Chapter 17
Floating Seaweeds and Their Communities

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17.1 Introduction

Floating seaweeds have fascinated sailors and naturalists since the first ships sailed across the oceans, where they discovered immense rafts of seaweeds far from shore. Christopher Columbus was one of the first who documented dense aggregations of floating algae. In September 1492, his crew encountered masses of floating seaweed as they were approaching the Bahamas: “They saw so much weed that the sea appeared to be covered with it. . ..and there was a great deal of weed and they found crabs in it” (Farlow 1914).

Floating *Sargassum natans* and *S. fluitans* from the Sargasso Sea and especially their specifically adapted fauna are remarkable biological communities. Full-grown algae that form dense masses without ever having been attached to the seafloor pass their entire floating life cycle via the propagation of vegetative fragments (Parr 1939). While floating algal populations in other seas appear to originate from benthic source populations, the size of algal rafts and the length of their ocean voyages equal or even surpass that of *S. natans* and *S. fluitans*.

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Centuries after Columbus' voyage, contemporary marine scientists have reported floating seaweeds from all major oceans (Ohno 1984; Kingsford 1992; Helmuth et al. 1994; Ingólfsson 1998; Hobday 2000a; Hirata et al. 2001; Macaya et al. 2005; Vandendriessche et al. 2006; Komatsu et al. 2008; Hinojosa et al. 2010). Recent studies confirm that floating algae can cross large ocean basins, facilitating the colonization of new habitats on remote shores by the algae themselves but also by organisms living associated with floating algae (Fraser et al. 2009, 2011; Macaya and Zuccarello 2010; Nikula et al. 2010). Accordingly, these authors emphasized the importance of dispersal of organisms via these floating islands.

There is a wide variety of positively buoyant seaweeds in the oceans that become detached by breakage of stipes, thallus fragmentation, erosion of holdfasts, storms, or grazing activities. Once detached, floating seaweeds continue to grow if environmental conditions are optimal, and they form habitat for many associated organisms. Also these algae are known to travel considerable distances at the mercy of winds and currents, having the potential to release spores or gametes at a new site and thereby connecting distant populations (Fraser et al. 2009). In order to understand the fate of floating seaweeds it is crucial to address a set of questions. Where can we regularly find floating algae and where do they come from? How do abiotic and biotic factors affect the persistence of floating algae at the sea surface? How can floating algae acclimate or withstand sea surface conditions? Which organisms are traveling with them and how can they affect raft viability? Answering these questions will help to understand the role of floating algae as dispersal agents in the world's oceans.

17.2 Spatial and Seasonal Distribution of Floating Seaweeds

A wide diversity of seaweeds can be found floating in the world's oceans, where they persist at the sea surface thanks to the presence of gas-filled tissues or pneumatocysts (Fig. 17.1). The dominant floating seaweeds in the world's oceans are brown algae belonging to the genera *Macrocystis*, *Fucus*, *Sargassum*, *Ascophyllum, Durvillaea, Carpophyllum, Phyllospora,* and *Cystophora*. Some red and green algae have also been reported floating, albeit with a more limited floating potential than brown algae (Thiel and Gutow 2005a; Gagnon et al. 2011). Besides a few entirely pelagic species such as *Sargassum natans* and *S. fluitans*, most floating algae grow in benthic habitats during their earlier life stages and can vary widely in size after detachment, ranging from a few centimeters to tens of meters. Floating seaweeds can aggregate at the sea surface and form large rafts of many individuals with biomasses of up to 300 kg wet weight per seaweed patch (e.g., Senta 1962 for the Japanese coast) or more (Mitchell and Hunter 1970 for the southern Californian coast and Baja California).

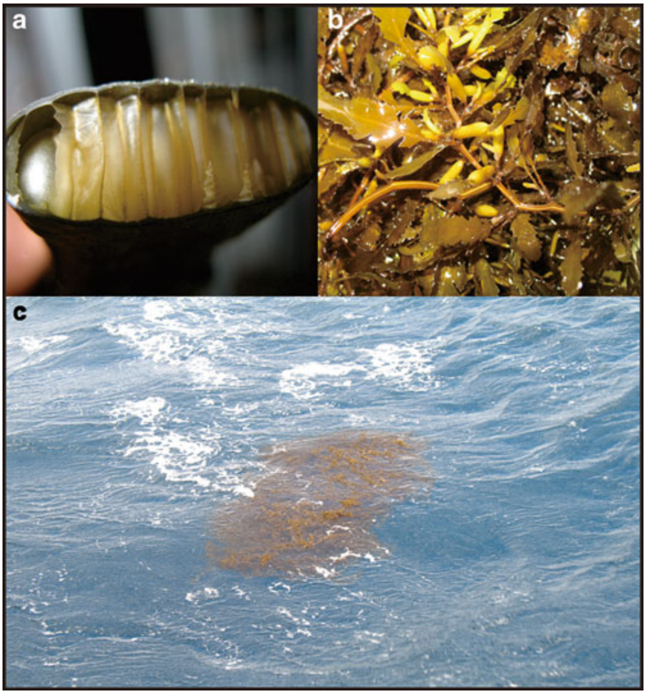

Fig. 17.1 (**a**) Cross section through a thallus of *Durvillaea antarctica* showing the gas-filled honeycomb structure; (**b**) vesicles of *Sargassum horneri*, providing positive buoyancy to the algae; and (**c**) raft of *S. horneri* floating in the eastern East China Sea

17.2.1 Global Distribution Patterns of Floating Seaweeds

The presence of floating algae at the sea surface strongly depends on their supply from benthic source populations. Most reports of floating macroalgae come from mid and high latitudes in both hemispheres (Kingsford 1992; Helmuth et al. 1994; Hobday 2000a; Macaya et al. 2005; Komatsu et al. 2008; Hinojosa et al. 2010; Thiel et al. 2011) (Fig. 17.2), where extensive benthic populations provide abundant supply (Lüning 1990; Graham et al. 2007). For instance, in the northern hemisphere algal rafts can be found in the NE Pacific where extensive subtidal kelp forests along the Pacific coast of North America nourish abundant floating populations of *Macrocystis pyrifera* (Kingsford 1995; Hobday 2000a). In the NW Pacific a diverse *Sargassum* community is floating in coastal waters around Japan (Ohno 1984; Hirata et al. 2001). In the N Atlantic pelagic *S. natans* and *S. fluitans* occur in the Gulf of Mexico, the Gulf Stream, and in the Sargasso Sea (Parr 1939) while floating fronds of *Ascophyllum nodosum* and *Fucus vesiculosus* are common along the northern N Atlantic >45°N (Tully and Ó Céidigh 1986; Ingólfsson 1998; Vandendriessche et al. 2006; Muhlin et al. 2008; Thiel et al. 2011).

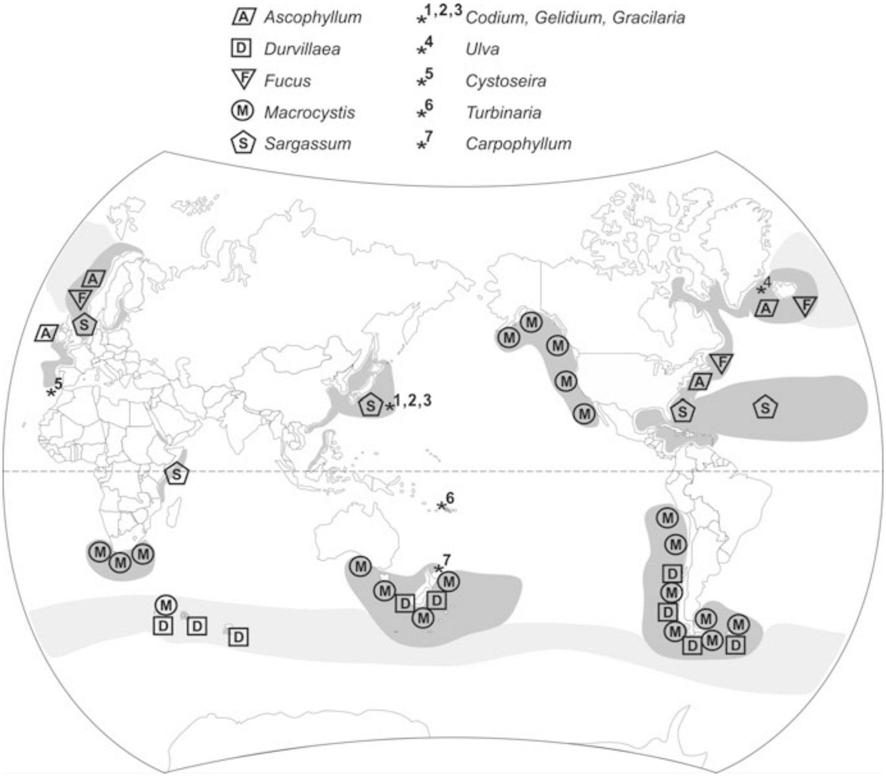

Fig. 17.2 Distribution of the most common genera of benthic algae (*indicated with symbols and letters*) that are positively buoyant, as well as examples of a few benthic genera (*indicated with asterisks and numbers*) that are less commonly found floating in the world's oceans. *Shadings* indicate areas where floating algae have been reported abundantly

M. pyrifera and *Durvillaea antarctica* are the most common floating seaweeds in the southern hemisphere. They occur in the SE Pacific along the Chilean coast (Macaya et al. 2005; Hinojosa et al. 2007, 2011), around Tasmania and New Zealand (Edgar 1987; Kingsford 1992) and throughout the entire West Wind Drift where floating sporophytes connect the algal populations of the sub-Antarctic islands (Smith 2002; Fraser et al. 2009). Also the Agulhas Bank region off South Africa "literally swarms with *Macrocystis*" (Hooker 1847). Whereas *Macrocystis* and *Durvillaea* are widespread throughout cold temperate waters of the southern hemisphere, other floating seaweeds have a more restricted distribution but may become locally very abundant. For example, high densities of floating *Carpophyllum* spp. and *Cystophora* spp. can be found in waters around New Zealand (Kingsford 1993) and buoyant *Turbinaria ornata* are common among the Polynesian islands (Stewart 2008). Although floating seaweeds can bridge large oceanic distances in subpolar regions, the warm waters of the tropics and the subtropics appear to be an impenetrable dispersal barrier mostly preventing the exchange of floating algae between the two hemispheres.

17.2.2 Regional Aggregations of Floating Seaweeds

Complex interactions between winds and mesoscale oceanographic features such as fronts, eddies, and currents determine the spatial distribution of algae at the sea surface. Accordingly, abundances of floating seaweeds vary substantially on a regional scale and are often highly unpredictable (Kingsford 1992; Ingólfsson 1998). For example, Kingsford and Choat (1986) observed consistently higher densities of floating algae inside than outside transient surface slicks, which were generated by tidally forced internal waves. In other regions, floating algae accumulate along fronts (Kingsford 1995) where single sporophytes may entangle at the sea surface to form large floating mats. Franke et al. (1999) reported that during calm summer conditions dense aggregations of floating algae form at boundary zones between tidal currents of different speeds and directions around the island of Helgoland (North Sea). Hinojosa et al. (2010) could show for the fjords of southern Chile that floating seaweeds are aggregated in an estuarine front in the large channel openings by an interaction of wind and the surface outflow of estuarine waters (Fig. 17.3). These regions are suggested to act as retention zones, which receive and accumulate floating seaweeds. Due to the aggregation of floating algae, other pelagic organisms, and organic matter, these retention areas are considered centers

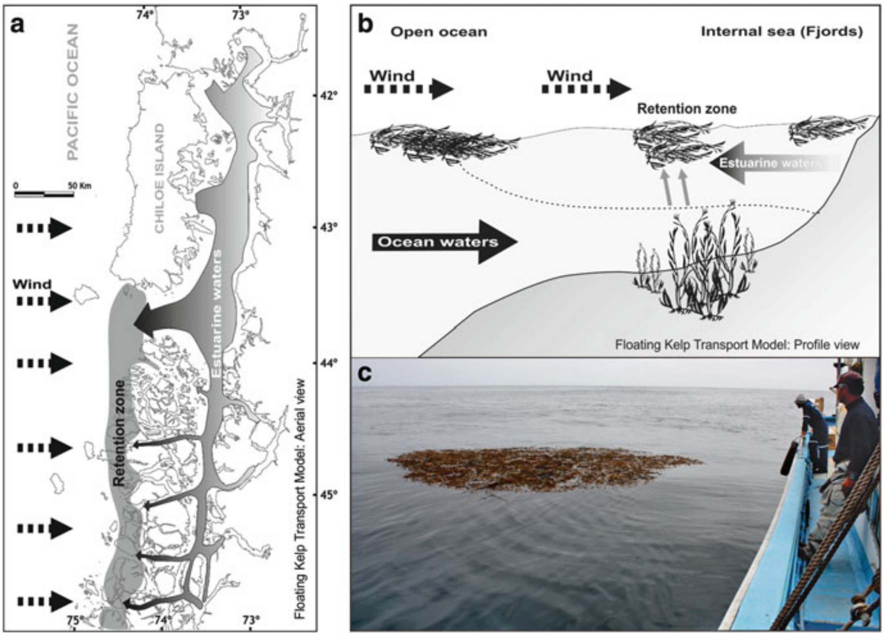

Fig. 17.3 Retention zones for floating seaweeds formed by winds, currents, and estuarine influence in the fjord regions of southern Chile, in (**a**) aerial view and (**b**) profile view; figure modified after Hinojosa et al. (2010). (**c**) Floating patch of *Macrocystis pyrifera*; image courtesy of Iván Hinojosa

of high biological activity, where decomposers that are associated with the floating algae recycle organic remains into nutrients and other compounds (Thiel and Gutow 2005b).

Floating seaweeds are often more abundant in coastal waters than in the open ocean (Segawa et al. 1961; Kingsford 1992; Ingólfsson 1995; Hobday 2000b). High nearshore densities of floating algae are primarily due to the proximity to coastal source populations. Additionally, floating algae are known to accumulate in coastal areas with complex current conditions and frontal zones (Segawa et al. 1961). Harrold and Lisin (1989) tracked floating *M. pyrifera* equipped with radio transmitters in coastal waters of California. They could show that the majority of algal rafts are deposited on beaches soon after detachment while others become entangled with benthic sporophytes in coastal kelp forests (see also Dayton et al. 1984; Graham et al. 1997). The onshore transport of floating *M. pyrifera* in coastal waters of California was confirmed by Hernández-Carmona et al. (2006) (Fig. 17.4). Results from experiments with artificial drifters revealed that directional net transport of floating algae in coastal systems is mainly the result of prevailing winds that interact with surface currents (Tapia et al. 2004). During periods of low wind, no substantial transport of the drifters by currents alone could be detected (Fig. 17.4). Apparently, only a relatively small fraction of detached seaweeds escapes to offshore waters where they might enter larger oceanic currents.

In offshore regions conspicuous amounts of seaweeds have repeatedly been observed in surface eddies that develop above seamounts in the NE Pacific (Parker and Tunnycliffe 1994). Additionally, floating algae often accumulate in the convergence zones of wind-induced Langmuir circulations (Faller and Woodcock 1964). In the N Atlantic, pelagic *Sargassum* has been observed in such windrows extending over tens to hundreds of miles (Carr 1986). Drift lines of floating *Sargassum* are transient structures that disintegrate when wind exceeds a certain threshold speed (Marmorino et al. 2011). Johnson and Richardson (1977) suggested that the downwelling of surface waters in the zones of convergence might carry *Sargassum* below a critical depth where the thalli lose buoyancy and finally sink to the seafloor, thereby exporting biomass from the surface to the deep sea benthos (Schoener and Rowe 1970).

17.2.3 Seasonal Patterns of Floating Populations

While large quantities of seaweeds appear during some periods of the year, floating algae can virtually disappear at other times. For instance, along the coast of Japan high densities of floating individuals of the annual *Sargassum horneri* can be found throughout spring and summer when the algae shed off most of their thalli during their reproductive season (Yoshida 1963; Ohno 1984; Hirata et al. 2001). Similar observations have been made by Kingsford (1992) for floating *S. sinclairii* from coastal waters of New Zealand, indicating that the appearance of large quantities of *Sargassum* is driven by their seasonal growth cycles. Additionally, the invasive

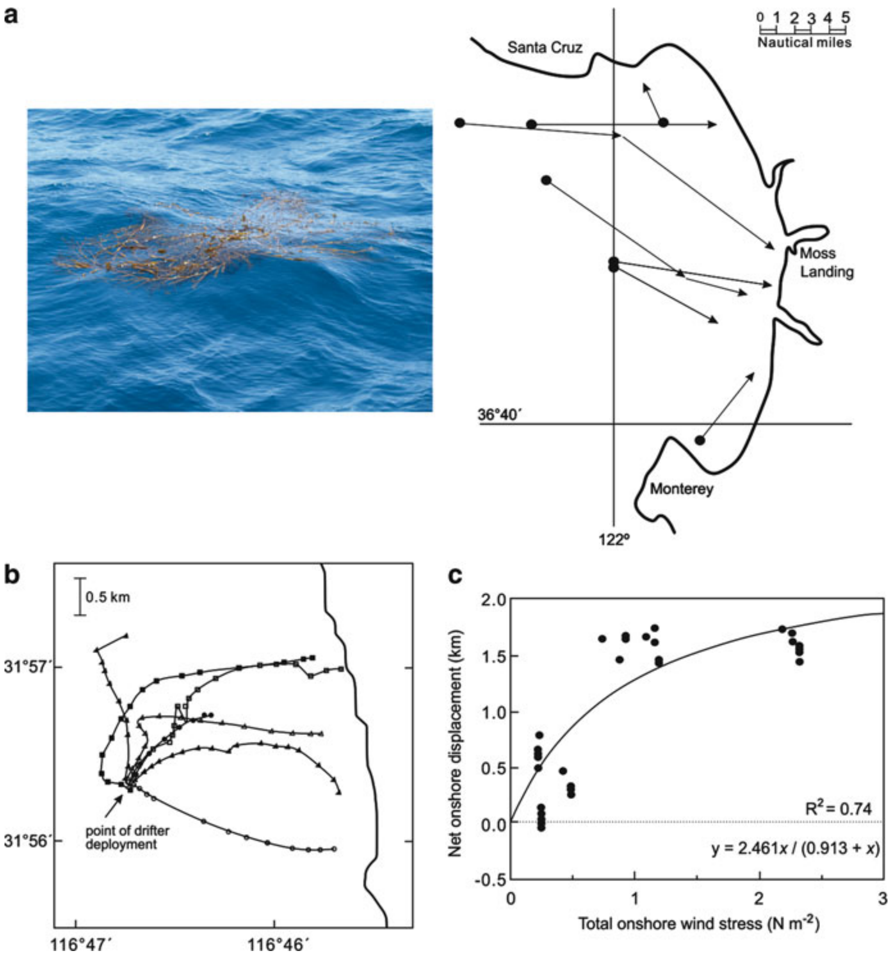

Fig. 17.4 Similar trajectories of (**a**) floating *Macrocystis pyrifera* and (**b**) artificial drifters towards the shore in coastal waters of California and Baja California, respectively. (**c**) Drift direction and velocity of the artificial drifters correlated with prevailing wind conditions. Figures modified after Hernández-Carmona et al. (2006) and Tapia et al. (2004)

species *S. muticum,* which originates from Japan, has been reported floating abundantly in May in the North Sea (Vandendriessche et al. 2006); thallus fragmentation and rafting dispersal may have facilitated the rapid spread of this species along the coasts of NW Europe (Rueness 1989; Harries et al. 2007). The holopelagic *Sargassum* species from the Gulf of Mexico seemed to have similar seasonal growth cycles, with highest amounts during March and June (Gower and King 2008). Seasonal variations of floating populations have also been revealed for perennial algae such as *M. pyrifera* and *D. antarctica* in southern Chile, with highest densities being found during austral spring (Hinojosa et al. 2010). Floating seaweeds can also reach high abundances after storms (Kingsford 1992), while during El Niño events, high water temperature and nutrient limitation can cause the disappearance of benthic seaweeds (Dayton et al. 1999), thus also leading to the elimination of the floating populations.

17.3 Ecophysiology of Floating Seaweeds

Growth and reproduction of floating seaweeds depend (as for their benthic counterparts) on a variety of abiotic and biotic conditions. At the sea surface, factors such as grazing activity, epibiont overgrowth, high water temperature, and solar radiation have been repeatedly inferred to have a negative effect on growth and health status of floating seaweeds. Also, it has been discussed that nutrient limitation might affect physiological functioning and growth of floating algae (Edgar 1987). While nutrient-limited open ocean waters suppress the physiological functioning of floating *S. natans* (Lapointe 1995), algae that accumulate in frontal systems where organic matter is efficiently recycled are thought to have sufficient nutrients to sustain algal growth (Thiel and Gutow 2005b).

Abrupt changes in environmental factors, as experienced especially by floating algae, can impact their photosynthetic apparatus, which is most susceptible to damage under stressful conditions. Stressed algae invest energy to adjust and maintain photosynthetic activity. However, this energy investment comes at the expense of algal growth. Consequently, algae respond with variable growth to changing environmental conditions because growth integrates all physiological costs and gains. Growth can be directly related to the overall health status of the algae and thus to their persistence at the sea surface (Fig. 17.5).

17.3.1 Light

At the sea surface floating algae are often exposed to intense visible (400–700 nm) and ultraviolet radiation (280–400 nm), which may induce photoprotective processes. In large outdoor mesocosm studies conducted along the Chilean coast, *M. pyrifera* reacted to high solar irradiance by lowering their pigment contents and by energy dissipation via heat (Rothäusler et al. 2011a, b). Similar physiological responses were observed for the holopelagic *S. natans,* floating in tropical waters of the Gulf of Mexico (Schofield et al. 1998). These processes are relevant because they permit algae to tolerate the stressful conditions of extreme irradiance and even to continue growing at the sea surface.

While the positively buoyant *M. pyrifera*, of which the attached sporophytes grow throughout the entire water column (up to 40 m in length), can efficiently acclimate to a broad range of irradiance prevailing along the Chilean Pacific coast (Rothäusler et al. 2011a, b), negatively buoyant seaweeds showed strong

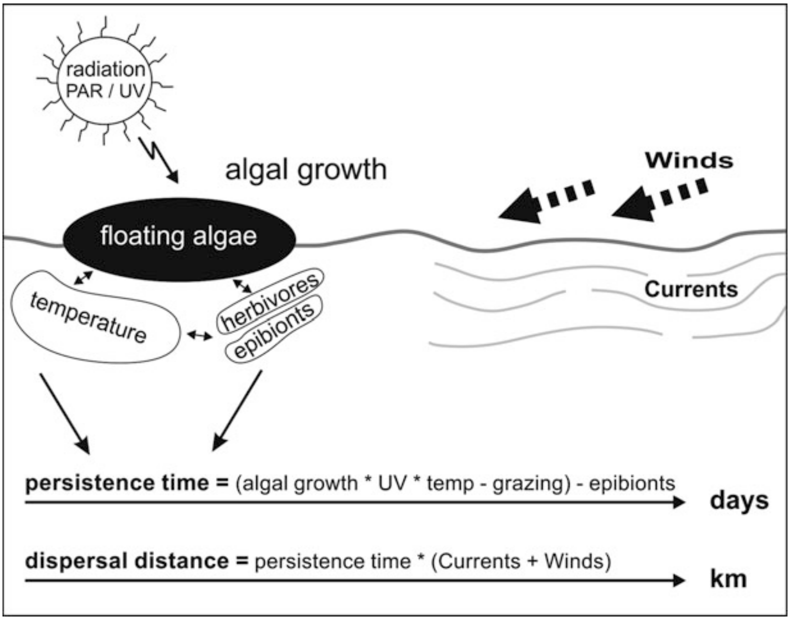

Fig. 17.5 Conceptual figure of the main abiotic and biotic factors affecting the growth of floating algae and thus their persistence at the sea surface

photoinhibition when transplanted close to the sea surface (Karsten et al. 2001). At low latitudes these photoacclimation responses were costly for *M. pyrifera*, which was reflected in their overall diminished growth responses, implying lower persistence due to combined effects of high water temperatures and high light conditions (Rothäusler et al. 2011a). While short-term exposure to UVA and UVB radiation induces the production of UV-absorbing phlorotannins in blades of benthic *M. pyrifera* (Swanson and Druehl 2002), at present it is not known whether floating *M. pyrifera* can also increase the phlorotannin content in response to elevated UV exposure as a protection of their photosynthetic tissues.

17.3.2 Temperature

Temperature is one of the most important factors controlling growth and persistence of floating seaweeds (Hobday 2000a; Rothäusler et al. 2009). For instance, algae from temperate waters lose biomass (Fig. 17.6), and thus floating capacity, when experiencing thermal stress on their floating voyages into warmer oceanic regions. Hobday (2000a) showed for the temperate *M. pyrifera* from southern California that the aging rate of kelp blades was low at surrounding water temperatures <20°C but substantially increased above this threshold. Recent

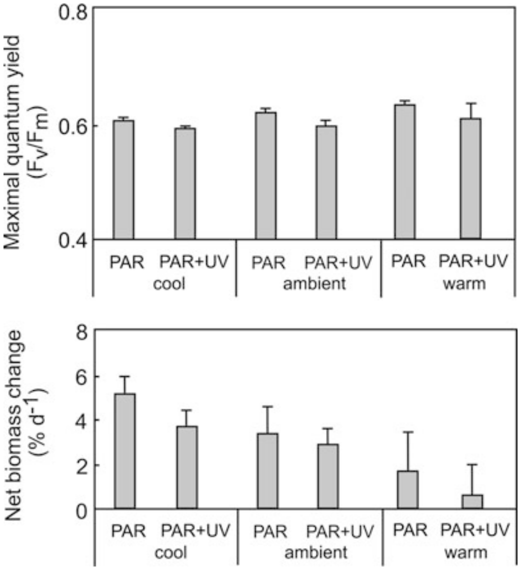

Fig. 17.6 Photosynthetic performance and growth of floating *Macrocystis pyrifera* maintained under different temperature and light conditions in outdoor mesocosm experiments. Figure modified after Rothäusler et al. (2011c)

studies in outdoor mesocosms confirmed that floating individuals of *M. pyrifera* lost biomass at water temperatures >20°C. A rapid disintegration of the algal thalli was observed at 24°C, where all algae sank after 5 days, even in treatments without grazers (Rothäusler et al. 2009). Similarly, floating persistence of temperate *A. nodosum* and *F. vesiculosus* from the southwestern North Sea was reduced at water temperatures >15°C due to high losses of biomass (Vandendriessche et al. 2007a). At equatorial latitudes in the Atlantic, John (1974) documented floating individuals of *A. nodosum* that were small (<0.5 m long) and not particularly robust. Possibly, high water temperatures are responsible for the rapid demise of floating algae in these oceanic regions. Besides temperature, also desiccation may affect the physiological functioning and thus the disintegration of algae, but this effect probably depends on the degree of buoyancy of each algal species (Thiel et al. unpublished).

Suboptimal water temperatures can also affect the reproductive activity of floating algae (Macaya et al. 2005; Rothäusler et al. 2009) (Fig. 17.7). Along the Chilean Pacific coast, in situ sampling and mesocosm experiments with floating *M. pyrifera* confirmed the absence of reproductive tissues (sporophylls) at low latitudes, while at higher latitudes many rafts had fertile sporophylls (Macaya et al. 2005). The authors inferred that unfavorable sea surface conditions, such as water temperatures >20°C, at low latitudes are responsible for the observed pattern. Overall, results imply that low water temperatures (and possibly also winter conditions) favor the persistence and reproductive success of temperate species at the sea surface, which consequently have higher potential for long-distance dispersal.

Contrary to meropelagic rafts, the tropical holopelagic *S. natans* and *S. fluitans* in the Sargasso Sea have growth optima and thus an optimal persistence at

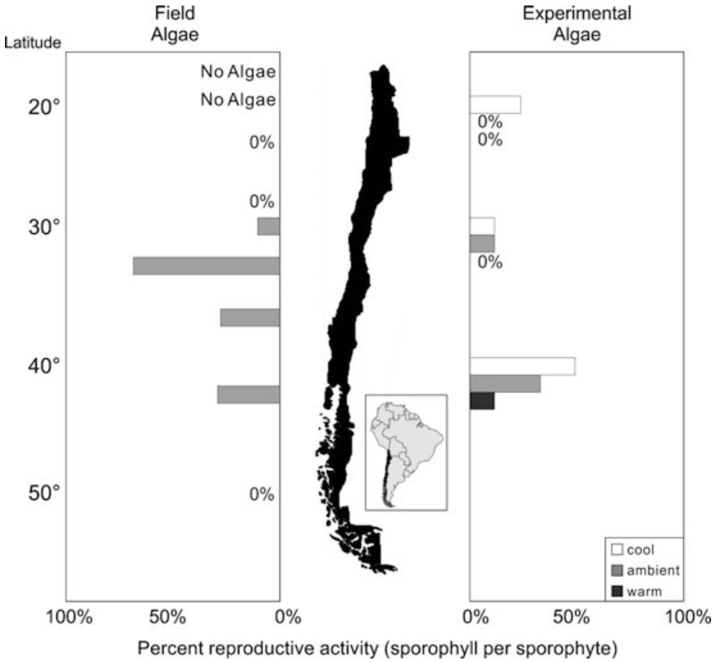

Fig. 17.7 Percent reproductively active sporophytes of freely floating *M. pyrifera* and in outdoor mesocosm experiments simulating the temperature gradient (ambient, cool, warm) along the Chilean Pacific coast. Figures modified after Macaya et al. (2005) and Rothäusler et al. (2009), respectively

temperatures between 18°C and 30°C (Hanisak and Samuel 1987). These algae, commonly known as gulfweed, appear to have evolved efficient protection mechanisms to endure surface levels of high temperature and irradiance (Schofield et al. 1998 for *S. natans*), which is in accordance with their distributional ranges in the tropical and subtropical N Atlantic. No growth was revealed for both species at water temperatures around 12°C (Hanisak and Samuel 1987).

17.3.3 Herbivory

Floating seaweeds are commonly inhabited by dense populations of mobile mesoherbivores such as amphipods and isopods, which can affect algal persistence by removing photosynthetic tissue and thereby weakening the ability to fix carbon (Gutow 2003; Thiel and Gutow 2005b; Vandendriessche et al. 2007a; Rothäusler et al. 2009). These grazers mainly feed on vegetative blades and it was shown for floating individuals of *M. pyrifera* in an outdoor mesocosm study that high densities of a herbivorous amphipod led to a reduction in pigment contents (e.g., by the

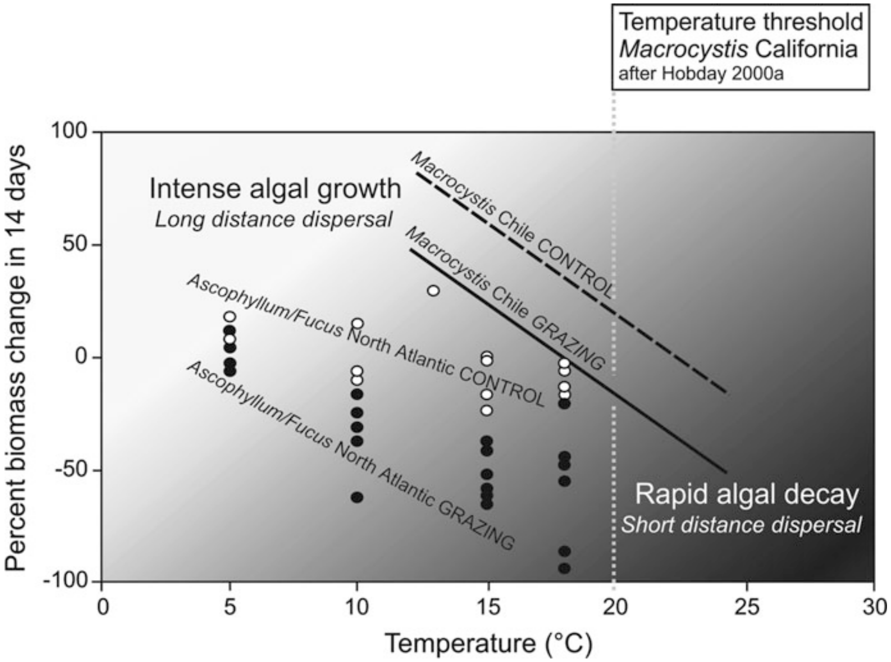

Fig. 17.8 Conceptual model of the influence of the combined effects of temperature and grazing (CONTROL versus GRAZING) on percent biomass change of floating algae during 14 days; data for *Ascophyllum nodosum* and *Fucus vesiculosus* were taken from Vandendriessche et al. (2007a), and data for *Macrocystis pyrifera* from Rothäusler et al. (2009)

allocation of N to the synthesis of other compounds) and algal growth at mid latitudes (Rothäusler et al. 2009, 2011b), while under moderate grazing pressure algae could compensate tissue loss by enhanced growth (Cerda et al. 2009). Grazing by isopods also provoked fast sinking of *A. nodosum* and *F. vesiculosus* but it seemed that the destructive effects of the grazers depended on water temperature and the availability of alternative food resources (Gutow 2003; Vandendriessche et al. 2007a). The negative effect of isopod grazing on the floating potential of the algae was enhanced by high water temperatures, which resulted in a reduced persistence of the brown algae at the sea surface (Vandendriessche et al. 2007a). Contrarily, in cooler waters (<15°C) grazing seemed to play only a minor role for the survival of floating algae because they can compensate grazer-induced tissue losses via growth (Vandendriessche et al. 2007a; Rothäusler et al. 2009) (Fig. 17.8). This might also explain why Ingólfsson (1998) observed no signs of decay in *A. nodosum* after >40 days of floating in cold Icelandic waters.

17.3.4 Epibiosis

Floating seaweeds are commonly colonized by larvae of sessile epibionts such as bryozoans and lepadid barnacles (Thiel and Gutow 2005b), which can influence algal growth by covering photosynthetic tissues. At mid latitudes in the Humboldt Current System, it was observed that bryozoan cover of *M. pyrifera* increased with distance from potential source populations and that physiological parameters (e.g., maximal quantum yield and overall photosynthetic efficiency) declined with increasing bryozoan size (Rothäusler et al. 2011d). Small benthic algae can maintain high photosynthetic activity under bryozoan cover by increasing the pigment content (Muñoz et al. 1998). However, such shade adaptation was not observed in benthic and floating *M. pyrifera* (Hurd et al. 2000; Hepburn et al. 2006; Rothäusler et al. 2011d). While dense epibiont cover can increase the specific density of floating algae and even cause sinking, uncalcified young bryozoan colonies might have a positive effect on algal tissue by shielding them against high solar radiation. Algae may also benefit from encrusting bryozoans through the provision of carbon dioxide and ammonium released directly from epibionts onto the algal tissue (Muñoz et al. 1998; Hurd et al. 1994, 2000), but these advantageous effects probably depend on the degree of colonization. In general, over long floating times, continuous epibiont growth and grazing pressure negatively affect algal persistence at the sea surface. However, depending on the presence of alternative food sources and the colonization progress, not all organisms associated with floating algae (e.g., detritus feeders, scavengers, and predators) may have the same destructive effects on their rafts.

17.4 Rafting Communities

Floating seaweeds carry with them a wide diversity of organisms (Thiel and Gutow 2005b and references therein). The composition of the rafting community and the abundance of individual species can be highly variable in time and space, and successional changes are probably related to travel time of the floating algae, their distance from the shore, competition, and predation.

Not all organisms are equally adapted to the rafting life style because not all of them can efficiently hold onto floating algae. Large invertebrates such as sea urchins, crustaceans, and gastropods immediately drop off when detached algae float to the sea surface. Also small organisms such as the boring peracarid isopods *Limnoria* spp. quickly left their burrows after kelp holdfasts were detached from benthic substrata (Miranda and Thiel 2008). Similarly, Gutow et al. (2009) showed that the densities of some peracarid crustaceans dropped immediately after algae became dislodged. Some species, such as ampithoid amphipods that build nest-like domiciles on algal blades (e.g., *Peramphithoe femorata* Cerda et al. 2010), may persist and even reproduce after detachment, resulting in a population increase during rafting journeys (see also Thiel 2003). Even though these motile organisms can stay and proliferate on algal rafts, other effective rafters are sessile organisms such as hydrozoans and bryozoans, which can form dense colonies on algal blades where they overgrow each other when competing for space (Thiel and Gutow 2005b and references therein). Some of these sessile epibionts colonize the rafting substrata at a later stage via the propagules from the water column.

The most common marine invertebrates on floating algae are peracarid crustaceans, which incubate their embryos in a marsupium, from which fully developed juveniles emerge. Direct development has been considered an important life history trait for rafters, because offspring can immediately recruit onto the algae (Ingólfsson 1998; Gutow 2003; Thiel and Haye 2006; Vandendriessche et al. 2006). Thus, their populations might not only persist but also increase over time. This mode of local recruitment is advantageous for rafters, since local populations on the algae can be maintained, even when the duration of the rafting journey exceeds the lifetime of the species (Thiel and Gutow 2005b). Direct development also favors successful colonization of new habitats.

17.4.1 Successional Changes of Epibiont Communities on Algal Rafts

Rafting communities can experience substantial changes during their journey. These changes are immediately initiated with the detachment of the algae from the benthic substratum (Kingsford and Choat 1985; Miranda and Thiel 2008; Gutow et al. 2009) and continue throughout the entire floating period. For instance, Helmuth et al. (1994) reported that with distance from their benthic source populations, kelp rafts had more sessile epibionts. Vásquez (1993), who tethered kelp holdfasts to a main line, demonstrated that densities of associated peracarid crustaceans increased towards the end of the experiment. In natural algal rafts around Iceland, Ingólfsson (1995) observed that the diversity of associated organisms decreased with increasing distance from source regions.

These temporal changes of rafting communities can be influenced by species interactions. Floating seaweeds attract fish (Kingsford 1992, 1995) and seabirds (Vandendriessche et al. 2007b), which prey upon associated organisms, thereby suppressing the populations of these organisms (including small grazers) on the rafts. In addition, rafters may compete with each other for food and space, which also affects species succession during a long voyage (Tsikhon-Lukanina et al. 2001).

17.5 Rafting Dispersal of Seaweeds and Associated Organisms

The dispersal of algae and their associated organisms strongly depends on the persistence of the rafts at the sea surface and on the capability of the organisms to withstand the rafting conditions. Under favorable conditions, algae can continuously grow and thus provide a long-lasting food source for herbivorous passengers. The floating thalli of, e.g., *M. pyrifera* even continue to reproduce while afloat, thereby acting as successful spore carriers, dispersing over hundreds of kilometers (Macaya et al. 2005; Hernández-Carmona et al. 2006). Thus, floating rafts facilitate population connectivity and expansion of geographic ranges of the floating algae themselves and of associated organisms. Winds and ocean currents mainly determine the floating directions, velocities, and distances that algae can cover.

17.5.1 Floating Velocities and Trajectories

Driven by the major oceanic currents, floating algae are transported across the world's oceans. While ocean currents determine large-scale algal movements, strong winds largely influence algal dispersal on a regional scale. Overall both forces in combination determine algal trajectories and velocities (Thiel and Gutow 2005a and references therein).

Following patches of *M. pyrifera*, Harrold and Lisin (1989) showed that rafts within Monterey Bay (California) occasionally move very slowly and at other times can advance very fast (0.2–2.3 km h^{-1}). Within the southern California Bight a similar trend was observed by Hobday (2000b) for satellite-tracked drifters. Very high velocities of up to 0.8 km h^{-1} have also been reported for algae floating in southern Japan (Segawa et al. 1962; Yoshida 1963), which are probably related to the prevailing current velocities (Thiel and Gutow 2005a).

Trajectories of floating algae and their associated organisms closely follow the directions of the major current systems (Thiel and Gutow 2005a). For instance, Helmuth et al. (1994), who sampled *M. pyrifera* rafts, underlined the importance of the West Wind Drift in the Southern Ocean in transporting algae in eastward direction between South America and sub-Antarctic islands (see also Chap. 14 by Huovinen and Gómez). A similar route in the West Wind Drift had been reported for *D. antarctica* (Smith 2002). Along the Chilean Pacific coast, within the Humboldt Current, floating seaweeds are generally displaced towards the north (Macaya et al. 2005) but southward movements are also observed occasionally. In the N Pacific, Hobday (2000b) underlined that floating *M. pyrifera* are transported in southward direction within the Californian Current. These observations confirm that algal rafts together with their passengers are transported with the main oceanic currents, both across vast areas of open ocean and over extensive distances in alongshore direction.

17.5.2 Connectivity of Populations

There is increasing evidence from molecular studies confirming population connectivity of floating seaweeds and their associated fauna (e.g., Thiel and Haye 2006 and references therein; Muhlin et al. 2008; Fraser et al. 2009; Coleman and Kelaher 2009; Nikula et al. 2010; Coyer et al. 2011; Buchanan and Zuccarello 2012). Bull kelp *D. antarctica* showed high genetic homogeneity among populations from different sub-Antarctic islands (Fraser et al. 2009) (Fig. 17.9). Similarly, results by Macaya and Zuccarello (2010) showed that a single haplotype of *M. pyrifera* dominated the populations from sub-Antarctic islands that are separated by thousands of kilometers (see green dots in Fig. 17.9). Results of both studies show strong evidence that *D. antarctica* and *M. pyrifera* can occasionally be transported across some of the world's largest gaps of open ocean (Fig. 17.9). Efficient dispersal of these floating kelps and of associated organisms is facilitated by the West Wind Drift, the strong surface current moving steadily in eastward direction (Waters 2008). Rafting on seaweeds can thus transport epifaunal organisms to distant shores as confirmed by, e.g., Nikula et al. (2010) for two peracarid crustaceans inhabiting the holdfasts of *D. antarctica*.

Algal rafting also contributes strongly to population connectivity over smaller spatial scales. The fucoid alga *Phyllospora comosa* from eastern Australia showed gene flow between populations that were separated by a 70-km distributional gap (Coleman and Kelaher 2009). Similarly, Muhlin et al. (2008) confirmed connectivity between *Fucus vesiculosus* populations from two adjacent peninsulas in the Gulf of Maine. Results suggest that floating of fertile thalli, which can release gametes when reaching a new site, is responsible for population connectivity. Floating dispersal also seems to affect the genetic population structure of some species of *Sargassum* along the coasts of SE Asia (Cheang et al. 2010, but see also Uwai et al. 2009). Along the European Atlantic coast, there is evidence of high genetic homogeneity between populations of *A. nodosum* (Olsen et al. 2010) and similar

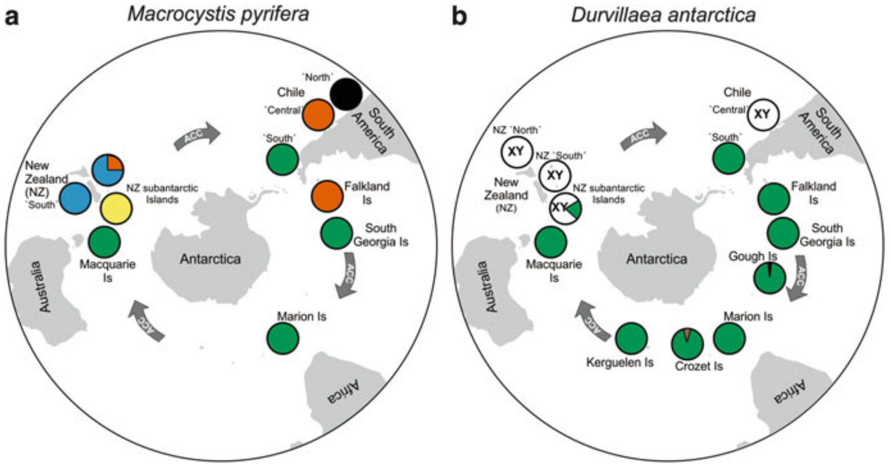

Fig. 17.9 Map of the sub-Antarctic region with different haplotype distributions for (**a**) *Macrocystis pyrifera* and (**b**) *Durvillaea antarctica*. *Different colors* indicate distinct haplotypes and XY denotes other haplotypes as shown. ACC: Antarctic Circumpolar Current. Figures modified after Macaya and Zuccarello (2010) and Fraser et al. (2009, 2010), respectively

results were shown for *Cystoseira amentacea* var. *stricta* from the Mediterranean Sea (Susini et al. 2007). While *A. nodosum* is highly buoyant, individuals of *C. amentacea* var. *stricta* lack vesicles but thallus fragments mix with other floating algae at the sea surface (Susini et al. 2007). Overall, the dispersal of gametes and spores via floating reproductive fragments or adults may also facilitate the reestablishment of algal populations after large-scale disturbances (such as El Niño events) (e.g., Dayton et al. 1999).

17.6 Outlook

Floating seaweeds can be found from the tropics to the Arctic and the sub-Antarctic islands. Since most studies on the physiology and ecology of floating algae were conducted at mid and high latitudes (e.g., Hobday 2000a, b; Macaya et al. 2005; Rothäusler et al. 2009), our knowledge about floating algae from tropical and subtropical regions is scarce. We propose that future research should examine the floating persistence of algae traveling in warm waters and under high radiation conditions, which will help to understand the role of low latitude algae as potential dispersal agents. In the face of global climate change, which predicts to drive species ranges towards the poles (see also Chap. 18 by Bartsch et al.; Parmesan and Yohe 2003), it can be expected that tropical and subtropical algae with positive buoyancy might expand farther towards mid latitudes, while the dispersal potential of temperate floating algae will be suppressed at mid latitudes (see above).

While afloat, algae can be concentrated in frontal systems (convergence zones) and eddies, which can result in the formation of huge biomass accumulations (e.g., Gower et al. 2006). Particulate organic matter such as algal detritus can also aggregate within these zones, contributing to biogeochemical cycles (Thiel and Gutow 2005b). Decomposers may use the organic matter as a substrate and nutrients released can be assimilated by the algae. Efforts should be made to better understand these processes within zones where floating algae and other floating items accumulate (Hinojosa et al. 2011).

So far, molecular studies have helped to reveal population connectivity of seaweeds and associated organisms over a broad range of spatial scales. However, they should also include the temporal scale. Rafting frequencies mainly depend on the availability and the persistence of the floating algae at the sea surface. Depending on latitude and local conditions, supply of floating algae can be spatially and temporally variable. Furthermore, the benthic distribution of floating algae might have changed substantially over evolutionary and ecological timescales. Future studies should therefore not only examine the relevance of rafting for recent population connectivity, but also how episodic rafting in the past has facilitated the establishment of isolated populations and subsequently led to allopatric speciation.

17.7 Conclusions

Floating seaweeds are an important component of the pelagic environment, predominantly in cold temperate and subpolar regions. Although most of the common floating algae naturally grow in benthic environments, these species show specific adaptations to the floating lifestyle which allow for persistence at the sea surface over prolonged time periods. These adaptations indicate selection for traits that facilitate floating persistence, suggesting that floating is a common and integral part of the species' life cycle (see e.g., Rothäusler et al. 2011a). Long-term floating supports genetic exchange between distant populations, natural range expansion, and regional population persistence through re-colonization after local extinctions.

Floating seaweeds significantly contribute to the complexity of the pelagic environment providing habitat for a rich community of associated rafters. Large patches of floating algae can be considered biodiversity hotspots, which catalyze the accumulation of species and the development of interspecific interactions among rafters and with their algal raft. For the associated rafters the patches of floating algae provide a highly dynamic habitat, which is subject to continuous changes depending on fluctuations of the biotic and abiotic environment. Considerable changes of the algal habitat during the pelagic journey are likely to exert strong selective pressure on the associated rafters.

Genetic homogeneity among distant populations of seaweeds and associated rafters, especially in the southern ocean, is the result of continuous exchange of floating individuals across extensive areas of open ocean. Continuous large-scale dispersal via floating algae adds a cosmopolitan dimension to marine biogeography that might not have been achieved through dispersal of larvae and spores alone.

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