwelling. The importance of upwelling is difficult to assess because glaciation cycles also caused changes in sea level that may have affected upwelling (Lindberg 1991) as well as the distribution and abundance of giant kelp (Graham et al. 2003). Because giant kelp can grow in deep water (e.g., Perissinotto and McQuaid 1992) and it is now known that other kelps occur in deep tropical waters (review in Graham, Kinlan, et al. 2007), the tropical thermal barrier appears to be less daunting and, historically, more permeable because the spread of kelp across the equator could potentially have occurred through submerged populations. The probability that spread across the equator could have occurred by surface drift of adult plants has also increased because we now know that rafts of giant kelp can be driven against currents by the wind, and can survive and produce viable spores for over 100 days and hundreds of kilometers if surface temperatures are suitable (Macaya et al. 2005, Hernández-Carmona et al. 2006, Rothäusler et al. 2011). Alberto et al. (2011) determined that current speed and direction, combined with spore production, explained more of the genetic differences in giant kelp populations than geographic distance and habitat continuity, at least on a regional scale. It remains to be determined, however, if spores from drift giant kelp can arrive in suitable habitats at great enough densities and with the genetic diversity likely to produce viable new populations. Drifters may not be important locally over short timescales, but may be important regionally over long timescales, especially if very large masses of giant kelp strand on shore and release spores.

We have outlined where *Macrocystis* occurs and potential influences on its range limits, but an intriguing question is, why doesn't it occur elsewhere, particularly along the coastlines of the western Pacific Ocean? This question is an old one, first posed in the literature by Setchell (1932). In discussing the worldwide distribution of *Macrocystis*, he noted that "the waters of the Bering Sea, of the Ochotsk, and the Kuriles are probably not colder than those of Cape Horn, South Georgia, the Falklands, and those of the Antarctic islands. Hence its absence presents the question: specific identities or seasonal or other variables?" Whatever the underlying mechanisms for the absence of giant kelp from the shores of the western Pacific, a combination of prevailing currents, cold temperatures, seasonal ice, low light, and competition with other kelps would have helped prevent the spread of *Macrocystis* westward. Furthermore, the ice bridge along the Bering Sea between Alaska and eastern Siberia may have prevented the spread of giant kelp over much of its history. During the Last Glacial Maximum (LGM), other algal taxa were not abundant. Caissie et al. (2010) pointed out that during the LGM through to the early deglacial period (23,000–17,000 years ago) there were more than 6 months of sea ice present each year, corresponding with low diatom concentrations. As ice-free conditions later prevailed, there was a transition from diatom assemblages dominated by sea-ice species to those dominated by species indicative of high productivity. Similarly, de Vernal et al. (2005) found that dinocyst concentrations were lower during the LGM, which they interpreted as being the result of limited biogenic production due to limited light because of permanent or quasi-permanent sea-ice cover. With respect to *Macrocystis*, both Graham et al. "Global ecology" (2007) and Macaya and Zuccarrello (2010a, 2010b) concluded that glaciations probably had a great effect on the distribution, abundance, and productivity of giant kelp. A more recent paper highlights this possibility for a similar large, drifting alga of the southern hemisphere. Fraser et al. (2009) used molecular techniques to assess the history of the southern bull kelp, *Durvillaea antarctica* (the largest fucoid alga, not a laminarian kelp), across the southern hemisphere landmasses. They found considerable genetic diversity among northern and southern Chilean sites, and around the coast of mainland New Zealand. Samples across the subantarctic islands, however, showed remarkable genetic homogeneity. Fraser et al. interpreted this similarity across the vast distances of the subantarctic islands as the result of subantarctic kelp populations being eliminated during the LGM due to ice scour, with recolonization occurring through a series of long-distance rafting events.

As in all areas where reconstructions, correlative evidence, and informed surmisal are involved, we will probably never know why giant kelp did not get to some regions of the Pacific basin and establish unless, of course, it suddenly appears there and we can determine how it did so. Nevertheless, many find it interesting to use the accumulating knowledge across a wide range of disciplines and continue the long tradition of speculation. The problems of origins, diversification, and spread will no doubt be areas of research and speculation in the future. As Druehl (1981, quoting Silva 1962) pointed out, however, "the field of phytogeography is vast, the literature is inexhaustible, its data capable of a variety of interpretation, extraordinary manipulation, and distortion. It has the fascination of a chess game. It is a valid, though treacherous, field of investigation."

HISTORY OF RESEARCH (UP TO 1970)

If you see beds of weede, take heed of them and keep off from them.

– sailing directions from the mid-1500s cited by Hooker (1847).

The ocean is an inexhaustible treasury of varied wealth, but its riches are stored in so attenuated a form that we are powerless to gather them without the aid of natural processes that go on continually. Marine plants include annually certain portions of this wealth, and offer it for our acceptance like dividends due; should we refuse, it is returned to the treasury and, as time advances, offered us again and again.

– Balch (1909)

No level of species' protection or reserve status will be effective if water quality, coastal run-off, increased sedimentation, and contamination impact the ability of giant kelp to survive and thrive.

– Foster and Schiel (2010)

Giant kelp forests have provided food, medicine, materials, and probably aesthetic value since the earliest humans inhabited temperate coasts (Dillehay et al. 2008). Forests and drift plants first entered the written record in the logs of European explorers in the mid-1500s. Cabrillo, one of the earliest Spanish explorers in the Northeast Pacific, was apparently the first to mention giant kelp in this region, which he observed while anchored at Bahía San Pablo in Baja California in 1542 (Kelsey 1986). Other explorers noted giant kelp in the Southern Ocean at around the same time and commonly used drifting and attached plants to indicate proximity to land and the presence of shallow, submerged rocks (Hooker 1847). The presence of "porra," individuals or rafts of clubbed-shaped drifting kelp, was especially significant for the Spanish Manila-Acapulco merchant galleons active between 1565 and 1815. Porra indicated they were near the often fog-shrouded west coast of California / Baja California on the eastward leg of their route and needed to bear south to Acapulco (Schurz 1917). Setchell (1908) noted that porra could have been *Nereocystis luetkeana*, *Pelagophycus porra*, or *Macrocystis pyrifera*, based on voyage narratives and depending on where the galleons arrived along the coast. Distributional records and descriptions of new species and forms proliferated as increases in ocean commerce and voyages of exploration led to more collections and observations. The resulting taxonomic descriptions, however, were commonly based only on portions of plants that were often collected as drift. Moreover, the descriptions were usually not done by the collector but by botanists who saw only the collected portion and not entire plants growing in the field (Setchell 1932). The early efforts to describe *Macrocystis* formally are exemplified by Bauhin (1651) who produced the first written description and drawing, naming giant kelp BULBUS MARINUS CRINATUS (figure 1.6), and by Linnaeus' official description (review in Womersley 1954). Bauhin clearly did not see an entire plant growing in nature. An even more inaccurate illustration of the plant appeared in Darwin (1890). To Darwin's credit, however, he was not responsible for the illustrations in this 1890 edition of what has become known as the "Voyage of the Beagle"; most drawings, including that of giant kelp, were done by the illustrator R. T. Pritchett after Darwin died. Pritchett supposedly made the sketches "on the spot with Mr. Darwin's book by his side" (publisher's prefatory notice to the 1890 illustrated edition), but this is unlikely for the *Macrocystis* illustration, which looks like a "tribrid" of the kelps *Macrocystis* and *Lessonia*, and the fucalean *Marginariella* (figure 1.6).

The accuracy of descriptions was greatly improved by Hooker (1847) and Skottsberg (1907) (figures 1.6B and 1.6C) who spent several years in the Southern Ocean observing and collecting drift and attached plants. Both of these field botanists showed that much of the morphological variation previously used to describe species was a result of limited collections of parts of plants. They concluded that the variation previously used to discriminate between species could often be found as a result of changes in a single plant during development, within a mature plant, and among plants along environmental gradients. Skottsberg's (1907) research is particularly noteworthy as he also accurately described how giant kelp plants developed, and critically reviewed and added

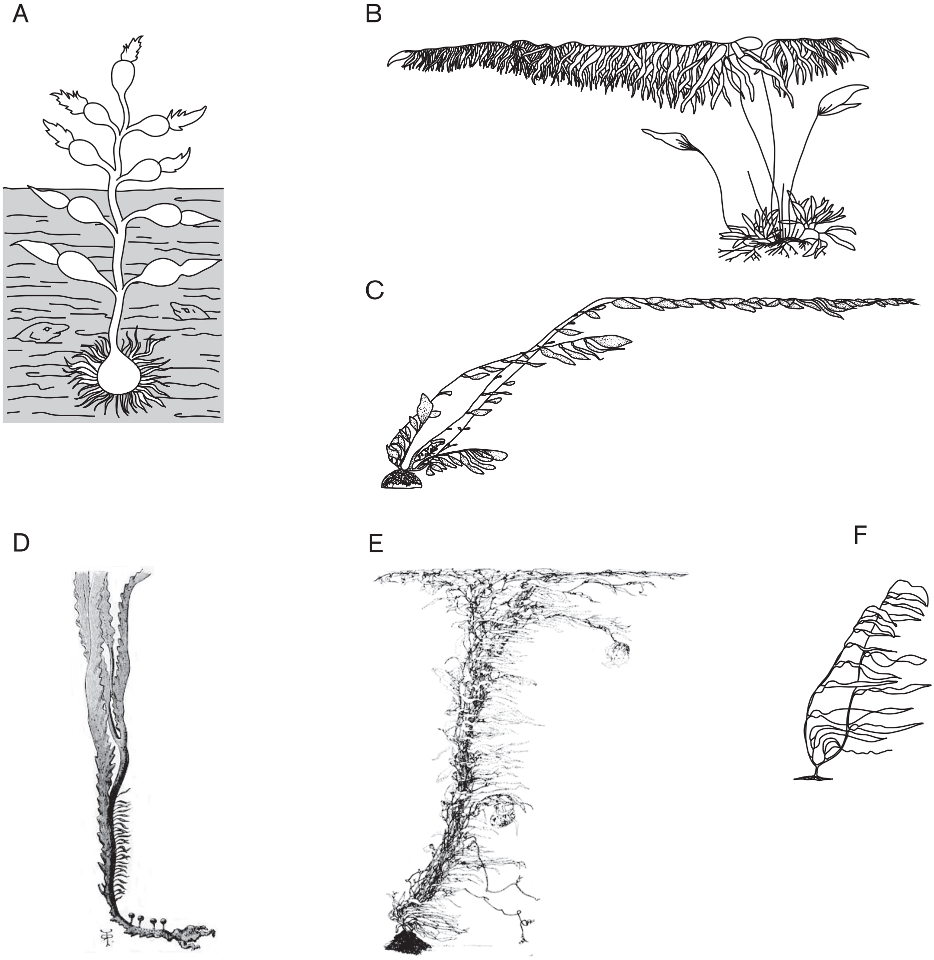


FIGURE 1.6
Evolution of giant kelp illustrations. The Skottsberg and Neushul illustrations are anatomically correct as they show all fronds arise from dichotomous branching (obscured in more fully developed plants) and that floats and blades occur from the base to the tip of vegetative fronds (see also figure 1.2).

SOURCE: Drawings from (A) redrawn from Bauhin (1651), (B) Hooker (1847) (from North 1971a and redrawn by L. G. Jones), (C) Skottsberg (1907), (D) Darwin (1890) by R. T. Pritchett, (E) and (F) Neushul (adult and juvenile forms) from Dawson et al. (1960). (B) is reprinted with permission from Schweizerbart Science Publishing (www.schweizerbart.de).

to the understanding of its internal morphology. This early research was summarized by Setchell (1932), Womersley (1954), and North (1971a). Setchell (1932) produced the first world map showing the distribution of the genus. Womersley (1954) reviewed and more completely described what were thought to be three species based on holdfast morphology, and mapped the distribution of species worldwide, a map very similar to the most recent one in figure 1.5.

As it has for many species, research and research funding increased significantly when giant kelp became economically important. With the outbreak of World War I, the U. S. government was concerned over the possible termination of potash supplies imported from Germany (Cameron 1915). Potash, composed of soluble salts of potassium, can be used as fertilizer as well as in the manufacture of gunpowder and numerous other materials. Potash was traditionally obtained by burning wood or other plant materials, extracting the soluble potash from the ashes with water and then evaporating the water. It became more readily available and cheaper with the discovery of large, subterranean deposits in Germany in 1852 (Neushul 1989). In 1912 and 1913 around 900,000 tons of potash worth about $13,000,000 (in US dollars at the time) were imported to the United States from German mines, primarily for use as fertilizer on east coast farms (Cameron 1915). In addition to growing concern over this loss of supply with the onset of war (imports from Germany were embargoed in 1916; Neushul 1989), there was also interest in new supplies for farms on the west coast, and Balch (1909) had shown that potash could be produced from giant and other large kelps in the west coast region. In response, the U. S. Department of Agriculture, Bureau of Soils, funded several studies of kelp, and particularly giant kelp, beginning in 1911. These studies included kelp distribution, abundance, and productivity, as well as harvesting and extraction methods (reviewed in Neushul 1989). Funding continued into the 1920s, stimulating the giant kelp harvesting and processing industry in southern California. The information on giant kelp biology appeared in government publications by Cameron (1915) and Brandt (1923) and was summarized along with other U. S. efforts to develop its own potash supplies by Turrentine (1926).

With the end of World War I and resumption of potash imports from German mines, it became uneconomical to produce potash and other war-related materials from giant kelp. Fortunately for the kelp harvesting industry, a relatively new product, alginate, could be extracted in quantity from giant kelp. Alginate (also referred to as algin or alginic acid) was discovered in kelp by Stanford (1883). It is a complex cell wall polysaccharide that absorbs water and forms a viscous gum that probably provides strength and flexibility to the thallus (review in Draget et al. 2005). Alginate in various chemically modified forms has numerous industrial uses, particularly in the food processing and pharmaceutical industries. Its extraction from fresh giant kelp sustained the California harvesting industry and stimulated considerable research through the 20th century. The potential for harvesting giant kelp as a source of alginate also stimulated growth, harvesting, and resource assessments in New Zealand (e.g., Moore 1943), Australia (Cribb 1954), and Canada (Scagel 1947) but given the large size of forests and their proximity to processing facilities, the alginate industry became centered in southern California. The California harvest for alginate ended in 2006 as dried kelp that was collected and processed in other countries became the major source.

The government-sponsored research as well as other studies in the early 1900s revealed the fundamentals of giant kelp biology and led to harvest management. Detailed maps were made of giant kelp distribution from Pacific Mexico to Puget Sound. Observations indicated that storms could greatly diminish stands and that they recovered in 2–3 years, and field experiments showed that fronds cut by harvesting degenerated but new fronds grew up from the base of plants to replace them (Crandall 1915). Brandt's (1923) extensive field and laboratory work is especially noteworthy. He followed the growth and survivorship of a cohort of juveniles in the low intertidal zone, confirming Skottsberg's (1907) observations on development. Brandt (1923) found it took 3 months for visible sporophytes to develop from spores in the laboratory, and an additional 7 months for juvenile sporophytes to develop into harvestable adults in the field. Like Crandall (1915), he noted that storms were a major source of adult mortality but fronds and plants also died during periods of warm, calm weather. In such conditions, portions of surface fronds turn black, a phenomenon called "black rot." The need to manage the California harvest became apparent as many harvesting companies increased the annual harvest to 400,000 wet tons by 1917 (Crandall 1918). The California Legislature gave management authority to the California Department of Fish and Wildlife (until January 1 2013, this was called the California Department of Fish and Game) which developed a numbering system for the various beds in southern California, required harvesters to purchase a license ($10.00), and collected a $0.015 fee per ton of wet kelp harvested. The method, location, and timing of harvests were also regulated to promote sustainable yields (Crandall 1918).

Other important early studies explored the relationship between giant kelp morphology and physiology and its ability to grow rapidly, and clarified its life history. With sufficient nutrients, average frond growth rates are in the order of 15 cm day^{-1} (Zimmerman and Kremer 1984), and the holdfast can grow in the shade of the canopy. These observations coupled with the presence in the stipe of sieve elements, the specialized cells morphologically similar to sieve elements in the phloem of terrestrial plants, led early investigators to speculate that giant and other kelps with similar structures could actively transport (translocate) the products of photosynthesis within the thallus (e.g., Skottsberg 1907). Sargent and Lantrip (1952) showed that translocation was necessary to support the growth of rapidly growing blades, and Parker (1965) used dye and C^{14} labeling to demonstrate that the products of photosynthesis were actively transported through the sieve elements. The life history of giant kelp was first completely determined by Levyns (1933) who showed it to be similar to other genera in the Laminariales with a large, parenchymatous sporophyte and small, filamentous, free-living male and female gametophytes. The sporophytes, the large visible structures that were the subject of almost all early investigations, are therefore only part of the plant if its entire life cycle is considered; knowledge of the biology and ecology of the gametophytes has become essential to understanding the dynamics of sporophyte populations.

The first insights into the community ecology of giant kelp forests were published by Darwin (1839) who was impressed by the diversity and abundance of associated species and by Skottsberg (1907) who observed that the holdfast "teemed with animal life." Population studies began with the research of Crandall (1915) and Brandt (1923) discussed above. These early observations and studies were necessarily made from the surface, on plants pulled from the bottom or on intertidal populations at low tide. Giant kelp forests are most luxuriously developed in the subtidal zone, however, and so progress in understanding them required a suitable air supply and a warm, flexible diving suit to enable sustained underwater work. The first in situ research in giant kelp forests was that of Andrews (1945) who used a diving helmet with air supplied through a hose from the surface to collect giant kelp holdfasts for identification and enumeration of their fauna. The difficulties of working easily, efficiently, and safely under water were essentially eliminated by the development of scuba by Cousteau and Gagnan in 1943 (Dugan 1965) and the neoprene wet suit for divers by Bradner in 1951 (Rainey 1998). A few marine science graduate students in southern California began using scuba soon after the first "Aqua-Lungs" were imported from France in 1949. The beginnings of the use of scuba to study kelp forests were largely due to the curiosity and efforts of Conrad Limbaugh (figure 1.7), a graduate student at Scripps Institution of Oceanography. He developed training procedures, offered informal training courses, and began the first institutional marine science diving program at Scripps in 1953 (Dugan 1965, Price 2008).

The use of this new technology in kelp forest ecological research was initially concentrated along the southern California mainland, stimulated by concerns over the effects of harvesting giant kelp on sport fishing and the effects of sewage discharges on the "health and sustenance" of kelp forests. Limbaugh (1955) was the first to investigate the effects of giant kelp harvesting on species other than kelp, providing information on habitat utilization and feeding habits of numerous kelp forest fishes, and the distribution of common invertebrates. His research included comparing fish assemblages in harvested and nonharvested stands, the first such field experiment in a kelp forest. Aleem (1956) used scuba to provide the first quantitative description of kelp forest zonation and the standing crop of algae and invertebrates. The studies of Limbaugh and Aleem were followed by those of Limbaugh's colleague Wheeler J. North (figure 1.7). North's investigations were focused on kelp harvesting and sewage discharge effects, and done primarily from the perspective of the effects on *Macrocystis* itself (North 1964, North and Hubbs 1968). North's early observations of sea urchin grazing in southern California kelp forests and his suggestion that this might be caused by overharvesting of sea otters (North and Pearse 1970) stimulated much additional research and controversy over the effects of sea urchins and their predators on kelp population dynamics (review in Foster and Schiel 2010). Michael Neushul (figure 1.7), collaborating with North as well as the macroalgal taxonomist E. Y. Dawson, expanded on Aleem's (1956) zonation studies with surveys of macroalgal distribution in many giant kelp forests in southern California and northern Baja California (e.g., Dawson et al. 1960). Neushul also did innovative field and laboratory experiments to examine giant kelp growth and reproduction (Neushul 1963, Neushul and Haxo 1963). These early studies provided most of the basic descriptive and life history information about kelp forests and their associated organisms, and the phenomena that affect their abundance and distribution in California (summarized in North 1971a).

FIGURE 1.7

Some pioneers of giant kelp research. Top (left to right): Johann Bauhin, Joseph Dalton Hooker, and Carl Skottsberg. Bottom (left to right): Conrad Limbaugh, Wheeler J. North, and Michael Neushul.

SOURCE: Credits: Bauhin (1651); Hooker (Henry Joseph Whitlock © National Portrait Gallery, London); Skottsberg (1911). Limbaugh and North photos are from Scripps Institution of Oceanography Archives, UC San Diego; Neushul photo by M. S. Foster.

In recent decades, *Macrocystis* research has expanded geographically and in scope. Studies in Canada (e.g., Druehl and Breen 1986), Chile (review in Graham et al. "Global ecology" 2007), New Zealand (Schiel 1990, Schiel et al. 1995, Schiel and Hickford 2001), the Subantarctic Islands (e.g., Beckley and Branch 1992), Australia (e.g., Ling et al. 2009), and Argentina (Barrales and Lobban 1975) have greatly improved our appreciation of the global differences in giant kelp communities. Furthermore, long-term programs, such as those of Paul Dayton, Mia Tegner, and colleagues around Point Loma (San Diego), which have been running since the 1970s, and the Santa Barbara Coastal LTER (long-term ecological research network of the U. S. National Science Foundation, begun in 2000) with the work of Principal Investigator Dan Reed and colleagues, have provided considerable new insights into temporal dynamics, production, dispersal, connectivity, and interactions with the physical environment of kelp forests.