

THE ECOLOGY OF RAFTING IN THE MARINE ENVIRONMENT. I. THE FLOATING SUBSTRATA

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Abstract Rafting has been inferred as an important dispersal mechanism in the marine environment by many authors. The success of rafting depends critically on the availability of suitable floating substrata. Herein currently available information on floating items that have been reported to carry rafting organisms is summarised. Floating items of biotic origin comprise macroalgae, seeds, wood, other vascular plants, and animal remains. Volcanic pumice (natural) and a diverse array of litter and tar lumps (anthropogenic) are the main floating items of abiotic origin. Macroalgae, wood, and plastic macrolitter cover a wide range of sizes while pumice, microlitter, and tar lumps typically are <10 cm in diameter. The longevity of floating items at the sea surface depends on their origin and likelihood to be destroyed by secondary consumers (in increasing order): nonlignified vascular plants/animal carcasses < macroalgae < driftwood < tar lumps/skeletal remains < plastic litter < volcanic pumice. In general, abiotic substrata have a higher longevity than biotic substrata, but most abiotic items are of no or only limited food value for potential rafters. Macroalgae are most abundant at mid-latitudes of both hemispheres, driftwood is of major importance in northern and tropical waters, and floating seeds appear to be most common in tropical regions. Volcanic pumice can be found at all latitudes but has primarily been reported from the Pacific Ocean. Plastic litter and tar lumps are most abundant near the centres of human population and activities. In some regions of abundant supply or zones of hydrography-driven accumulation, floating items can be extremely abundant, exceeding 1000 items km⁻². Temporal supply of floating items is variable, being seasonal for most biotic substrata and highly sporadic for some items such as volcanic pumice. Most reported velocities of floating items are in the range of 0.5–1.0 km h⁻¹, but direct measurements have shown that they occasionally are transported at much faster velocities. Published trajectories of floating items also coincide with the main oceanic currents, even though strong winds may sometimes push them out of the principal current systems. Many studies hint toward floating items to link source regions with coastal sinks, in some cases across long distances and even entire ocean basins. Fossil evidence suggests that rafting has also occurred in palaeo-oceans. During recent centuries and decades the composition and abundance of floating items in the world's oceans have been strongly affected by human activities, in particular logging, river and coastline regulation, and most importantly oil exploitation and plastic production. The currently abundant supply and the characteristics of floating items suggest that rafting continues to be an important dispersal mechanism in present-day oceans.

Introduction

... If these hints did not convince the experts, what about the driftwood carved with some instrument other than an iron one, not like wood worked in Europe, which Columbus's brother-in-law had picked up on the beaches of Porto Santo? Or the canes so thick that a joint would hold two quarts of wine, also found on Porto Santo? Bamboo did not grow in Europe — it was a calling card from Asia!!!

Sanderlin (1966), documenting the difficulties Columbus encountered to find support for his voyage

While the contemporaries of Columbus misinterpreted the sources of floating items stranding on the shores of Porto Santo off the coast of Portugal, they correctly inferred that these items came from distant shores. Since then many beach strollers have combed the flotsam of shores worldwide and wondered about the origin of the items cast ashore by wind and waves. Often these items carry dense populations of marine organisms, giving testimony to the long voyage these items have taken along the sea surface. Again, Columbus was one of the first who reported on floating items collected at sea, and he also found the first indication for organisms rafting on these items. On October 11, 1492, his men fished a small stick out of the water that was loaded with barnacles (Sanderlin 1966). During the centuries after Columbus, numerous reports of organisms rafting on diverse suites of floating items have been published. Many authors have suggested that rafting is an important dispersal mechanism for marine and terrestrial organisms (e.g., Johannesson 1988, Niedbala 1998, Gathorne-Hardy & Jones 2000, Sponer & Roy 2002).

Many marine and terrestrial organisms are capable of autonomous dispersal either as adults or as highly specialised pelagic larvae (McEdward 1995), and rafting is probably of little importance for them. These species release propagules (gametes and pelagic larvae) that are transported passively by the major oceanic currents. Modelling exercises have demonstrated that the geographic distribution of marine invertebrates with pelagic larvae is largely determined by oceanic currents (Gaylord & Gaines 2000). Species with long-living pelagic larvae often have a wide geographic distribution (Scheltema 1988, Glynn & Ault 2000). It is generally believed that the length of larval life has a strong effect on dispersal of many marine invertebrates (Eckman 1996), but there is also increasing evidence that the duration of pelagic stages is not directly correlated with dispersal distances (Strathmann et al. 2002). Marine invertebrates that lack pelagic larvae often are thought to be limited in their dispersal capabilities, but not all species fit the expected patterns of restricted distributions (e.g., Scheltema 1995, Kyle & Boulding 2000). The populations of some marine invertebrates with direct development extend over wide geographic ranges or feature little genetic structure (e.g., Ayre et al. 1997, Edmands & Potts 1997, Ó Foighil et al. 2001), suggesting that dispersal events occur frequently. Because these species possess no pelagic larval stages, they must rely on other mechanisms to reach new habitats. Rafting has been brought forward as a possible dispersal mechanism for these organisms (e.g., Johannesson 1988, Ingólfsson 1992, Ó Foighil et al. 1999, Sponer & Roy 2002).

Two major lines of evidence are used to infer the importance of rafting in the marine environment: (1) the distributional line of evidence and (2) the rafting line of evidence. The first line of evidence is based on the distribution pattern of benthic organisms, which can be either (a) disjunct populations of organisms separated by large expanses of unpopulated coastlines or even entire ocean basins or (b) extensive geographic ranges of organisms that lack pelagic larval stages. The second line of evidence is based on observations of organisms travelling on floating substrata, which can be either (a) rafting organisms on floating substrata at sea or (b) floating substrata colonised by rafters and cast up on beaches.

Many authors have utilised the geographic distribution of organisms (the distributional inference) to infer that the observed pattern might result from rafting (Johannesson 1988, Ó Foighil 1989, Wares 2001, Westheide et al. 2003). For example, the snail *Littorina saxatilis*, which lacks a pelagic larval stage, has been reported from island shores in the northern North Atlantic, and it

has been suggested that this species reached these locations via rafting on floating substrata (Johannesson 1988). Similarly, Ó Foighil (1989) found that brooding species of the bivalve genus *Lasaea* had a wide geographic distribution and were also found on oceanic islands far from continental source populations. He also suggested that these species are dispersed via rafting on floating substrata. Even the distribution pattern of terrestrial invertebrates (Gathorne-Hardy & Jones 2000) and vertebrates (Hafner et al. 2001, Rieppel 2002) has been used to infer that rafting on floating substrata is an important dispersal mechanism. This inference carries with it the implicit assumption that not only have organisms travelled long distances on floating items, but that after such a voyage, successful colonisation occurred. In many cases where authors have inferred rafting as a dispersal mechanism based on distributional evidence, possible alternative explanations have not been considered. Castilla & Guíñez (2000) have followed a more rigorous approach by analysing and evaluating several alternative hypotheses. While their analysis confirmed rafting as the most likely dispersal mechanism in most examined species, in some cases they revealed that other processes (e.g., anthropogenic transport) may be more likely than rafting to explain disjunct distribution patterns of benthic organisms. For example, during recent times organisms may have been transported over long distances by means of shipping or aquaculture activities (see, e.g., Carlton 1989). In the 1940s, the barnacle *Elminius modestus* was introduced accidentally from Australia into British waters most probably as a fouling organism on ship hulls from where it spread rapidly along the shores of NW Europe (Crisp 1958). The Pacific oyster *Crassostrea gigas* has been introduced intentionally to NW Europe after the demise of the commercially important *Ostrea edulis*. Favoured by warm water temperatures, the former species is now established as a permanent member of benthic communities in NW Europe (Reise 1998). These and many other similar examples (e.g., Ruiz et al. 2000) illustrate that distributional evidence for rafting as a dispersal mechanism has to be examined very carefully and, ideally, should be examined by considering alternative hypotheses.

The rafting line of evidence is based on organisms found on floating substrata, either at sea or after being cast ashore. Several authors have collected floating items with rafting organisms at variable distances from the shores (Kingsford 1992, Davenport & Rees 1993, Bushing 1994, Ingólfsson 1995, Hobday 2000a, Donlan & Nelson 2003) and inferred that these organisms possibly could colonise distant shores. For example, Helmuth et al. (1994a) collected a small bivalve, *Gaimardia trapesina*, on floating macroalgae more than 1000 km away from potential source regions. Similarly, Yeatman (1962) found littoral harpacticoid copepods on floating algae in the open Atlantic Ocean. The rafting line of evidence is particularly intriguing when rafts are found far out at sea, because this suggests that they might travel long distances before arriving at new shores.

Whether an organism can reach distant coastal habitats via rafting, however, depends on several factors, including adaptations of the rafting organisms to survive a long voyage on floating substrata. Many organisms may not be capable of colonising floating items in the first place (Winston 1982). Some mobile species actively leave substrata (e.g., macroalgae) after these start to float (Takeuchi & Sawamoto 1998, Edgar & Burton 2000). Other rafters such as large echinoderms or crustaceans may be lost during the voyage because they are not capable of holding on or returning to the substratum (e.g., Kingsford & Choat 1985, Hobday 2000a) or because they are preyed upon by fishes or other predators (Shaffer et al. 1995, Ingólfsson & Kristjánsson 2002). Many small organisms also may not live sufficiently long to survive long trips, but this limitation may be overcome in brooding species where offspring could recruit directly onto the maternal habitat (e.g., Helmuth et al. 1994a). These considerations suggest that some organisms may be better suited for dispersal via rafting than others. Successful dispersal by rafting, though, depends not only on the rafting organisms but also on the availability and suitability of the floating substrata.

A voyage on a floating item can only result in a successful journey between distant shores if the item is resistant to destruction and sinking at sea. Floating items differ widely in size, habitable space, nutritive value, buoyancy, and longevity (e.g., Kingsford 1992, Hobday 2000b, Edgar &



Figure 1 Tree of 5–6 m in length encountered in the Mediterranean ($38^{\circ} 17'N$, $01^{\circ} 48'E$). The tree harboured numerous hydrozoans, goose barnacles, isopods, and caprellids.

Burton 2000). Some items such as trees or macroalgae are large (Figure 1) and may form extensive patches of several metres in length or diameter, whereas others such as small plastic items or volcanic pumice usually are only a few millimetres or centimetres in diameter (Figure 2). Large floating items can be used as rafts by large organisms, including terrestrial vertebrates (e.g., Censky et al. 1998), whereas small items may only harbour small or unicellular organisms (e.g., Minchin 1996). Floating items of biotic origin may provide food resources to rafting organisms: macroalgae and wood typically harbour a diverse fauna of grazing and boring invertebrates (Ingólfsson 1995, Hobday 2000a, Vishwakiran et al. 2001) that feed on their substrata. Most of these organisms do



Figure 2 Pieces of volcanic pumice collected in flotsam near Puerto Montt, southern Chile.

not occur on abiotic substrata because these offer no food resources. For example, the herbivorous isopod *Idotea baltica* is very common on floating macroalgae in the North Atlantic (Ingólfsson 2000). In the Mediterranean Sea, however, where macroalgae are largely absent from the flotsam (Dow & Menzies 1958), *I. baltica* is rarely found in the neuston (Hartmann 1976) even though it is commonly reported from benthic habitats (Guarino et al. 1993). In the context of rafting one of the most important properties of floating items is their buoyancy and longevity at the sea surface. For several reasons, floating items may lose their buoyancy at sea and sink to the seafloor. Abundant reports of wood (Wolff 1979), plastic debris (Holmström 1975), and patches of macroalgae (Schoener & Rowe 1970) in the deep sea give testimony that this frequently occurs in the world's oceans. Besides these qualitative characteristics of floating substrata, their availability in different regions of the world's oceans also may vary substantially, affecting the probability of rafting opportunities. These considerations demonstrate that it is important to know the main properties and availability of floating substrata in order to understand the process and ecological importance of rafting.

The wide expanses of large ocean basins may represent unsurpassable barriers for many terrestrial and coastal organisms unable to survive in the open ocean. Floating substrata may enable some of these organisms to cross these barriers. Columbus and his men (and some of their predecessors) demonstrated that oceanic barriers can be surpassed if vehicles well equipped for long voyages across the sea surface are used. There is increasing distributional and rafting evidence that a wide diversity of organisms are dispersed over long distances across the sea, but information about the quality and availability of potential dispersal vehicles is widely scattered throughout the

scientific literature. This complicates the evaluation of rafting as a dispersal mechanism in the marine environment. In the present contribution we therefore address a set of questions related to floating substrata. Which substrata are floating through the world's oceans? How long do these substrata survive at the surface of the sea? Are these substrata sufficiently abundant to serve as dispersal vehicles for rafting organisms? Where do these substrata occur? What are the main routes that floating items take? Answering these questions is essential to reveal the role of floating substrata for the dispersal of rafting organisms. Building on the qualitative and quantitative description of the floating substrata in the present review, we will deal with the evaluation of the rafting biota and the ecological importance of rafting in a future review.

Types and sizes of substrata

A wide diversity of floating items travels the world's oceans. Floating items can be categorised according to their origin (natural or anthropogenic) and to their organic nature (biotic or abiotic) (Table 1). Among biotic substrata, Sinitsyn & Reznichenko (1981) distinguished between plants and animals and named the most important items found in each category. Natural substrata of abiotic origin comprise volcanic pumice, tar balls (from natural seeps), and ice. Anthropogenic substrata include a whole suite of items that can be categorised as manufactured wood, tar balls (from oil industry), and plastics of various sizes, shapes, and surface characteristics (Table 1). The sizes of floating items of different origin also vary substantially. Smallest items of only a few millimetres in diameter are plastic microlitter, plant seeds, and volcanic pumice, while large items can exceed several metres in diameter or length. The largest items floating in the world's oceans are whale carcasses and trees. While in evolutionary history floating objects have been almost exclusively of natural origin, during recent times human activities have contributed to an increase in abundance of some natural substrata (e.g., wood) and to the introduction of new substrata such as plastics (Barnes 2002, Masó et al. 2003).

Macroalgae

Among natural floating objects, macroalgae probably represent the quantitatively most important substrata. Most macroalgae are negatively buoyant and sink to the seafloor when detached from the primary substratum, but some species possess high buoyancy, as can be seen from the fact that adult plants may even lift and transport rocks of considerable size from the substratum (Emery & Tschudy 1941, Emery 1963, Norton & Mathieson 1983). The dominant floating macroalgae are brown algae, but there are also some red and green algae that have been reported floating (Table 2). In most species, air-filled pneumatocysts provide floatation allowing large plants to extend photosynthetic tissues into the light-saturated surface waters. Species from the genera *Macrocystis*, *Sargassum*, *Ascophyllum*, and *Fucus* have thalli with many small pneumatocysts (typically <1 cm in diameter). The number of pneumatocysts can vary. Friedland & Denny (1995) reported that subtidally growing plants of *Egregia menziesii* were positively buoyant, whereas intertidal plants had fewer pneumatocysts per length of stipe and were negatively buoyant. In the kelp *Nereocystis luetkeana*, individual pneumatocysts can reach a volume of up to 1 l (Hurka 1971). The kelp *Pelagophycus porra* also has a single large pneumatocyst. The gas composition within the pneumatocysts was analysed for *Sargassum* cf. *leptopodium* Sonder (Hurka 1971). They contain a mixture of oxygen, nitrogen, and carbon dioxide in varying relative proportions depending on the physiological status of the plant and the partial pressure of the particular gas in the surrounding medium. These gas-filled pneumatocysts provide buoyancy and let entire plants float to the sea surface after becoming detached from their substratum (e.g., Kingsford & Choat 1985). The blades of the bull kelp *Durvillaea antarctica* possess gas-filled cells that provide sufficient buoyancy to keep entire plants with the attached holdfast at the sea surface (Figure 3). In contrast to the brown algae with pneumatocysts, most red and green algae that have been reported floating obtain their buoyancy by means of gas bubbles trapped between or in the algal thalli (Dromgoole 1982, Bäck et al. 2000).

Table 1 Categories of floating substrata and the main size classes in which they have been reported.



Note: Dots indicate diameters of individual items: small, 0.1–10 cm; intermediate, 11–100 cm; large, >100 cm.

Source: Table slightly modified after Simitsyn & Reznichenko (1981).

Table 2 Geographical distribution and estimates of the approximate abundances of algal and sea grass species reported floating at the sea surface

Species	Region	Abundance	Method	Reference
Algae				
<i>Ascophyllum nodosum</i>	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
	Iceland	Abundant	VSS	Ingólfsson 1995, 1998, 2000
	Iceland	Common	Plankton net	Ólafsson et al. 2001
	Sargasso Sea	n.i.	n.i.	John 1974
	Sargasso Sea	Present	Plankton net	Winge 1923
	Equatorial Atlantic	n.i.	n.i.	John 1974
	North Sea	Common	VSS	Franke et al. 1999
	New Zealand	Common	VSS	Kingsford 1992
<i>Carpophyllum angustifolium</i>	New Zealand	Common	VSS	Kingsford 1992
<i>Carpophyllum flexuosum</i>	New Zealand	Common	VSS	Kingsford 1992
	New Zealand	Abundant	VSS	Kingsford 1993
<i>Carpophyllum maschalocarpum</i>	New Zealand	Abundant	VSS	Kingsford 1992, 1993
	New Zealand	Common	Beach survey	Marsden 1991
<i>Carpophyllum plumosum</i>	New Zealand	Abundant	VSS	Kingsford 1992, 1993
<i>Chaetomorpha</i> sp.	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
<i>Chorda filum</i>	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
	Iceland	Common	VSS	Ingólfsson 1998
	Iceland	Common	Plankton net	Ólafsson et al. 2001
<i>Codium fragile</i>	Japan	Present	VSS	Hirata et al. 2001
<i>Codium</i> sp.	New Zealand	Present	VSS	Kingsford 1992
<i>Colpomenia sinuosa</i>	Japan	Present	VSS	Hirata et al. 2001
<i>Cystophora scalaris</i>	New Zealand	Present	Beach survey	Marsden 1991
<i>Cystophora</i> sp.	New Zealand	Present	VSS	Kingsford 1992
	New Zealand	Abundant	VSS	Kingsford 1993
<i>Cystophyllum sisymbroides</i>	Japan	n.i.	VSS, beach survey	Segawa et al. 1959a
<i>Cystophyllum turneri</i>	Japan	n.i.	VSS, beach survey	Segawa et al. 1959a
<i>Cystoseira osmundacea</i>	California	n.i.	Beach survey	Kohlmeyer 1972
	Baja California	Common	VSS	Mitchell & Hunter 1970
<i>Cystoseira tamariscifolia</i>	French Atlantic coast	Present	VSS	Personal observations
<i>Cystoseira</i> spp.	California	Present	VAS	Kingsford 1995
	Netherlands	n.i.	Beach survey	van den Hoek 1987

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Table 2 (continued) Geographical distribution and estimates of the approximate abundances of algal and sea grass species reported floating at the sea surface

Species	Region	Abundance	Method	Reference
<i>Durvillaea antarctica</i>	New Zealand	Present	VSS	Kingsford 1992
	New Zealand	Abundant	Beach survey	Marsden 1991
	South of Tasmania	Abundant	VSS	Smith 2002
	Chile	Common	VSS	Personal observations
<i>Ecklonia maxima</i>	St. Helena	n.i.	VSS	Arnaud et al. 1976
	South Africa	Abundant	Beach survey	Griffiths & Stenton-Dozey 1981
<i>Ecklonia radiata</i>	New Zealand	Present	VSS	Kingsford 1992
<i>Ectocarpus</i> sp.	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
<i>Egregia laevigata</i>	Baja California	Common	VSS	Mitchell & Hunter 1970
<i>Egregia menziesii</i>	California	Present	VAS	Kingsford 1995
<i>Egregia</i> sp.	California	Common	VSS	Bushing 1994
<i>Enteromorpha intestinalis</i>	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
	Baltic Sea	Common	Beach survey	Bäck et al. 2000
<i>Enteromorpha</i> spp.	Iceland	Present	VSS	Ingólfsson 1998
<i>Eusargassum</i> spp.	Japan	n.i.	VSS, beach survey	Segawa et al. 1959a
	Japan	Common	VSS	Ohno 1984a
<i>Fucus distichus</i>	Iceland	Common	VSS	Ingólfsson 1995
	Iceland	Present	VSS	Ingólfsson 1998, 2000
<i>Fucus serratus</i>	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
<i>Fucus spiralis</i>	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
	Iceland	Present	VSS	Ingólfsson 1995, 2000
<i>Fucus vesiculosus</i>	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
	Iceland	Common	VSS	Ingólfsson 1995
	Irish Sea	Abundant	Neuston net	Tully & Ó Ceidigh 1986
	Iceland	Abundant	VSS	Ingólfsson 1998, 2000
	Iceland	Common	Plankton net	Ólafsson et al. 2001
<i>Fucus</i> spp.	North Sea	Abundant	VSS	Franke et al. 1999
	NE Pacific	Abundant	VSS	Shaffer et al. 1995
<i>Halidrys dioica</i>	California	n.i.	Beach survey	Kohlmeyer 1972
<i>Halidrys siliquosa</i>	Netherlands	n.i.	Beach survey	van den Hoek 1987
<i>Himantalia elongata</i>	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
	Irish Sea	Present	Neuston net	Tully & Ó Ceidigh 1986
	Netherlands	n.i.	Beach survey	van den Hoek 1987

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Table 2 (continued) Geographical distribution and estimates of the approximate abundances of algal and sea grass species reported floating at the sea surface

Species	Region	Abundance	Method	Reference
	North Sea	Present	VSS	Franke et al. 1999
<i>Hizikia fusiformis</i>	Japan	n.i.	VSS, beach survey	Segawa et al. 1959a
	Japan	Common	VSS	Ohno 1984a
	Japan	Common	VSS	Hirata et al. 2001
	Japan	Present	VSS	Hirata et al. 2003
<i>Homosira banksii</i>	New Zealand	Present	VSS	Kingsford 1992
	New Zealand	Common	Beach survey	Marsden 1991
<i>Laminaria hyperborea</i>	North Sea	Present	VSS	Personal observations
<i>Laminaria saccharina</i>	North Sea	Present	VSS	Personal observations
<i>Laminaria</i> sp.	Irish Sea	Present	Neuston net	Tully & Ó Ceidigh 1986
	California	Present	VSS	Bushing 1994
<i>Leathesia difformis</i>	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
<i>Lessonia variegata</i>	New Zealand	Common	Beach survey	Marsden 1991
<i>Lethisia</i> sp.	New Zealand	Present	VSS	Kingsford 1992
<i>Macrocystis angustifolia</i>	California	Common	VSS	Bushing 1994
<i>Macrocystis integrifolia</i>	California	Common	VSS	Bushing 1994
<i>Macrocystis pyrifera</i>	New Zealand	Abundant	Beach survey	Marsden 1991
	Baja California	Abundant	VSS	Mitchell & Hunter 1970
	California	Abundant	VAS	Kingsford 1995
	California	Common	VSS	Bushing 1994
	California	Abundant	Beach survey	Harrold & Lisin 1989
	California	Abundant	VSS	Hobday 2000a,b,c
	Tasmania	n.i.	VSS	Edgar 1987
	Chile	Present	Beach survey	Rodríguez 2003
	Scotia Arc	Present	VSS	Helmuth et al. 1994a
	Falklands	n.i.	Beach survey	van Tussenbroek 1989
<i>Marginariella boryana</i>	New Zealand	Present	Beach survey	Marsden 1991
<i>Myagropsis myagroides</i>	Japan	Common	VSS	Ohno 1984a
	Japan	Present	VSS	Hirata et al. 2003
<i>Nereocystis luetkeana</i>	NE Pacific	Abundant	VSS	Shaffer et al. 1995
	California	Present	VSS	Bushing 1994
<i>Pelagophycus giganteus</i>	California	Present	VSS	Bushing 1994
<i>Pelagophycus porra</i>	California	Common	VSS	Bushing 1994
	Baja California	Common	VSS	Mitchell & Hunter 1970

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Table 2 (continued) Geographical distribution and estimates of the approximate abundances of algal and sea grass species reported floating at the sea surface

Species	Region	Abundance	Method	Reference
<i>Pelvetia</i> sp.	California	Present	VAS	Kingsford 1995
<i>Phyllospora comosa</i>	Australia	Common	VSS	Druce & Kingsford 1995
<i>Pterygophora californica</i>	Baja California	Common	VSS	Mitchell & Hunter 1970
<i>Saccorhiza polyschides</i>	French Atlantic coast	Present	VSS	Personal observations
<i>Sargassum confusum</i>	Japan	n.i.	VSS, beach survey	Segawa et al. 1959a
<i>Sargassum filipendula</i>	Florida Current	Common	VSS	Dooley 1972
<i>Sargassum fluitans</i>	U.S. Atlantic coast	n.i.	Beach survey	Kohlmeyer 1972
	NW Atlantic	Common	VSS	Howard & Menzies 1969
	Sargasso Sea	n.i.	VSS	Johnson & Richardson 1977
	NW Atlantic	Abundant	VSS	Conover & Sieburth 1964
	NW Atlantic	Common	Neuston net	Stoner 1983
	NW Atlantic	Abundant	VSS	Stoner & Greening 1984
	North Atlantic	n.i.	VSS	Carpenter & Cox 1974
	Sargasso Sea	Abundant	Neuston net	Parr 1939
	Sargasso Sea	Abundant	Plankton net	Winge 1923
	Florida Keys	Abundant	VSS	Bomber et al. 1988
	Florida Current	Common	VSS	Dooley 1972
	Sargasso Sea	Common	VSS	Calder 1995
<i>Sargassum horneri</i>	Japan	n.i.	VSS, beach survey	Segawa et al. 1959a
	Japan	Abundant	VSS	Ohno 1984a
	Japan	n.i.	n.i.	Ohno 1984b
	Japan	n.i.	n.i.	Kimura et al. 1958
	Japan	Abundant	VSS	Hirata et al. 2003
<i>Sargassum hystrix</i>	Brazil Current	Common	VSS	de Oliveira et al. 1979
	Florida Keys	Present	VSS	Bomber et al. 1988
<i>Sargassum muticum</i>	North Sea	Present	VSS	Franke et al. 1999
	Japan	Common	VSS	Hirata et al. 2003
<i>Sargassum natans</i>	U.S. Atlantic coast	n.i.	Beach survey	Kohlmeyer 1972
	NW Atlantic	Common	VSS	Howard & Menzies 1969
	Sargasso Sea	n.i.	VSS	Johnson & Richardson 1977

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Table 2 (continued) Geographical distribution and estimates of the approximate abundances of algal and sea grass species reported floating at the sea surface

Species	Region	Abundance	Method	Reference
	NW Atlantic	Common	VSS	Conover & Sieburth 1964
	NW Atlantic	Common	Neuston net	Stoner 1983
	NW Atlantic	Abundant	VSS	Stoner & Greening 1984
	North Atlantic	n.i.	VSS	Carpenter & Cox 1974
	Sargasso Sea	Abundant	Neuston net	Parr 1939
	Sargasso Sea	Abundant	Plankton net	Winge 1923
	Florida Keys	Abundant	VSS	Bomber et al. 1988
	Florida Current	Common	VSS	Dooley 1972
<i>Sargassum patens</i>	Japan	n.i.	VSS, beach survey	Segawa et al. 1959a
	Japan	Abundant	VSS	Ohno 1984a
	Japan	n.i.	n.i.	Ida et al. 1967
	Japan	n.i.	n.i.	Ohno 1984b
	Japan	Abundant	VSS	Segawa et al. 1961a
	Japan	Common	VSS	Hirata et al. 2003
<i>Sargassum platycarpum</i>	Brazil Current	Common	VSS	de Oliveira et al. 1979
<i>Sargassum ringgoldianum</i>	Japan	n.i.	n.i.	Ida et al. 1967
	Japan	n.i.	VSS, beach survey	Segawa et al. 1959a
	Japan	Present	VSS	Ohno 1984a
	Japan	Abundant	VSS	Hirata et al. 2003
<i>Sargassum serratifolium</i>	Japan	n.i.	VSS, beach survey	Segawa et al. 1959a
	Japan	Common	VSS	Ohno 1984a
	Japan	n.i.	n.i.	Ida et al. 1967
	Japan	n.i.	n.i.	Ohno 1984b
	Japan	Abundant	VSS	Segawa et al. 1961a
<i>Sargassum sinclairii</i>	New Zealand	Abundant	VSS	Kingsford 1993
	New Zealand	Present	Beach survey	Marsden 1991
	New Zealand	Common	VSS	Kingsford 1992
<i>Sargassum tortile</i>	Japan	n.i.	VSS, beach survey	Segawa et al. 1959a
	Japan	Abundant	VSS	Ohno 1984a
	Japan	n.i.	n.i.	Ohno 1984b
	Japan	Abundant	VSS	Segawa et al. 1961a
<i>Sargassum</i> sp.	California	Present	VSS	Bushing 1994

-- continued

Table 2 (continued) Geographical distribution and estimates of the approximate abundances of algal and sea grass species reported floating at the sea surface

Species	Region	Abundance	Method	Reference
	New Zealand	Abundant	VSS	Kingsford 1993
<i>Scytosiphon lomentaria</i>	New Zealand	Present	Beach survey	Marsden 1991
<i>Turbinaria turbinata</i>	Florida Keys	Present	VSS	Bomber et al. 1988
	Caribbean	Common	VSS	Calder 1991
<i>Ulva lactuca</i>	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
Sea Grass				
<i>Phyllospadix iwatensis</i>	Japan	n.i.	Neuston net	Yoshida 1963
<i>Phyllospadix japonicus</i>	Japan	Common	VSS	Hirata et al. 2001
<i>Phyllospadix</i> sp.	California	Present	VSS	Bushing 1994
<i>Zostera asiatica</i>	Japan	n.i.	Neuston net	Yoshida 1963
<i>Zostera caespitosa</i>	Japan	n.i.	Neuston net	Yoshida 1963
<i>Zostera marina</i>	Irish Sea	Common	Neuston net	Tully & Ó Ceidigh 1986
	Japan	n.i.	Neuston net	Yoshida 1963
	Japan	Common	VSS	Hirata et al. 2001
	California	Common	Beach survey	Worcester 1994
<i>Zostera noltii</i>	NW Europe	Common	Beach survey	Personal observations
<i>Zostera</i> spp.	Irish Sea	n.i.	Neuston net	Davenport & Rees 1993
	U.S. Pacific coast	Common	VSS	Shaffer et al. 1995
	Japan	Common	VSS	Segawa et al. 1961a

Note: VSS = visual ship-based survey; VAS = visual aerial survey; n.i. = no information.

Apart from a few entirely pelagic species, most floating macroalgae grow in benthic habitats during early life (Lüning 1990). Entire plants or parts of these attached algae may become floating by various mechanisms, namely, breakage of the stipe, detachment of the holdfast, and lifting of the attachment substratum. Breakage of the stipe may occur regularly during the life cycle of some macroalgae, as in many species from the genus *Sargassum*, which fragment during and toward the end of the growth season (Norton 1977, Ohno 1984a, Arenas et al. 1995). Grazers may also contribute to breakage of stipes (Chess 1993, Duggins et al. 2001). Similarly, grazers may weaken the holdfast of macroalgae and cause these to detach from the primary substratum. In southern California, the sea urchin *Strongylocentrotus franciscanus* inhabits the holdfasts of *Macrocystis pyrifera* where it feeds on the hapters, making the holdfasts more susceptible to detachment (Tegner et al. 1995). Large kelps, such as *M. pyrifera* and *Durvillaea antarctica* have comparatively large holdfasts that harbour a wide diversity of organisms (e.g., Ojeda & Santelices 1984, Edgar 1987, Smith & Simpson 1995, Edgar & Burton 2000, Thiel & Vásquez 2000). Some of these inhabitants excavate burrows into the holdfasts, and thereby contribute to a weakening of the attachment strength of kelp plants (Thiel 2003). In many algal species, breakage of stipes and detachment of holdfasts are greatly enhanced during storms when drag forces on plants increase (Duggins et al. 2001). For the giant kelp *Macrocystis pyrifera* highest detachment rates of plants have been observed during winter storm seasons in California (ZoBell 1971). Many



Figure 3 Floating plant of *Durvillaea antarctica* encountered off the central-northern Pacific coast of Chile, where this species can frequently be found floating; diameter of tracking buoy = 9 cm.

intermediate-size species (*Sargassum* spp., *Fucus* spp., *Ascophyllum nodosum*, *Himantalia elongata*) possess small, yet firmly attached holdfasts. Algae growing on pebbles may float away when drag increases beyond a certain limit (Vallentin 1895, Emery & Tschudy 1941, Shumway 1953, Gilbert 1984) and when the weight ratio of alga:pebble is >3 (Kudrass 1974). Emery (1963) reported holdfasts of *Macrocystis pyrifera* attached to the shells of abalone (*Haliotis* spp.). Organisms serving as growth substratum for *Sargassum muticum* or other macroalgae may face a similar fate (e.g., Critchley et al. 1987). Ohno (1984a) remarked that many *Sargassum* plants found floating in nearshore waters of SE Japan had intact holdfasts, suggesting that they had come from nearby coastal habitats. Other authors also remarked that it is not unusual to find entire plants with complete holdfasts (e.g., Helmuth et al. 1994a, Hobday 2000c). Regardless of the detachment mechanism, floating plants or parts thereof may become entangled in attached plants (Dayton et al. 1984), increasing the drag on these (Seymour et al. 1989). Floating macroalgae also may be accumulated, forming large patches that consist of several algal species (Hirata et al. 2001).

Some of the most intensively studied floating macroalgae belong to the genus *Sargassum*. The two holopelagic species *S. natans* and *S. fluitans* are characteristic of the open North Atlantic. These plants, commonly known as gulfweed, circulate mainly in an area from 20–40°N and from 30°W to the west coast of the Florida Current extending over approximately 7 million km² (Carpenter & Cox 1974). Particularly high densities of gulfweed are found in the Sargasso Sea (Winge 1923) and the adjacent Gulf Stream (Howard & Menzies 1969). Single plants can become several metres long but are typically much smaller (Coston-Clements et al. 1991). Plants frequently aggregate into large windrows in convergence zones of wind-induced Langmuir cells (Faller & Woodcock 1964). The importance of North Atlantic *Sargassum* as a neustonic habitat can be derived from the description of a veritable *Sargassum* community of associated vertebrates and invertebrates (Butler et al. 1983, Dooley 1972). Besides these holopelagic species there are many other *Sargassum* species that have been reported floating. The highest diversity of *Sargassum* spp. has been reported from the NW Pacific around Japan, where the species *S. horneri*, *S. serratifolium*, *S. patens*, *S. tortile*, and *S. confusum* are often found floating in coastal waters (Senta 1962, Hirotsaki 1963, 1965, Ikehara & Sano 1986, Hirata et al. 2001). In the Brazil Current the species *S. hystrix* and *S.*

platycarpum have been reported (de Oliveira et al. 1979). *Sargassum sinclairii* is commonly found floating in coastal waters of northeastern New Zealand (Kingsford & Choat 1985, Kingsford 1992). Following the accidental introduction of *S. muticum* in NW Europe through aquaculture activities, it has been inferred that this alga disperses via floating fragments (Norton 1976, Fernández 1999), and floating plants have indeed been observed in the North Sea (Franke et al. 1999). The floating behaviour of branches after fragmentation and the species' high tolerance to changes in environmental factors such as temperature and salinity allow the benthic *S. muticum* to be dispersed rapidly in coastal waters, as observed at the West Coast of North America in the 1970s (Norton 1976) or the Swedish west coast during the late 1980s (Karlsson & Loo 1999).

Floating macroalgae common to the Northern Hemisphere include other brown algae such as *A. nodosum*, *H. elongata*, and *Fucus* spp. (Ingólfsson 1995, Shaffer et al. 1995). *Ascophyllum nodosum* usually lives in wave-sheltered intertidal areas and individual plants may reach considerable sizes (Bertness 1999). *Himantalia elongata* typically grows subtidally and floating plants have occasionally been observed (Davenport & Rees 1993, Franke et al. 1999). *Fucus vesiculosus* and other species from that genus grow abundantly on many rocky shores of the northern North Atlantic (Bertness 1999). Individuals of other brown algae (e.g., *Cystoseira tamariscifolia*, *Saccorhiza polyschides*) are occasionally found floating in nearshore waters (personal observations).

Fell (1967) stated that epipelagic transport of animal species by large brown algae is more significant in the world's Southern Hemisphere because kelp species are generally larger there and thus more persistent. The most conspicuous species belongs to the genus *Macrocystis*, which displays an antitropical distribution. It grows in temperate subtidal regions of the entire Southern Hemisphere and along the Pacific coast of western North America. The giant kelp *M. pyrifera* is found along the coasts of every major landmass and most oceanic islands in that region (Coyer et al. 2001). The size of single floating plants varies from 20 cm (Kingsford 1995) to up to 30 m (Coyer et al. 2001). Accumulation of plants as a consequence of entanglement increases the size of algal patches significantly (Emery & Tschudy 1941, Dayton et al. 1984). Rafts with a volume of up to 4 m³ have been reported to consist of more than 200 individual plants (Helmuth et al. 1994a). Extending well below the surface, large clumps of drift algae increase the complexity of the pelagic environment substantially (Kingsford 1995). Wet weight of patches of floating *Macrocystis pyrifera* has been reported to range from 1.4 kg for a single plant to 450 kg for entire clumps (Mitchell & Hunter 1970).

In the Southern Hemisphere there are other large macroalgae that are also frequently found floating. The bull kelp *Durvillaea antarctica* features large gas-filled cells in its characteristic blades (Hay 1994). It usually grows in the low intertidal zone in wave-exposed areas, and during strong storms entire plants may become detached from the primary substratum. Bull kelp has been reported to dominate floating macroalgae in the Southern Ocean (Smith 2002), but its suitability as a dispersal agent for rafting organisms has been questioned because its holdfast is very compact, providing little space for potential travellers (Edgar & Burton 2000).

Some smaller macroalgae can also occasionally be observed floating, for example, *Myagropsis myagroides*, *Hizikia fusiformis*, *Codium fragile*, *Colpomenia* spp., *Ulva* spp., *Carpophyllum* spp., *Chaetomorpha* spp., *Enteromorpha* spp., or *Pachymeniopsis* spp. (Segawa et al. 1959a, Hirotsaki 1963, Ohno 1984a, Kingsford & Choat 1985, Worcester 1994, Cho et al. 2001, Hirata et al. 2001, personal observations). Most of these macroalgae rarely exceed 25 cm in length and their buoyant properties are limited (Dromgoole 1982). They may nevertheless be of importance as rafting substrata in particular habitats (e.g., coastal bays) where they may contribute to small-scale dispersal of some organisms. Some of these macroalgae only become positively buoyant at specific times. For example, *Codium fragile* accumulates oxygen bubbles on or in the thallus as a result of photosynthesis during the day, and subsequently, relative density decreases and the algae may float (Dromgoole 1982). Similar observations have been reported for *Cladophora* spp. (Norton & Mathieson 1983). Bäck et al. (2000) also observed that mats of *Enteromorpha intestinalis* floated to the sea surface during spring and summer. This usually occurred during

calm and sunny weather, and the authors remarked that abundant gas bubbles were observed under these mats. The brown alga *Colpomenia peregrina*, which grows in bulbous shapes, may become air-filled at low tide and float away when the tide recedes (Norton & Mathieson 1983). When floating, *C. peregrina* may carry with it the attachment substratum. This temporarily floating alga has gained fame as the oyster thief because it often grows on oysters, which are transported away from oyster beds by this process (Ribera & Boudouresque 1995). Because most of these algae only float for specific and relatively short periods, it is most likely that they are only dispersed over relatively short distances, e.g., within an estuary.

The importance of floating and rafting for long-distance dispersal of macroalgae is underscored by two facts, namely, that (1) island flora in many cases is dominated by algal species that are positively buoyant and that (2) distances between local algal populations and potential source regions are far beyond the dispersal range of spores (van den Hoek 1987). The spores of many macroalgae have a very limited dispersal potential and may be dispersed over only a few metres, while adult plants or parts thereof may float over long distances and either reattach or release spores near new habitats (e.g., Hoffmann 1987). The fact that rafting may be an efficient dispersal mechanism is also underlined by the extensive geographic distributions of some of these floating macroalgae themselves. In the subantarctic region, phytogeography is characterised by a high degree of shared species between different continents (Meneses & Santelices 2000), which might be because some species (*Macrocystis pyrifera*, *Durvillaea antarctica*) are highly adapted to floating over long distances. A recent genetic study by Coyer et al. (2001) showed that species from the genus *Macrocystis* show very little genetic differentiation, justifying their unification as a single species. The authors note that this floating macroalga is very efficiently dispersed with major oceanic currents. For the elk kelp, *Pelagophycus porra*, however, Miller et al. (2000) implied that island populations along the Californian coast might experience less genetic exchange than mainland populations. Local currents may limit efficient genetic exchange of this floating macroalga.

Vascular plants

Sea grasses

In coastal areas sea grass blades are frequently found floating (e.g., Worcester 1994, Shaffer et al. 1995). Segawa et al. (1961a) reported that *Zostera* spp. is typically found floating in bay areas. Blades of *Zostera* spp. and of *Phyllospadix japonicus* were also found in coastal waters of Asia, namely, Japan (Segawa et al. 1961a, Hirosaki 1963, 1965, Hirata et al. 2001) and off South Korea (Cho et al. 2001). Large amounts of sea grass blades are frequently cast onto beaches toward the end of the growth season (Kirkman & Kendrick 1997, Ochieng & Erfteimeijer 1999), suggesting that during that time many sea grass remains float at the sea surface. The large amounts of blades of *Thalassia testudinum* reported from the deep sea off the Caribbean coasts (Wolff 1979) provide similar evidence for the local abundance of floating sea grass since they must have reached their final destiny via the sea surface.

Due to their limited buoyancy and longevity at the sea surface, sea grasses probably are primarily of importance in coastal bays where they may play an important role in short-scale dispersal (Worcester 1994). Genetic structure of local sea grass populations suggests that gene flow is limited and depends largely on vegetative dispersal (Procaccini & Mazzella 1998, Reusch et al. 1999). Fruits and seeds of sea grasses have been reported to float over periods of hours and days (Lacap et al. 2002). These authors estimated that during extreme weather conditions the fruits of the common sea grasses *Enhalus acoroides* and *Thalassia hemprichii* may be transported over distances of several 100 km, but typically their dispersal range is within tens of kilometres or even less. The dispersal distances of seeds of the sea grass *Zostera marina* also appear to be very limited (Orth et al. 1994, Ruckelshaus 1996). In the Chesapeake Bay, Orth et al. (1994) frequently observed reproductive shoots of *Z. marina* containing seeds that were floating at the sea surface, and they

suggested that long-distance dispersal and colonisation of distant habitats may be achieved via these floating plants. Because sea grass seeds are comparatively small and have limited longevity, they could only carry microorganisms (microalgae, fungi) as travellers over short distances.

Terrestrial grasses, bushes or shrubs

Plants from beaches or salt marshes are among the most commonly reported nonlignified vascular plants. For example, Worcester (1994) reported *Salicornia virginica* and *Spartina foliosa* floating in a North American estuary. Carlquist (1967) also remarks that parts or entire plants of *Portulaca lutea*, *Sesuvium portulacastrum*, and *Lycium sandwichense* have the capacity to float. Stems of *Salsola kali* have been observed floating by Guppy (1906). Davenport & Rees (1993) collected terrestrial plants such as straw and bamboo in the Irish Sea. In tropical regions large amounts of floating freshwater plants have been observed to be transported to the sea (King 1962). Some of these rafts made up of water hyacinths (*Eichhornia* spp.) and grass (*Panicum* spp.) were estimated to be >500 m² in size (King 1962). Bamboo has also been observed floating in tropical regions (Zarate-Villafranco & Ortega-García 2000) where it may be common, as can be inferred from its frequent presence on beaches in those regions (Heatwole & Levins 1972, Prasannarai & Sridhar 1997). In tropical estuaries leaves from deciduous trees such as mangroves may also be abundant (Wehrmann & Dittel 1990). Nonlignified terrestrial plant remains may be of local importance for short-distance dispersal and for terrestrial invertebrates.

Wooden plants and trees

Some of the largest floating substrata are lignified plants or parts thereof (wood *sensu lato*). Most natural wood is delivered to the sea by large rivers and may also reach the ocean as a consequence of coastal erosion (Emery 1955, Goda & Nishinokubi 1997). Similar to macroalgae, burrowing invertebrates may weaken the stem or root system of trees, thereby causing these to fall over and possibly float away. This process may be of particular importance in mangrove forests where arthropod borers excavate extensive burrows in roots of mangrove trees (e.g., Svavarsson et al. 2002).

Wood in the oceans comes in a wide diversity of species and sizes, as whole trees, trunks, or branches (Maser & Sedell 1994). The wood of different tree species may vary substantially in important properties, such as buoyancy and resistance to destruction. In general it can be said that hardwoods (e.g., teak and mahogany) possess relatively high resistance to destruction, but they may have very little positive buoyancy. Borges et al. (2003) showed that hardwoods suffer very little from attacks by boring marine isopods. In contrast, lightwoods (e.g., balsa) may be highly susceptible to destruction but are very buoyant. Abe (1984) suggested that hardwood is more resistant to entry of seawater than softwood and therefore might be comparatively suitable for survival of rafting insects (termites). The properties of wood may also vary depending on the sites or seasons where and when wood was removed from its original site (e.g., Alsar 1973).

A wide diversity of tree species have been reported either as floating at sea or as driftwood after being cast ashore. In tropical regions mangrove trees and remains thereof (*Rhizophora* spp., *Avicennia* spp.) are commonly reported as driftwood (Hyde 1989, Si et al. 2000). At high latitudes of the Northern Hemisphere, primarily coniferous trees (*Abies* spp., *Pinus* spp., *Larix* spp., *Picea* spp., *Tsuga* spp.) have been reported as driftwood (Emery 1955, Strong & Skolmen 1963, Maser & Sedell 1994, Dyke et al. 1997, Johansen 1999, 2001). Deciduous trees (e.g., *Salix* spp., *Betula* spp., *Populus* spp., *Alnus* spp., *Quercus* spp.) appear to be more typical as driftwood in temperate regions (Johansen 1999). Emery (1955) remarked on a gigantic kauri tree (*Agathis australis*) that was 3 m in diameter and held a large boulder between its roots. The majority of driftwood in coastal regions is probably made up from parts of smaller tree or shrub species such as *Arctostaphylos* spp., *Juniperus* spp., *Hibiscus* spp., and others (Emery 1955, Volkmann-Kohlmeier & Kohlmeier 1993).

The importance of trees as transport vehicles had already been recognised by Darwin (1879), who suggested that large rocks had reached remote coral islands via driftwood. Many trees may entangle and form large rafts, sometimes referred to as floating islands, which may harbour a wide diversity of organisms (Wheeler 1916, King 1962), including terrestrial vertebrates such as lizards (Censky et al. 1998). Large rafts that would be sufficient in size to carry large mammals have been reported many kilometres seaward from the mouths of large tropical rivers (St. John 1862, Matthew 1915, both cited in Brandon-Jones 1998). Several authors inferred that the present distribution of large vertebrates (primates, reptiles) in some regions may be based on dispersal via rafting on wood (Brandon-Jones 1998, Rieppel 2002).

Highest abundances of naturally occurring wood are mainly reported from the northern oceans recruiting from large forests in North America and Siberia. Entire uprooted trees may be delivered to the sea by large rivers passing through forest areas (Maser & Sedell 1994, Dyke et al. 1997). Emery (1955) gathered several reports on entire trees floating far out in the ocean. He remarked that wood might be important as transport mechanisms in tropical regions, where large macroalgae are absent. Abundant amounts of driftwood have also been reported from beaches at low latitudes (Abe 1984). In the Southern Ocean wood appears to be of minor significance because of a lack of large forests at higher southern latitudes (Barnes 2002). The presence of wood in the deep sea, far from terrestrial source regions (Wolff 1979, Turner 1981), indicates that wood may potentially be transported over long distances.

There are also large amounts of manufactured wood floating on the surface of the sea. Wooden planks, boards, and entire pallets have been reported (Heatwole & Levins 1972, Reznichenko 1981, Zarate-Villafranco & Ortega-García 2000). For the logs stranded on beaches in a fjord and on the outer coast of Washington State (NW America), Dayton (1971) estimated that 50 and 15%, respectively, had been cut during logging activities. On beaches of subantarctic islands, Convey et al. (2002) found equal proportions of manufactured and natural wood.

Seeds or fruits

Many plants produce positively buoyant seeds or fruits, which can be found on beaches worldwide (Guppy 1906, 1917, Nelson 2000). Some seeds, due to their buoyancy and hard shell, may stay afloat for weeks or months (Skarpaas & Stabbertorp 2001), i.e., sufficiently long to cross entire ocean basins (Table 3). Some of these seeds may have particular adaptations to float at the sea surface (Nelson 2000). For example, the seeds of the blister pod *Sacoglottis amazonica* possess an endocarp full of empty, air-filled cavities or lightweight corky or fibrous tissues, which reduces the specific weight leading to high buoyancy of the seeds. Often an impermeable coat inhibits the absorbance of water so that the seeds will stay afloat for long periods (Nelson 2000). Guppy (1906) examined buoyancy of the seeds from 320 British vascular plants and found that almost 25% of all tested plants possess seeds that float for at least 7 days (Table 4). Floating seeds appear to be of particular importance in tropical regions, where they can be found in high diversity and abundance on beaches (Green 1999). Wolff (1979) also reported several coconuts from the deep sea off the Caribbean coasts. Some very resistant seeds may float for several years and during this time become dispersed throughout the world's oceans, as appears to be the case of the sea hearts from the Fabaceae, *Entada gigas* (= *scandens*), that can be found growing on all major continents (Guppy 1906). Recent molecular studies have confirmed that some terrestrial plant species are efficiently dispersed over long distances via floating seeds (Hurr et al. 1999). Carlquist (1967) also remarked on the high proportion of littoral flora that is thought to be dispersed via floating seeds (or plants). Among floating mangrove seeds, which have been reported by several authors (Steinke 1986, Jokiel 1989), *Rhizophora* is considered a dispersal specialist because its seeds can float for long periods (Duke 1995). Sizes of these so-called sea beans or nickar nuts range from a few millimetres up to about 30 cm in the case of coconuts. The latter have occasionally been observed to be populated by marine (Guppy 1917, Gerlach 1977, Nelson 2000) and terrestrial (Heatwole & Levins 1972)

organisms. Most floating seeds are small, offering little space for epibionts, but some appear sufficiently large to harbour rafting organisms, which may be dispersed during the voyage of the floating seeds. But even small seeds of about 3–6 mm in diameter such as the sea pea *Lathyrus japonicus* subsp. *maritimus* have been found to be overgrown by colonies of the goose barnacle *Lepas fascicularis* (Minchin & Minchin 1996, cited in Nelson 2000).

Animal remains

Dead animals or parts thereof are known to float at the surface providing potential substrata for rafting organisms. The carcasses of marine mammals and seabirds may float for days or weeks at the sea surface (e.g., Baduini et al. 2001). Following death, decomposition processes produce gases, which may accumulate in the body cavity and lead to positive buoyancy, offering the potential for colonisation by flora and fauna. Guppy (1906) provides a particularly vivid account of large numbers of floating animal carcasses from northern Chile. Dead whales floating at the sea surface have also been reported by several authors (Dudley et al. 2000, Verriopoulou et al. 2001, Zarate-Villafranco & Ortega-García 2000, Castro et al. 2002).

Skeletal remains of some marine organisms are positively buoyant, the most typical being calcareous shells of cephalopods. Shells of some species start floating after the animal's death and following decomposition of soft tissues. Skeletons of cephalopods may occasionally be very abundant. Deraniyagala (1951, cited in Deraniyagala 1960) reported an extensive area with abundant floating shells of cuttlefish in the Indian Ocean west of Colombo. Large numbers of *Nautilus* shells can be found during the monsoon season on some beaches in the Bay of Bengal (Teichert 1970). Mark and recapture experiments proved that long distances can be covered by postmortem drift of *Nautilus* shells (Saunders & Spinosa 1979). Based on the degree of shell degradation and the fouling community of *Nautilus* shells found in Thailand, Hamada (1964) inferred that these may have floated at the sea surface for relatively long periods. Observations of a heavily fouled floating *Nautilus* shell by Jokiell (1989) support the suggestion that these may remain afloat for several months. Similar observations have been made for the shells of other cephalopods (Taylor & Monks 1997). A widespread distribution of fossil nautilid shells of the genus *Aturia* indicates that this mechanism has already been active in palaeo-oceans (Zinsmeister 1987, Chirat 2000).

Some reef corals are also known to float after their dried cellular structures are filled with air (DeVantier 1992). Typical rafters such as goose barnacles and bryozoans found growing on coral specimens recently deposited at beaches demonstrate the corals' importance as a neustonic substratum (Kornicker & Squires 1962). Some coral species that have been found floating belong to the genera *Colpophyllia* and *Solenastrea* (Gulf of Mexico, Kornicker & Squires 1962) and *Symphillia* (Great Barrier Reef, DeVantier 1992).

Egg capsules of chondrichthyan fishes and other marine organisms (e.g., molluscs) also float at the sea surface, as can be inferred from their frequent appearance in flotsam deposited on the shore (W. Vader, personal comment). Smith & Griffiths (1997) reported large numbers of egg cases from various species of sharks and skates stranded on South African beaches.

Volcanic pumice

A naturally occurring but abiotic substratum for rafting organisms is floating pumice that has been found to be abundant throughout the atolls of the Pacific (Jokiell 1990). Eruptions of submarine or coastal volcanoes produce large quantities of pumice that are deposited into the sea. Additionally, land-derived pumice is carried to the sea by rivers. Generally, fragments of pumice range in size from rough gravel or pea and marble size (Walker 1950, Coombs & Landis 1966) to walnut or potato size to as large as a man's head, corresponding to about 0.1 m³ (Richards 1958). Jokiell (1984) reported blocks of pumice that exceeded 1 m in diameter and were sufficiently buoyant to support the weight of children who used them as rafts, and fragments of pumice with similar

Table 3 Sizes, buoyancy (longevity at sea surface), and origin of sea beans found on European beaches

Species	Vernacular name	Systematic group	Size (cm)	Buoyancy	Distribution
<i>Acrocomia</i> sp.	Prickly palm	Areaceae	3.5	>2 yr	Tropical America, West Indies
<i>Astrocaryum</i> spp.	Starnut palm	Areaceae	3–4	~2 yr	Tropical America, West Indies
<i>Barringtonia asiatica</i>	Box fruit	Lecythidaceae	1.5	>15 yr	Tropical America
<i>Bertholletia excelsa</i>	Brazil nut, Pará nut	Lecythidaceae	2–3	Few months	Tropical South America
<i>Caesalpinia bonduc</i>	Nickar nut, ash-coloured nickar, gray nickernut, tearna Moire, ritta nut, sea pearl, nickarbean, cat's claw	Fabaceae	2	>19 yr	Tropical America, West Indies, Florida
<i>Caesalpinia</i> sp.	Nickar nut	Fabaceae	2–2.5	Long-distance drift seed	Tropical America
<i>Calophyllum</i> cf. <i>calaba</i>	Calaba (tree)	Clusiaceae	4	~2 yr	Tropical America
<i>Canavalia maritima</i>	Bay bean	Fabaceae	1–2	>19 yr	Tropical America, West Indies, southern Florida
<i>Canavalia nitida</i>		Fabaceae	1.5–2.5	Long-distance drift seed	West Indies
<i>Carapa</i> sp.	Crabwood	Meliaceae	2.5	>4 yr	Tropical America
<i>Carya aquatica</i>	Water hickory	Juglandaceae	3.5	~1 yr	Temperate North America
<i>Carya illinoensis</i>	Pecan	Juglandaceae	2–3	1 yr	Temperate North America
<i>Cocos nucifera</i>	Coconut	Areaceae	20–30	n.i.	America
<i>Calystegia</i> spp.	Bindweeds	Convolvulaceae	0.6	~1.5 yr	Western Europe
<i>Ipomoea</i> spp.	Morning glories	Convolvulaceae	1.7	>19 yr	America
<i>Operculina</i> spp.		Convolvulaceae	0.7	n.i.	America
<i>Dioclea reflexa</i>	Sea purse, cluster pea, vulture's eye	Fabaceae	3.5	>18 yr	Tropical America
<i>Entada gigas</i>	Sea bean, sea heart, Mary's nut, Cuban heart	Fabaceae	2.5–6	>19 yr	Tropical America, West Indies
<i>Erythrina</i> sp.	Coral bean	Fabaceae	1–2	>1 yr	Tropical America
<i>Hemandia sonora</i>		Hernandiaceae	1.5	>3 yr	Tropical America, West Indies
<i>Juglans nigra</i>	Black walnut	Juglandaceae	3–4	~1.5 yr	Eastern North America
<i>Lathyrus japonicus</i> subsp. <i>maritimus</i>	Sea pea, beach pea	Fabaceae	0.4	7 yr	Temperate North America

<i>Manicaria saccifera</i>	Sea coconut, sleeve palm, golf-ball bean	Areaceae	4-5	19 yr	Tropical America
<i>Maximiliana maripa</i>	Maripa	Areaceae	2.5-4	Long-distance drift seed	Tropical South America, West Indies
<i>Merremia discoidesperma</i>	Mary's bean, Mary's kidney, crucifixion bean	Convolvulaceae	2-2.5	~6 yr	Tropical Central America, West Indies
<i>Mucuna sloanei</i>	Horse eye, (true) sea bean, donkey's eye	Fabaceae	2.5	>5 yr	Tropical America
<i>Mucuna</i> sp.	Horse-eye bean	Fabaceae	2.5-4	Long-distance drift seed	Tropical America, West Indies
<i>Pangium edule</i>	Vegetable ivory, ivory nut	Flacourtiaceae	5	>19 yr	Southeastern Asia, Melanesia
<i>Phytalephas</i> sp.	Castor oil (plant), castor bean	Areaceae	4-5	Few months	Tropical America
<i>Ricinus communis</i>	Blister pod, hand grenade, cojon de burra	Euphorbiaceae	1.5	>15 yr	Ubiquitous in frost-free, subtropical regions
<i>Sacoglottis amazonica</i>	Tropical almond, Indian almond, country almond	Humiriaceae	3-4	~5 yr	Tropical South America, West Indies
<i>Terminalia catappa</i>		Combretaceae	5-7	2 yr	Asia, cultivated in Caribbean and Central America

Note: n.i. = no information.

Source: Based on Nelson (2000).

Table 4 Numbers and percentages of British plant species with seeds that float at least 1 wk in freshwater

Minimum time afloat (days)	Total number	Percentage
7 days	20	6.3
30 days	21	6.6
180 days	18	5.6
360 days	20	6.3
Total plants floating	79	24.7
Total plants not floating	241	75.3

Note: A total of 320 species were examined by Guppy (1906), who tested approximately 260 species himself and added information from other authors, including Darwin.

diameters had been reported by Coombs & Landis (1966). Since floating pumice has only little freeboard and the emergent part is quite streamlined, some authors suggest that dispersal of pumice is controlled by currents rather than by wind (Richards 1958, Jokiel 1990). Walker (1950), however, remarked that floating pumice is only half submerged and therefore should be exposed to wind forces. These contrasting reports suggest that the buoyancy characteristics of pumice from different eruptions may vary. Compositional characteristics of pumice can be determined by microscopic and chemical analysis methods allowing for determination of the fragment's origin and its trajectory and travel speed (Frick & Kent 1984, Ward & Little 2000).

Ice

A seasonally occurring phenomenon at high latitudes is floating ice. Complete icebergs or sea, river, or lake ice become stranded in shallow waters where it freezes to the sediment at low tide (Nürnberg et al. 1994, Allard et al. 1998). Occasionally, waves also swash sediment on the top of stranded blocks. At high tide, when the blocks refloat again, large quantities of sediment with inhabiting organisms may be taken away and transported over long distances (Gerlach 1977, Wollenburg 1993, Nürnberg et al. 1994, Reimnitz et al. 1998). Large stones may also be moved after becoming frozen into ice (Bennett et al. 1996). These stones can be transported over considerable distances and become deposited on the seafloor during degradation of the primary floating substratum (plants or ice). In the northern North Atlantic this process was very important during the Holocene and Pleistocene periods (Oschmann 1990), but sediments are still transported by sea ice today (Ramseier et al. 1999, Hebbeln 2000). Rouch (1954) even mentioned floating icebergs near Bermuda and south of the Azores. In many cases, distances of ice rafting are probably limited, but dormant stages frozen into the ice may be transported over long distances (Johansen & Hytteborn 2001). In northern New England the displacement of ice-frozen blocks of salt marsh peat containing intertidal organisms such as the ribbed mussel *Geukensia demissa* from higher to lower elevations on the tidal flats causes significant impact on the intertidal community (Hardwick-Witman 1985). Schneider & Mann (1991) report on patches of sea grass that become frozen to the underside of ice "pans" of several square metres in Nova Scotia (Canada). Similar observations have been made for the brown algae *Fucus vesiculosus* (Rönnerberg & Haahtela 1988) and *Ascophyllum nodosum* (Mathieson et al. 1982), which are lifted from the substratum when the ice floats up again at high tide. Low temperatures do not present an immediate problem because attached animals frozen to the underside of ice are still in contact with the seawater. Furthermore, it has been shown that

meiofauna species can survive periods of being totally frozen into sediment (Jansson 1968). Members of the specialised under-ice fauna (e.g., Werner 1999) may also be dispersed via ice transport, as has been observed for under-ice diatoms (Fischer et al. 1988).

Floating marine debris of human origin

Anthropogenic debris can be found in a variety of shapes and sizes in all parts of the world's oceans. Due to its low specific gravity and durability, a high proportion of anthropogenic debris may remain afloat for long periods before being cast ashore. In some areas, anthropogenic litter may be far more abundant than natural floating substrata. For example, Castro et al. (2002) remarked that most floating objects found by fishermen are of anthropogenic origin. Input of litter from land occurs via rivers and drainage systems or as a result of recreational activities on beaches. During the 1970s and 1980s large amounts of anthropogenic litter also originated from shipping activities, with the main contributor among the vessels being merchant ships, with a proportion of about 85% (Pruter 1987). It is assumed that the amount of ship-generated debris has decreased since then, due to improved legislation and land-based disposal facilities. Plastic items, consisting of low-density polyethylene, polystyrene, or polypropylene (Pruter 1987), are the most common man-made objects floating in the oceans. Pieces of plastic, which mainly represent primary or secondary packaging material such as plastic bottles or cups and plastic bags, make up 60–70% of floating debris in the Mediterranean Sea (Morris 1980a) and 86% in the SE Pacific off the Chilean coast (Thiel et al. 2003a). Similar proportions are reported from beach surveys in many other parts of the world (Derraik 2002).

Commercial fisheries are responsible for significant input of anthropogenic debris into the sea. Each year, large quantities of fishing gear are dumped or lost in the world's oceans (Derraik 2002). Especially in regions with intensive fishery activities such as Alaska, many remains of nets, floats, and fish boxes can be found cast up on beaches (Merrell 1984). Fishermen themselves construct floats to attract fishes (Castro et al. 2002, Nelson 2003), but at present it is not known what proportion of these floats is lost annually to start independent voyages attracting and carrying rafting organisms through the world's oceans. Cornelius (1992) also reports that buoys with a rich rafting fauna occasionally reach the shores of the Azores. Aquaculture facilities throughout the world are suspended on large rafts or buoys, providing a large potential for the input of items with a very high buoyancy and longevity. In some regions of the world, large numbers of buoys are placed in the sea to support suspended cultures, and a large proportion of these buoys may be lost annually. Buoys originating from aquaculture facilities have occasionally been reported unattached and floating in coastal waters (Jara & Jaramillo 1979, Thiel et al. 2003b).

All these items (Styrofoam, plastic and glass bottles, bags, buoys) are relatively large in size (>>1 cm in diameter) and can thus be characterised as macrolitter. Besides these large items there is a whole suite of floating plastics substantially smaller than 1 cm in diameter. The majority of these are small (1–5 mm in diameter) polystyrene spherules (also called plastic pellets) that have their origin in plastic-producing or -processing plants (Colton et al. 1974). Microalgae and bacteria may grow on these plastic pellets (Carpenter & Smith 1972). Since these pellets are similar in size to many neustonic invertebrates, they are frequently ingested by seabirds (Vlietstra & Parga 2002).

Tar lumps

Tar lumps, which are in the same size range as plastic pellets, are commonly found floating at the sea surface along major shipping routes but also in regions of heavy oil exploitation and processing plants (Cordes et al. 1980). Tar lumps represent residues of oil or petroleum, which have been exposed to a variety of biological, chemical, physical, and geological processes that alter their chemical composition and physical form (Levy & Walton 1976). Analytical chromatographic

methods revealed a high concentration of iron in most of the tar lumps, indicating that they were most likely released into the marine environment from tankers as a result of offshore hull washing (Shaw & Mapes 1979). Shortly after release the heavier and waxier fraction of crude oil forms into tar lumps (Butler 1975). Lumps ranging in size from 1–2 mm up to 10 cm (Horn et al. 1970, Ehrhardt & Derenbach 1977) are regularly found to be colonised by algae and animals such as isopods and barnacles (Wong et al. 1974, Butler 1975, Minchin 1996). Because tar lumps are distributed mainly by surface currents, a frequent co-occurrence with pelagic *Sargassum* in the North Atlantic is not surprising (Cordes et al. 1980). Tar lumps and other floating items, such as macroalgae, often stick together (Cordes et al. 1980). Colour, shape, and consistency of lumps vary with time of exposure to marine conditions. Shortly after formation tar lumps are soft, but with increasing time they become harder (Cordes et al. 1980). Toxicity for rafting organisms could not be proved. Limited growth of barnacles on tar lumps compared with specimens associated with pumice cannot be attributed unequivocally to a toxic effect of oil compounds (Horn et al. 1970).

Floating sediments

Under certain conditions sediments may briefly float at the sea surface, but they rarely remain floating for more than a few hours. In shallow subtidal waters, agglutinations of benthic microalgae form dense mats on the sediment surface and may occasionally become positively buoyant. The mats are primarily composed of blue-green algae (Phillips 1963) or dinoflagellates (Faust & Gullede 1996). During the day, the microalgae photosynthesise, producing oxygen bubbles that become entrapped in the mucus matrix (locally termed *gunk* or *scum*). In calm conditions (e.g., in well-protected embayments or lagoons) these mats may then rise to the water surface during the day, but during the late afternoon, when photosynthetic production of gases decreases, the mats sink back to the sediment surface (Phillips 1963, Faust & Gullede 1996). Many organisms (entrapped microalgae, ciliates, nematodes, copepods) are lifted to the sea surface with these floating algal mats (Phillips 1963, Faust & Gullede 1996), but dispersal probably occurs on a highly local scale, rarely exceeding 100s of metres.

Nordenskiöld (1900) reported small “floating stones”, on which he observed small gaseous bubbles. He suggested that these bubbles may be produced by a thin layer of algae covering these small stones. Sediment grains themselves may be held at the water surface by surface tension. This process may transport individual grains several 100 m from the site of origin before they become wet and sink (Möller & Ingólfsson 1994), but it is unlikely that this process is of ecological importance for rafting organisms.

Chemical and physical properties of floating items

Floating items differ substantially in their chemical composition and physical characteristics. The chemical composition of a floating item will primarily determine its nutritional value to rafting organisms, as well as its resistance to weathering. Physical characteristics include the specific gravity, surface texture, and surface area of a floating item. These factors have an important influence on (1) potential rafting organisms and (2) the longevity of a floating item. Chemical and physical properties of floating items have been little studied in the past. Herein these characteristics are only briefly explored in the context of rafting and specific studies are referred to where these are available.

Biotic items have a high content of organic carbon. Most floating plants are rich in carbohydrates, but concentrations of lipids and proteins are usually low (Hay 1994, North 1994). A specialised assemblage of grazing or boring animals may feed on floating plants. Some macroalgae can produce secondary metabolites that deter grazers (Hay & Steinberg 1992, Hammerstrom et al. 1998), but it is not known to what extent this is also true for floating macroalgae. Wood commonly is high in lignin and tannin compounds rendering these items unattractive as food sources for most

organisms, with the exception of a few highly specialised boring organisms (e.g., Smith & Simpson 1995, Cragg 2003). Seeds are high in lipid and protein content and they are often protected by lignified shells. Guppy (1906) provides an interesting account on the specific gravity of the seeds of some coastal trees (e.g., *Rhizophora mangle*). These have a specific gravity between 1.000 and 1.025, which means that most seeds float in seawater but sink in freshwater. In contrast, the seeds of most inland plants have a substantially higher specific gravity and immediately sink in sea water. Animal carcasses are high in nitrogen and phosphate compounds (lipids and proteins), which renders them attractive to a wide variety of scavenging organisms (e.g., Dudley et al. 2000). Floating skeletal remains consist mainly of CaCO_3 and are of no nutritional value. Floating objects such as macro- and microlitter, namely, plastics, primarily consist of cyclic hydrocarbons and typically have a low specific gravity. These objects have little nutritional value for metazoans but may be prone to microbial attack. This is also true for tar lumps, which are largely decomposed by microorganisms (Gunkel 1988).

The specific gravity of floating items determines their buoyancy, but relatively little is known about the specific gravity of most floating items. As a result of degradation processes or penetration by water, the specific gravity of many floating items may change with time. Also, the rafting organisms themselves contribute to changes in specific gravity of the floating assemblage (= item + fouling community), as has been suggested for macroalgae overgrown with bryozoans (Hobday 2000a). The specific gravity of unfouled plastics may vary between 0.88 and 0.92 (Styrofoam = 0.045), but with increasing growth of the fouling community the specific gravity of the entire assemblage also increases, which results in sinking (Ye & Andrady 1991). Holmström (1975), who found plastic films on the seafloor of the Skagerrak (180 to 400 m water depths), suggested a similar process. Items such as glass bottles or volcanic pumice are mainly composed of silica oxides (SiO_2) (Frick & Kent 1984) and are of no nutritional value to potential rafters. Most floating items owe their buoyancy to enclosed gas (air). This is true for most macroalgae, many seeds, corals, volcanic pumice, and floating sediments.

The chemical composition of a floating item will influence not only its buoyancy but also the rafting organisms capable of colonising it. Some biotic substrata may have a high nutritional value, but others may be rather unattractive to secondary consumers. Most grazing organisms can only colonise macroalgae or large floating items with algal epiflora. Similarly, some sessile organisms may only settle on abiotic materials. For example, Winston (1982) found the bryozoan *Electra tenella* to be abundant on plastic items but not on equally available *Sargassum* spp. She considered that the larvae of *Electra tenella* might not be able to attach to *Sargassum* spp. or might avoid this alga in response to chemical compounds. In this context it should be noted that plants of *Macrocystis pyrifera* often are heavily encrusted with the bryozoan *Membranipora isabelleana* (Muñoz et al. 1991), but blades of *Durvillaea antarctica*, which grows in the same region, usually are completely free from bryozoan epibionts (personal observations). The chemical composition or the surface characteristics of the floating substratum may affect whether a potential rafting organism can settle successfully on a floating item (Steinberg & de Nys 2002). Larvae of sessile invertebrates are highly substratum specific (Steinberg et al. 2002), and it can therefore be expected that this is also true for floating substrata. The hydrophobic or hydrophilic nature of substrata apparently may have relatively little effect on larval settlement (Dobretsov & Railkin 1996, Holm et al. 1997), but surface area or rugosity may determine which and how many organisms can settle and establish successfully on floating substrata, as similarly observed on benthic substrata (Wahl & Hoppe 2002). Maser & Sedell (1994) discuss the surface texture of floating wood and its effect on the assemblage of organisms colonising it.

The specific surface area of most substrata has not been examined in detail, even though it can be assumed to have a strong influence on the number of rafting organisms able to inhabit a floating item. The specific surface area has been identified for common plastic microlitter. It ranges from 9–217 $\text{cm}^2 \text{g}^{-1}$ for rope and plastic bags, respectively (Ye & Andrady 1991). Reznichenko (1981) measured the total surface area of some medium-size floating items: a piece

of foam rubber had a total surface area of 10 cm², whereas a large piece of wood had 5000 cm². These authors also counted the individuals of gooseneck barnacles *Lepas* spp. on these substrata and found a significant positive relationship between the surface area of a floating item and the number of lepadids growing on it. Donlan & Nelson (2003) reported a significant positive relationship between the surface area of floating items and the species richness of rafting fauna. On items with a complex surface, such as macroalgae, ropes, Styrofoam, and pumice, the specific surface area available for organisms may be substantially higher than that on structurally simple items such as plastic bottles. Several authors have acknowledged the importance of structural complexity and the number of rafting organisms. Bushing (1994) remarks that the morphology of the holdfasts of different floating macroalgae may vary substantially, thereby influencing their suitability as rafting habitat. Holdfasts of *Macrocystis pyrifera* are characterised by their extensive haptera leaving many interstitial spaces that can be inhabited by potential rafters. In contrast, *Pelagophycus porra* or *Durvillaea antarctica* have rather compact holdfasts offering relatively little interstitial spaces (Edgar & Burton 2000). However, grazers and borers may excavate wide cavities in these holdfasts (Smith & Simpson 1995), thereby increasing the surface area accessible to potential rafting species. Future studies should examine how the specific surface area of a floating item affects the composition of the rafting assemblage.

The different floating substrata also differ substantially in their sizes (Table 5). Similar to surface area, the size of a floating item may have a strong influence on the number of species and individuals that can colonise it. Small items such as plastic pellets (microlitter) or tar lumps are mainly colonised by unicellular or small clonal organisms (Carpenter & Smith 1972), and it has been emphasised that these items rarely host larger solitary organisms (Minchin 1996). Medium-size items, such as plastic bottles, small algae, animal remains, or volcanic pumice, may harbour larger organisms such as stalked barnacles or hydroid colonies (Reznichenko 1981). Macroalgae may form large patches (Figure 4), which commonly are inhabited by dense populations of associated animals (e.g., Hobday 2000a). Very large floating items, such as trees or “floating islands,” may harbour large organisms, including terrestrial vertebrates (Censky et al. 1998, Raxworthy et al. 2002). Rouch (1954) mentions one floating island from the Atlantic that was approximately 4000 m² in area. Floating islands of several metres in diameter and consisting of trees, grasses, and even soil have been reported by a variety of authors (Moseley 1879, Guppy 1906, Rouch 1954, King 1962), but to our knowledge no specific studies on the assemblage of rafting organisms on these floating islands have been conducted. In general, it can be assumed that the size of a floating item has a strong influence on the abundance and diversity of the rafting assemblage, such as has been shown for many floating items (Figure 5) (see also Fine 1970, Butler et al. 1983, Stoner & Greening 1984, Ingólfsson 1995, 1998, Calder 1995, Hobday 2000a, Ólafsson et al. 2001). Large items also harbour dense assemblages of many individuals forming small local populations, i.e., demes (Gutow & Franke 2003).

Longevity and dynamics of floating objects

At present it is difficult to obtain estimates for the longevity of floating substrata at the sea surface, and most estimates have been obtained by indirect measures. For example, Tsikhon-Lukanina et al. (2001) used growth rates of stalked barnacles to estimate the age of floating objects in the NW Pacific. Helmuth et al. (1994a) and Hobday (2000b) used morphological measures of algal blades to estimate the longevity of *Macrocystis pyrifera* at the sea surface. Other authors used known delivery dates of floating items to the sea and recapture dates in order to obtain a measure for the duration of floating. For example, the dates of some volcanic eruptions in the Pacific Ocean are well known and have been used to estimate longevity of volcanic pumice (e.g., Richards 1958, Coombs & Landis 1966). Similarly, the accidental input of large amounts of well-identifiable plastic items has been used to track the routes and longevity of these items (Ebbesmeyer & Ingraham 1992). Some authors also marked floating items and followed them over time or monitored the

Table 5 Sizes and weights of different floating objects

Substratum	Region	Size	Weight (kg item ⁻¹)	Reference
Macroalgae	Tropical and subtropical Atlantic	<0.5 m (L)		John 1974
Macroalgae	California		0.2–75	Kingsford 1995
Macroalgae	California		Ranging from a few grams to 100s of kilograms	Gerard 1976, cited in Harrold & Lisin 1989
Macroalgae	California	1–15 m		Hobday 2000c
Macroalgae	California		2–160	Hobday 2000a
Macroalgae	Mexico		1.4 to >450	Mitchell & Hunter 1970
Macroalgae	Japan		0.1–4.0	Ida et al. 1967
Macroalgae	Japan		5–150	Ikehara & Sano 1986
Macroalgae	Japan	2.0–72.5 m ² (SA)		Mitani 1965
Macroalgae	Japan		<1.0 to ~6	Ohno 1984b
Macroalgae	Japan		15–150	Segawa et al. 1959a
Macroalgae	Japan		>40	Segawa et al. 1959b
Macroalgae	Japan		<1 to >300	Senta 1962
Macroalgae	Japan		3.7–7.7	Tanigawa 2001
Macroalgae	Japan	0.5–4.0 m ² (SA)	0.5–5.0	Ohno 1984a
Macroalgae	New Zealand		Mostly < 0.5	Kingsford 1993
Macroalgae	New Zealand		0.003–1.4	Kingsford & Choat 1986
Macroalgae	Australia		0.1–3.8	Druce & Kingsford 1995
Macroalgae	Scotia Arc	1–6 m		Helmuth et al. 1994b
Macroalgae	Iceland		0.01–1.2	Ingólfsson 1995
Macroalgae	Iceland		0.2–0.35	Ingólfsson 1998
Macroalgae	Iceland		0.006–6.1	Ingólfsson 2000
Mangrove propagules	South Africa	~0.03 m		Steinke 1986
Sea beans	South Africa	0.1 m		Muir 1934
Sea beans	European beaches	0.004–0.3 m		Nelson 2000
Tree	Costa Rica	0.3 m, 10 m (L)		Hunter & Mitchell 1967
Wood	Puerto Rico	0.06 m, 0.6 m (L)		Heatwole & Levins 1972
Sediment rafts	New Zealand	<0.03 to >0.2 m		Hicks 1988

-- continued

Table 5 (continued) Sizes and weights of different floating objects

Substratum	Region	Size	Weight (kg item ⁻¹)	Reference
<i>Nautilus</i> shells	Thailand	0.09–0.2 m		Hamada 1964
Floating corals	Gulf of Mexico		0.5–43.6	Kornicker & Squires 1962
Pumice	Hawaii	0.1 m		Jokiel 1984
Pumice	South Africa	0.02–0.1 m		Walker 1950
Pumice	Hawaii	~1 m		Jokiel 1984
Pumice	Hawaii	0.000001–0.1 m ³ (V)		Richards 1958
Pumice	New Zealand	Up to about 0.45 m		Coombs & Landis 1966
Pumice	Australia	~0.03 m		Jokiel 1990
Pumice	Japan	0.001–0.02 m		Fushimi et al. 1991
Tar lumps	North Atlantic	<0.01 to ~0.04 m		Levy & Walton 1976
Tar lumps	Mediterranean	0.001–0.1 m		Butler 1975
Tar lumps	NW Atlantic	Up to 0.02 m		Cordes et al. 1980
Tar lumps	NE Atlantic	0.001 to ~0.07 m		Ehrhardt & Derenbach 1977
Tar lumps	North Atlantic	0.001–0.1 m		Horn et al. 1970
Tar lumps	North Atlantic	0.002–0.035 m		Minchin 1996
Micro litter	Central North Pacific		2×10^{-5}	Moore et al. 2001
Micro litter	South Africa		1.0×10^{-7} to 1.9×10^{-5}	Ryan 1988
Plastic pellets	Lebanon	0.002–0.005 m	5×10^{-6} to 7×10^{-6}	Shiber 1979
Plastic spherules	NW Atlantic	0.0001–0.002 m		Carpenter et al. 1972
Plastic particles	Sargasso Sea	0.003–0.005 m	1×10^{-5} to 2×10^{-4}	Carpenter & Smith 1972
Plastic particles	NW Atlantic	0.0002–0.005 m	1.0×10^{-7} to 2.5×10^{-5}	Colton et al. 1974
Micro litter	North Pacific		1×10^{-5} to 4×10^{-5}	Day & Shaw 1987
Plastic granules	New Zealand	~0.005 m	3×10^{-5}	Gregory 1978
Micro litter	California	0.0004 to >0.005 m		Moore et al. 2002
Macrolitter (60–70% plastics)	Mediterranean	>0.02 m		Morris 1980a
Buoys from fishing gear	Hawaii	0.2–0.3 m		Jokiel 1984
Buoys from aquaculture	Chile	0.24–0.37 m ² (SA)		Thiel et al. 2003b
Fishing nets	Alaska		5–11.5	Merrell 1984

Note: Values represent diameter unless noted otherwise. SA = surface area; L = length; V = volume.



Figure 4 Large patch of floating macroalgae (*Macrocystis pyrifera* and *Durvillaea antarctica*) from southern Chile.

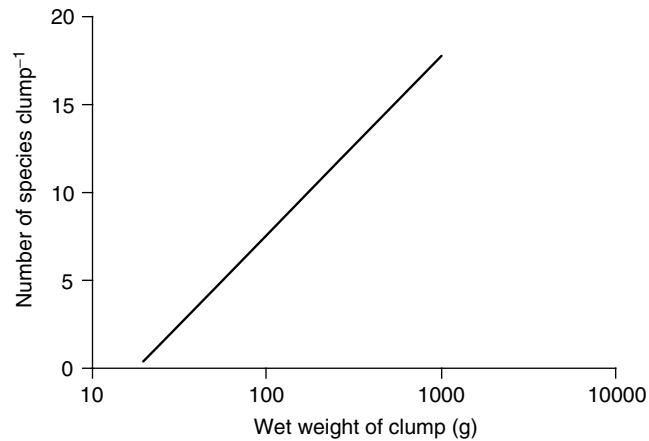


Figure 5 Relationship between substratum size and species number on floating macroalgae collected in coastal waters of SW Iceland; algal patches (≥ 62 g WW) consisted mainly of *Ascophyllum nodosum* and *Fucus vesiculosus*. (Modified after Ingólfsson 1998.)

arrival dates at the shoreline (Segawa et al. 1962, Harrold & Lisin 1989). The simplest method to obtain estimates of the longevity of a floating item at the sea surface is to maintain it in seawater in the laboratory, as has been done extensively for a wide diversity of plant seeds by Darwin (1859), Guppy (1906, 1917), Nelson (2000), and Skarpaas & Stabbertorp (2001).

Longevity of floating objects at the sea surface is limited by three major processes: raft destruction, loss of buoyancy, and stranding on a shoreline. According to their consistency and resistance to degradation, different substrata show different degrees of susceptibility to these processes. Raft destruction may be due to biological and physical processes. Organisms may feed or burrow into floating items. Biotic substrata are particularly prone to attack from organisms. A variety of rafting organisms are known to feed on macroalgae, wood, and animal remains, and they may thereby contribute to the demise of floating items. Abiotic substrata such as skeletal remains, pumice, or plastics are less susceptible to biologically caused degradation. Exposure to light, temperature variations, or chemical substances may primarily be responsible for the progressing degradation (weathering) of these floating items. Different mechanisms may cause a loss of buoyancy, but the two most important ones are penetration by water and overgrowth with fouling organisms. Most floating items owe their buoyancy to the presence of air-filled spaces. When these spaces become filled with water, the items will become negatively buoyant and sink to the seafloor. While afloat, many items become overgrown by a wide diversity of organisms, most of which are negatively buoyant. When the epibiont load of a floating item exceeds its buoyant capacity, the

respective item will start to sink (Ye & Andrady 1991). As long as floating items resist destruction and loss of buoyancy, they float at the sea surface at the mercy of winds and currents. In many cases wind and waves may be responsible for the final decommissioning of floating items by throwing them up onshore.

The survival times of floating items at the sea surface vary considerably. Some items start sinking after floating for a few hours, whereas others can potentially remain afloat for many years (Table 6). As a consequence of their high resistance to biological destruction, many abiotic substrata feature high longevity, but some biotic substrata may retain their floatability for long periods.

Many macroalgae are perfectly able to survive after being detached from their primary substratum (Norton & Mathieson 1983). Floating branches of macroalgae survive, continue rapid growth, and can even become fertile for at least several weeks after detachment (Norton 1976). Some floating macroalgae fragment actively, possibly as a mechanism of asexual reproduction. Fragmentation has been reported for, e.g., *Macrocystis pyrifera* (van Tussenbroek 1989) and *Codium fragile* (Chapman 1999). Fragments broken from attached sporophytes of giant kelp continued to grow for at least 3 months thereafter and these thalli developed normally, forming blades and pneumatocysts (van Tussenbroek 1989). On the stipes of detached fragments of *Macrocystis pyrifera* new hapters may form (van Tussenbroek 1989), possibly facilitating reattachment of these fragments on hard substrata.

Other macroalgae (e.g., *Sargassum* spp.) are also known to continue growth while floating (Winge 1923, Parr 1939), but very little is known about growth rates of floating macroalgae. Over a 2-wk period of growth experiments in the laboratory, Howard & Menzies (1969) reported an increase in weight of 47% and in length of 20% in floating fragments of *Sargassum*. However, while attached algae gain sufficient nutrients from passing waters, detached algae move along within the same body of water over long periods. Growth of *Macrocystis pyrifera* is mainly limited by nitrate (Brown et al. 1997). Resulting metabolic deficiencies may cause damage and tissue loss, which compromise the buoyancy of a plant if the pneumatocysts are affected. Regions of low dissolved nitrogen content such as the Tasman Sea may therefore act as efficient barriers for epipelagic transport by drift algae because of insufficient plant growth resulting in negative buoyancy (Edgar 1987). Even if *M. pyrifera* was able to maintain growth for about 2 wk in low-nitrogen waters by using internal reserves (Gerard 1982), accumulation of water in the pneumatocysts reduces floating capacity, especially of older plants (Cribb 1954). In laboratory experiments, pneumatocysts of *M. integrifolia* lost their buoyancy within about 7 days (Yaninek 1980, cited in Harrold & Lisin 1989). However, when floating in waters with sufficient nutrient supply, *M. pyrifera* has proven to be much more persistent. Measuring changes in blade length, Hobday (2000b) estimated floating periods of up to 100 days for *M. pyrifera* in the Southern California Bight (water temperatures of 15–23°C). Based on current directions and distance from potential source regions, Helmuth et al. (1994b) suggested similar survival times for rafts of *M. pyrifera* in the West Wind Drift, east of Cape Horn. For Japanese waters, Ohno (1984a) mentions that floating mats composed of *Sargassum* spp. may remain afloat for 2–4 wk. The species *S. natans* and *S. fluitans* from the Sargasso Sea are holopelagic and no benthic populations are known (Parr 1939). To our knowledge the floating populations of all other macroalgae are continuously resupplied from benthic populations. The particular adaptations of *S. natans* and *S. fluitans* to their holopelagic existence remain to be revealed.

Temperature has been shown to strongly affect survival of attached plants of giant kelp (e.g., Kirkman & Kendrick 1997, Tegner et al. 1997, Dayton et al. 1998). During incursions of warm waters (e.g., during El Niño events), kelp beds virtually disappear (Ladah et al. 1999). Similar effects can be expected for floating algae, which could explain the rapid decay of detached *Macrocystis pyrifera* at high temperatures (see e.g., Hobday 2000b). Interestingly, floating *Sargassum* spp. from the Sargasso Sea proper appear to have an optimum survival at high water temperatures. Several authors have noted that *S. fluitans* and *S. natans* cannot survive in waters of <18°C (Winge 1923, Parr 1939).

The temperature of the seawater may control not only the physiological status of the macroalgae but also the metabolism of prevailing grazers. The isopods *Phycolimmoria* spp. have been found to

cause significant loss of holdfasts (the most densely populated parts of the plant) by boring activity (Edgar 1987). Destruction of algae by grazing organisms appears to be highly correlated with temperature. Low metabolic rates of consuming animals at high latitudes result in low consumption of algal material. In cold Icelandic waters, the fucoid brown alga *Ascophyllum nodosum* did not show any signs of decay after more than 40 days afloat (Ingólfsson 1998). The same algal species is destroyed rapidly by grazing isopods at moderate temperatures in the North Sea, with a consumption rate of up to $60 \text{ mg animal}^{-1} \text{ d}^{-1}$ (Gutow 2003). For *Macrocystis pyrifera*, Hobday (2000b) demonstrated that loss of biomass increases dramatically when temperatures exceed 20°C (Figure 6). Vásquez (1993) also witnessed a rapid degradation of tethered kelp holdfasts during the buildup of large populations of common mesograzers. Some of the most important grazers on floating macroalgae are isopods and amphipods (Edgar 1987, Ingólfsson 1998, Hobday 2000a, Gutow 2003), and their metabolism may increase with temperature (e.g., Bulnheim 1974 for *Idotea baltica*).

Observations by Parr (1939) on floating *Sargassum* spp. indicate the importance of consumers and epibionts in causing loss of buoyancy in macroalgae. He mentioned that large quantities of *Sargassum* spp. are carried into the Gulf of Mexico, where plants apparently degrade and sink to the seafloor. He further remarked that *Sargassum* plants caught in the northwestern Gulf of Mexico are heavily overgrown with bryozoans (*Membranipora* spp.) and other epifauna. Similar observations were made by Helmuth et al. (1994a) for floating patches of *Macrocystis pyrifera* in the West Wind Drift east of Tierra del Fuego, Argentina. The farther away patches were from potential source regions (Tierra del Fuego), the more signs of degradation and overgrowth with rafting epifauna did they present. Both authors suggested that downcurrent regions may represent sinks for these floating macroalgae. In this context, the observation by Safran & Omori (1990) that floating *Sargassum* toward the east of Japan decreased in size with increasing distance from the coast might be indicative of the progressing degradation with distance from the source region.

In general, macroalgae appear to be important as vectors for large-scale dispersal of associated animals mainly at mid- and high latitudes (Fell 1967). In these regions, macroalgae generally are large and thus more resistant to the degrading effect of herbivorous organisms, which themselves exhibit lower metabolism at low temperatures. At present it is not known whether floating macroalgae produce antiherbivore substances, as has been shown for many attached macroalgae such as *Ascophyllum nodosum* (Pavia et al. 1997).

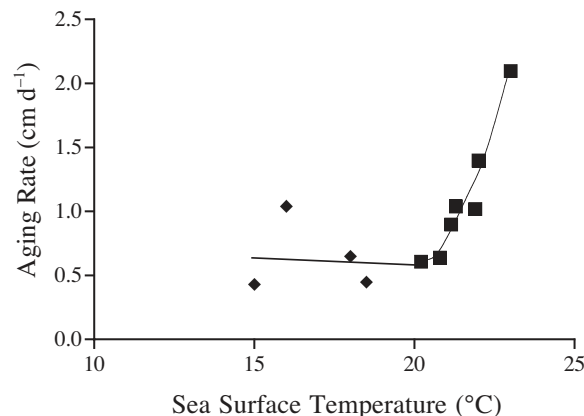


Figure 6 Estimates of the effect of temperature on the ageing rate of floating *Macrocystis pyrifera* tethered in nearshore waters of California; ageing rate based on decrease in blade length. (Modified after Hobday 2000b.)

Table 6 Longevities of different floating objects

Substratum	Region	Longevity (days)	Method	Remarks	Reference
Macroalgae	Scotia Arc	75–100	Estimate of drift period		Helmuth et al. 1994a
Macroalgae	Japan Sea	Up to 50	Mark and recapture		Segawa et al. 1962
Macroalgae	Southern Ocean	>260	Estimate of drift period		Smith 2002
Macroalgae	Japan Sea	~170	Mark and recapture		Ida et al. 1967
Macroalgae	Japan Sea	60	Mark and recapture		Yoshida 1963
Macroalgae	Japan Sea	14–30	Determined from records of fishery stations		Ohno 1984a
Macroalgae	Southern Ocean	~150	Estimate of drift period		Arnaud et al. 1976
Macroalgae	Tasmania	Up to 180	Estimated from feeding rates of inhabiting isopods	Longevity refers <i>only</i> to the holdfasts of the plants	Edgar 1987
Macroalgae	Iceland	>43	Mark and recapture		Ingólfsson 1998
Sea grass fruits (<i>Enthalus acoroides</i>)	Philippines	~6	Floating experiments		Lacap et al. 2002
Sea grass fruits (<i>Thalassia hemprichi</i>)	Philippines	~2.5	Floating experiments		Lacap et al. 2002
Seeds (<i>Mertensia maritima</i>)	North Atlantic	>60	Floating experiments		Skarpaas & Stabbetorp 2001
Mangrove propagules (<i>Avicennia marina</i>)	South Africa	~7	Floating experiments		Steinke 1986
Floating mangrove detritus	Belize	~0.5	Direct observation		Faust & Gullledge 1996
Mangrove propagules	Panama	3–55	Floating experiments	Propagules of some species can regain buoyancy after an initial sinking period	Rabinowitz 1978
Seeds of terrestrial plants (<i>Anchusa crispera</i>)	Mediterranean	Up to 1	n.i.		Quilichini & Debussche 2000
Sea beans	European beaches	>1000	Floating experiments		Nelson 2000
Wood (frozen into ice)	Arctic	>1000	Estimate of drift period		Dyke et al. 1997
Logs	Southern Ocean	>1000	Estimate of drift period		Deacon 1960
Seabird carcasses	Bering Sea	~14	Direct observation		Badumi et al. 2001
Corals		5 to >240	Floating experiments		Kornicker & Squires 1962

Corals	Australia	>30	Estimated from the size of sessile rafters	DeVantier 1992
<i>Nautilus</i> shell				
Pumice	Hawaii	>140 >1000	Mark and recapture Estimated from the size of sessile rafters	Saunders & Spinosa 1979 Jokiel 1984
Pumice	Australia	>1000	Estimate of drift period	Jokiel 1990
Pumice	Palau Islands	>790	Estimate of drift period	Richards 1958
Pumice	Tasmania	>600	Estimate of drift period	Sutherland 1964
Pumice	New Zealand	>600	Estimate of drift period	Coombs & Landis 1966
Plastic shoes	North Pacific	>300	Estimate of drift period	Ebbesmeyer & Ingraham 1992
Plastic debris	Florida	~120	Estimate of drift period	Winston 1982
Plastic debris	Florida	50-60	Estimate of specific gravity	Ye & Andraday 1991
Plastic debris	Southern Ocean	>300	Estimated from the size of sessile rafters	Barnes & Fraser 2003
Tar lumps	Mediterranean, NE Atlantic	>60	Estimated from the size of sessile rafters	Horn et al. 1970
Tar lumps	North Atlantic	~60	Estimated from the relation of input rate vs. average density	Levy & Walton 1976
Tar lumps	Gulf of Mexico	~360	n.i.	Cordes et al. 1980

Note: Estimates based on field and laboratory experiments or approximate drift periods. n.i. = no information.

Grazers may also partially destroy pneumatocysts, thereby permitting entry of water. However, even if associated animals do not destroy the algae by grazing activity, overgrowth with sessile organisms may reduce buoyancy, especially of older plants, because epibionts contribute to an increase in the specific gravity of the floating assemblage (Hobday 2000a). In particular, bryozoans are expected to increase the plant's weight significantly because of their calcareous skeleton. Additionally, macroalgae fouled by bryozoans suffer greater blade loss than plants that are not overgrown because fouled blades become fragile and break off easily and because fishes bite off chunks of blade while foraging on the attached bryozoans (Dixon et al. 1981). Once their floatability is seriously compromised by epibionts, macroalgae may be easily submerged in the convergence zones of Langmuir circulations (Barstow 1983). The largest Langmuir cells occurring at strong wind forces might cause *Sargassum* plants to sink below the critical depth of 100 m at a downward circulation speed of 10 cm s^{-1} . Once sunk below this critical depth, the hydrostatic pressure causes ruptures in the wall of the plant's pneumatocysts. Air bubbles escaping from the rupture indicate an irreversible loss of buoyancy (Johnson & Richardson 1977) and plants will sink to the seafloor where they may become food to benthic organisms. Schoener & Rowe (1970) presented images of entire *Sargassum* plants at depths of >5000 m, with a brittle star being a major consumer of algal material.

Generally, it can be expected that floating objects caught in coastal current systems have a high probability of being cast up onshore (Harrold & Lisin 1989). This is illustrated by the fact that all different types of floating objects have been found on beaches worldwide. The height at which an object becomes stranded on the beach depends on wave action and size and weight of the particular object. During storms and spring tides floating items may be washed up high on the shore. The higher an object is cast up, the lower the probability of being resuspended in the water (Yaninek 1980, cited in Harrold & Lisin 1989). Especially macroalgae growing in coastal waters are in great danger of being washed ashore. In Monterey Bay (California) most detached *Macrocystis pyrifera* apparently remain within the bay and are deposited on the shore during the first few days after detachment (Harrold & Lisin 1989). A large proportion of kelp rafts (45%) floating in offshore waters of Southern California Bight return to the Californian coast after an average of 10 days and a displacement of 56 km (Hobday 2000c). Probably, the majority of uprooted macroalgae is cast up on the beach shortly after detachment by strong onshore waves. Once stranded, algae are degraded rapidly (Inglis 1989) by beach-dwelling insects and amphipods (Griffiths & Stenton-Dozey 1981, Marsden 1991). In western Australia the amphipod *Allorchestes compressa* feeds on large accumulations of detached macrophytes sweeping around in the surf zone of sandy beaches (Robertson & Lucas 1983). High densities (>100 individuals g dry weight^{-1} of vegetation) of *A. compressa* consume stranded kelp *Ecklonia radiata* at considerable rates, especially at high summer temperatures. Similar processes have been invoked for algae caught on rocky shores, which are rapidly consumed by sea urchins and other shore-dwelling organisms (Rodríguez 2003). After making contact with the shore substratum, algae may also be covered by sediments. Regardless of the process (decomposition by animals or covering by sediment), there appears to be little likelihood that an alga returns to the sea in a floatable stage after being cast up on the shore. The fate of beach-cast material has been extensively reviewed by Colombini & Chelazzi (2003).

The same mechanisms found to reduce the longevity of macroalgae can be expected to act on other floating objects as well. Biotic items are particularly prone to destruction by secondary consumers. Wood, for example, is colonised by a wide variety of organisms (e.g., Kohlmeyer et al. 1995, Singh & Sasekumar 1996), but despite the intensive boring pressure of marine animals such as isopods or shipworms, the resistance of wood to sinking appears much higher than that of macroalgae. At low and mid-latitudes a wide variety of arthropod and mollusc borers may contribute to the destruction of floating wood (Maser & Sedell 1994). Softwood is exposed primarily to arthropod borers, but hardwood is not out of harm's way, because mollusc borers apparently exhibit preferences for hardwood (Si et al. 2000). While Häggblom (1982, cited in Dyke et al. 1997) estimated floating wood to persist for 10–17 months at the sea surface, Dyke et al. (1997) report

on transit times of 3–6 yr for wood in arctic waters. Reports of intense epibiont loads on wood logs (Carr 1986) also suggest a longevity of several months (Emery 1955). For mangroves, Duke (1995) cites Steinke (1975) as mentioning that the buoyant longevity of *Avicennia* propagules is hardly sufficient to cover 200 nautical miles at sea. More than 70% of the propagules lose buoyancy within the first 10 days (Steinke 1986). In contrast, *Rhizophora* propagules may float for several months at the sea surface (Rabinowitz 1978, cited in Duke 1995).

For floating seeds, longevity has been experimentally shown to range from a few months up to 19 yr (Nelson 2000). Not all seeds of one species have the same longevity at the sea surface. Some sink very quickly, whereas others may remain afloat for long periods (Guppy 1906). In this context, Skarpaas & Stabbetorp (2001) found that after 9 wk, >70% of seeds of *Mertensia maritima* remained afloat, further indicating high variability within a species. Epibionts or boring species may contribute to the loss of buoyancy of seeds. Penetration of water or germination may also provoke seeds to be lost as floating items (Guppy 1906).

Animal carcasses are highly attractive to a wide variety of scavengers and are therefore prone to destruction (e.g., Dudley et al. 2000). For carcasses of seabirds, Baduini et al. (2001) mention periods at the sea surface of approximately 2 wk. Longevity of skeletal remains of animals depends on an object's resistance to physical disintegration and its floatability. A recapture of an empty *Nautilus* shell 138 days after the living animal had been marked (Saunders & Spinosa 1979) probably represents a minimum estimate of persistence at the sea surface. Because the shells of living animals are not encrusted, a dense overgrowth of empty shells with sessile plants and animals is usually taken to indicate a long postmortem floating time (Chirat 2000). Based on the rafting organisms found on floating corals, it has been suggested that these may remain afloat at least for several months (DeVantier 1992). Floating periods of air-filled corals have been determined experimentally to range from 5 to more than 240 days (Kornicker & Squires 1962). Buoyancy of floating corals can be prolonged by occasional periods of exposure to air on beaches (Kornicker & Squires 1962).

Because the time and location of volcanic eruptions are often well known, it is possible to infer when and where pumice entered the ocean. Based on findings of stranded pumice originating from known eruptions, many authors have suggested that pumice can stay afloat for many months, up to several years. The distances to sampling sites can be related to average drift speed along probable routes in order to determine drift time. Fragments of pumice originating from the island of San Benedicto off the Mexican coast have been found at the Palau Islands (Richards 1958). Assuming an average drift speed of 0.7 km h⁻¹ along the distance of 12,000 km results in a drift period of 790 days, which must be considered a minimum value for the longevity of this particular piece of pumice. Fouling with corals will eventually cause pumice to sink (Jokiel 1990). Using the size of coral colonies growing on floating pumice found at Hawaii, these pumice pieces were estimated to have been afloat for about 2 yr, which is probably sufficiently long to travel across the tropical Pacific Ocean (Jokiel 1984). The first arrival of pumice from well-dated volcanic eruptions at distant shores has also been used by other authors to estimate the floating periods of pumice. For example, pumice from a submarine volcanic eruption occurring in March 1962 in the South Sandwich Island Group (55°S, 30°W) showed up 20 months later in Tasmania (Sutherland 1964) and New Zealand (Coombs & Landis 1966). One of the most impressive accounts of the longevity of volcanic pumice is by Frick & Kent (1984), who report that “after one century specimens from the Krakatoa eruption are still found on the beaches of the countries bordering the Indian Ocean.” Most likely these items conducted stepwise voyages with interludes of variable length on the shore (see also “beach hopping” below).

No reliable method exists for the age determination of plastics found in the marine environment. Consequently, no precise information is available about the longevity of plastic items. However, using well-dated release events of floating plastics, it is possible to arrive at realistic estimates for the floating periods of plastic items, similar to what has been done for volcanic pumice (see above). Some of the best examples are plastic shoes that were thrown overboard from a merchant ship

during a heavy storm in May 1990 in the North Pacific (Ebbesmeyer & Ingraham 1992). Many of these shoes were recovered thousands of kilometres from the release site several months after they had been spilled. The authors remarked that “even after a year in the ocean, many of the shoes were wearable after washing,” indicating that plastic shoes can float for long periods. Tracing plastic items back to a potential source has also been used by other authors, who were mainly interested in determining the sources of plastic litter (Garrity & Levings 1993). Ageing or weathering of plastic is accelerated by sunlight or by leaching out of substances added to increase the durability of plastic. Oxidative ageing of plastics lets them become brittle and susceptible to fragmentation (Cundell 1974). Most plastics are highly resistant to natural decay (Cundell 1974), and biodegradation by plastic-consuming bacteria is limited (Gregory 1978). Plastic spherules without additives found on New Zealand beaches are expected to persist there for 5–10 yr and spherules with additives for 30–50 yr (Gregory 1978). Heavy wave action smashes larger pieces into smaller fragments (Pruter 1987), which in general have lower buoyancy than large pieces. Finally, overgrowth with fouling animals and plants might cause plastic pieces to sink (Holmström 1975). Heavy fouling resulted in loss of buoyancy of most plastic items tethered in a shallow bay on the Florida coast (Ye & Andrady 1991), but the authors suggested that after sinking, some items regained buoyancy after losing some of their epibiont load. Smaller fragments have often been found in the course of stomach content analysis of fishes and seabirds (Gregory 1978, Vlietstra & Parga 2002), but it is not known how gut passage affects buoyancy.

Tar is not as immune to weathering as plastic. Lumps are only transient states of petroleum in the sea breaking up into fine particles that remain dissolved or as particulate hydrocarbons in the water column. In the presence of nutrients, tar is rapidly degraded under laboratory conditions by microorganisms such as bacteria, yeasts, and fungi (Butler 1975). Resulting longevity of tar balls ranges from about 2 months (Horn et al. 1970) up to about 1 yr (Cordes et al. 1980). Tar lumps can be expected to persist long enough to be transported along for one or more complete circles around the North Atlantic gyre (Levy & Walton 1976). With increasing temperature the rate of microbial degradation of tar lumps probably increases, as has been reported for surface-absorbed or liquid oil residues exposed to natural seawater (Gilbert & Higgins 1978, Minas & Gunkel 1995). Tar lumps in the vicinity of sandy shores may also incorporate sand grains, which leads to loss of buoyancy and subsequent sinking (Zsolnay 1978). Accidental consumption of tar lumps by fishes such as the Mediterranean saury *Scomberesox saurus* and by sea turtles has also been reported (Horn et al. 1970, Witherington 2002).

Substrata that lose their positive buoyancy at sea, due to either epibiont load or biotic or abiotic destruction, will inevitably sink to the seafloor. If this happens to floating algae in shallow waters, they might join the assemblage of drifting algae, which tumble over the seafloor at shallow water depths (Holmquist 1994, Brooks & Bell 2001). These are detached algae; their buoyancy is (or became) insufficient for floating, but nevertheless they are dispersed by tidal or wind-induced currents. Benz et al. (1979) reported a wide diversity of these drift algae in Florida lagoons, Virnstein & Carbonara (1985) mentioned seasonal dynamics of drift algae, and Belsher & Meinesz (1995) suggested that *Caulerpa taxifolia* may be dispersed by drift above the sea bottom.

In particular in the deep sea, items falling from surface waters may represent small islands that provide food and habitat for a variety of organisms (Schoener & Rowe 1970, Gage & Tyler 1991, Smith et al. 1998). The fact that several highly specialised species have evolved on sunken wood and animal remains in the deep sea (Knudsen 1970, Distel et al. 2000) suggests that these natural floating items are carried to the open ocean in sufficient quantities to sustain this fauna, and also were supplied regularly throughout evolutionary history. Not only biotic substrata such as macroalgae or wood items sink to the seafloor, but also a wide variety of anthropogenic macrolitter, including large amounts of plastics (Galgani et al. 1995, 1996, Galil et al. 1995).

Floating items that are caught in coastal and tidal currents may be cast ashore. A wide variety of floating items finally end up on the shores around the world (Guppy 1906, 1917, ZoBell 1971, Barnes 2002). Onshore winds may favour stranding of floating items (Winston 1982, Vauk & Schrey

1987, Johansen 1999). Floating items that reach rocky shores may break into pieces upon reaching the coast and thereby lose their buoyancy (Pruter 1987). Items cast ashore on sandy beaches remain intact, but most marine inhabitants will die. This loss of epibiont load may cause heavily overgrown items to regain some of their initial buoyancy, as has been reported by Ye & Andrady (1991) for sinking plastic items. Drying out on beaches should also have positive effects on the buoyancy of items such as wood, coral skeletons, and pumice, but it may accelerate destruction of floating macroalgae. Stranded items may also be taken out to sea again during spring tides or storms. Lee (1979) observed that during extreme high tides large amounts of driftwood and wrack were removed from a beach in southern California and redeposited at other sites. Similar patterns of “beach hopping” (*sensu* Lee 1979) of floating items can be expected in many other areas, e.g., estuaries and lowland coasts. ZoBell (1971) also noted that most stranded macroalgae were returned to the sea during storms or spring tides. Also, in the Arctic, driftwood may become waterborne again during strong storms and be carried with currents to new areas, as has been suggested by Dyke et al. (1997).

In summary, the probabilities of a floating item to disintegrate, sink to the seafloor, or become stranded depend on their propensity to be attacked by secondary consumers, to be overgrown by epibionts, and to be cast ashore. Presently, it is not known what proportion of floating items follow the above pathways (disintegration, sinking, and stranding). However, it appears safe to assume that many biotic items such as macroalgae and wood may disintegrate in response to consumer attack, whereas only few abiotic items will face this fate. Items from all categories are prone to loss of buoyancy, but given the fact that air-filled spaces may become destroyed by consumers, biotic items are more susceptible to sinking at sea. The high resistance of abiotic floating substrata suggests that a very high proportion of these will end up on shorelines around the world, as indeed has been shown by the high proportions of plastic litter from beaches at low, mid-, and high latitudes (Garrity & Levings 1993, Walker et al. 1997, Ribic 1998, Barnes 2002). Items that have sunk to the seafloor most likely will not return to become floating. Some of the items stranded on beaches may be returned to the sea during high tides or storms, but the proportion of items that refloat after stranding is usually very low (Garrity & Levings 1993).

Abundance of floating items (spatial and temporal distribution)

Methods to estimate abundance

Different methods have been applied for the quantitative assessment of floating objects. The most widely used method is the collection of stranded material on beaches. However, beach surveys may provide limited information about the origin of the floating items and their abundance in the open ocean because items may become concentrated in certain areas (e.g., Kirkman & Kendrick 1997, Acha et al. 2003). In some cases, objects found on the beach may derive from the sea, but an anthropogenic introduction from land cannot always be precluded (e.g., Debrot et al. 1999). Only if stranded items are overgrown by aquatic organisms can one conclude without doubt that these items have been floating at the surface of the sea. Furthermore, items may accumulate and persist on the beaches over long periods. For example, Dyke et al. (1997) and Dyke & Savelle (2000) emphasised that driftwood on shores in the Canadian Arctic has been accumulated over tens and hundreds of years. Similarly, there exists the risk of underestimation because after stranding on the beach, light objects such as plastic bags are likely to be blown away by wind or buried in the sand (Gregory 1978, Garrity & Levings 1993). These considerations show that it is difficult to infer from beach surveys (densities usually expressed as number of items per square kilometre of shoreline) the abundance of floating items in adjacent waters where items are distributed in an area, i.e., a two-dimensional space (densities usually expressed as number of items per kilometre sea surface). Consequently, beach surveys provide only qualitative and semiquantitative estimates of the abundance of floating items at sea. Estimates may be highly dependent on local hydrography,

beach dynamics, and environmentally influenced survival of an item at the beach. Quantitative comparisons among different sites are therefore problematic, even though they can provide a very useful first approximation to detect regional and global spatial trends (see, e.g., Unepetty & Evans 1997a, Barnes 2002).

Beach surveys, however, may provide very important information in the context of rafting if they report arrival rates of floating items. Surveys conducted at regular time intervals (e.g., every high tide) provide data that allow the estimation of arrival rates. Furthermore, the results from beach surveys provide information on the proportion of different floating items. This information is important because the quality of different items (size, nutritional value, longevity) will have a strong influence on potential rafting organisms.

Surveys at sea (by ship or plane) are well suited for quantitative comparisons because they operate in the target environment, and estimates usually are directly comparable between studies and regions. In visual ship-based surveys, objects floating at the sea surface are typically counted in a transect strip (see, e.g., Segawa et al. 1960). Small objects are likely to be overlooked by this method and thus abundance estimates based on visual surveys are only useful for relatively large floating items, e.g., macrolitter. Abundance estimates are then obtained by dividing the number of floating items counted in a given transect by the area covered (transect length \times transect width; for a detailed description of the method, see Matsumura & Nasu 1997, Thiel et al. 2003a). This method harbours another source of uncertainty because open water provides only few spatial features for allowing a precise estimate of transect width. Furthermore, quantitative estimates of floating items in ship-based surveys may be strongly dependent on weather conditions and sea state. Besides affecting the physical capabilities of human observers, sea state may influence the visibility of floating items on the sea surface. Therefore, ship-based surveys usually are only conducted during good weather conditions. These sources of uncertainty may be even more serious for visual aerial surveys, which are only useful to determine the abundance of very large floating items (>50 cm length or diameter). Some authors have also measured the time interval between sightings of two items in order to estimate the abundance of floating items (e.g., Hirata et al. 2001). High accuracy can be achieved by appropriate use of neuston nets. The width of the net's opening combined with fixed hauling distances provides relatively precise estimates of the area covered by this method. However, similar to visual surveys, the efficiency of the neuston net also depends on sea state, and Morris (1980b) remarked that the sampling efficiency of his neuston net typically ranged from 25 to 50%. Nevertheless, the neuston net is considered most appropriate for sampling small floating items quantitatively. The minimum size of the collected material is determined by the mesh size. On the other hand, neuston nets are not useful for estimating the abundance of macrolitter because (1) the area covered usually is not sufficient for representative sampling of these and (2) large items have to be avoided in order not to destroy the net.

This brief overview indicates that different sampling methods should be employed depending on the size of the target items and the specific objectives of a study. Some authors also have collected items, which previously had been floating at the sea surface, from the seafloor. This approach may be useful to determine potential sinks of floating items.

Spatial abundance of floating items

Macroalgae

The abundance of floating macroalgae varies substantially between studies, most likely depending on survey methods and study area. Abundance estimates vary from <1 up to 12,000 items km⁻² (Table 7). In general, the number of floating macroalgae is higher in coastal waters than in the open ocean, with one exception being the Sargasso Sea. Intensive studies on the spatial distribution of floating macroalgae (mainly *Sargassum* spp.) have been conducted in Japanese waters. Most authors emphasised that abundances of floating macroalgae were substantially higher in coastal

waters than in open-ocean waters (Segawa et al. 1959b, Senta 1962, Ohno 1984a, Hirata et al. 2001). Similar patterns with high abundances in coastal waters have been reported from other areas of the world (North Atlantic, Ingólfsson 1995; California, Hobday 2000c; New Zealand, Kingsford 1992). In the Mediterranean Sea, floating macroalgae are almost entirely absent (Dow & Menzies 1958). Guppy (1906) had already noted the absence of (natural) floating debris on beaches of the Mediterranean. For Californian coastal waters, Kingsford (1995) reported maximum abundances of floating *Macrocystis pyrifera* of about 1100 items km⁻². There is strong spatial variation, as is emphasised by the fact that mean abundances at different sampling sites, separated by 6–7 km, varied from about 1–400 items km⁻². In the same region, Hobday (2000c) found 0.8–7.0 rafts of the same species km⁻², but he emphasised that these values represent underestimates because only rafts larger than 0.5 m in diameter were considered. In the South Pacific, Smith (2002) reports an average of 3.7 algal rafts km⁻² (primarily *Durvillaea antarctica*) in the West Wind Drift south of Tasmania. This value is similar to that given by Helmuth et al. (1994a), who revealed a patchy distribution of floating *Macrocystis pyrifera* in the West Wind Drift along their trip from South Georgia to Punta Arenas (Chile), with abundances varying from about 0.2–5.0 rafts km⁻² (raft sizes were 1–6 m in diameter). The highest abundances of floating algae have been reported by Kingsford (1992) from New Zealand waters. Densities varied between 0 and 12,000 algal clumps km⁻² between stations that were separated by distances of 400–700 m. This author used a small boat for his survey, suggesting that the observer was close to the sea surface, possibly permitting the registration of small algal thalli not observable from larger ships. Kingsford & Choat (1986) estimated the number of items and the wet weight of floating macroalgae in surface slicks and the surrounding water. Within the slicks they found numbers and biomass of floating macroalgae about two orders of magnitude higher than outside these slicks, but they also noted the ephemeral nature of these slicks.

These last comparisons show that the abundance of floating macroalgae not only varies between regions, but also on relatively small scales within regions. Rafts of macroalgae accumulate in patches or drift lines, and their abundance on a small scale is often highly unpredictable (Kingsford 1992, Ingólfsson 1998). Nevertheless, the presently available information (Table 7) indicates that the abundance of floating macroalgae in many areas of coastal oceans typically varies between 1 and 1000 items km⁻², occasionally even exceeding values of 10,000 items km⁻².

Weight estimates confirm the high spatial variability previously reported for the abundances of floating macroalgae (Table 7). Along the Californian coast, estimates for *M. pyrifera* varied between 0 and 10,400 kg wet weight (WW) km⁻² (Kingsford 1995). These values are similar to the estimates by Hobday (2000c) of about 40–1000 kg WW km⁻² from the same region. In the NW Pacific in Japanese waters, the mass of floating *Sargassum* varied from 0.3 (Mitani 1965) to 3000 kg WW km⁻² (Segawa et al. 1960). Further evidence for the high spatial variability of floating macroalgae is provided by Segawa et al. (1961b), who reported that mass differed markedly between the coastal Iki Passage (~1700 kg WW km⁻²) and the wider Tusima East Passage (~600 kg WW km⁻²). In coastal waters of New Zealand the mean mass of floating macroalgae reached about 210 kg WW km⁻², although local variations (0–1813 kg WW km⁻²) were almost as high as in the North Pacific (Kingsford 1992).

For the central North Atlantic, Parr (1939) estimated a total of around 7 million tons (WW) of *Sargassum* spp. for the entire Sargasso Sea proper, which corresponds to mean values between 580 and 1570 kg WW km⁻². This author also remarked on the high spatial variability; areas with high amounts of floating *Sargassum* were immediately adjacent to areas with almost no floating macroalgae. Estimates of 525 kg WW km⁻² reported by Niermann et al. (1986) from the Sargasso Sea match the findings of Parr (1939). However, these authors found only little spatial variations throughout their sampling area, and their results did not confirm the suggestion by Stoner (1983) that the amount of *Sargassum* in the Sargasso Sea had decreased between the 1930s and the late 1970s. The reported interdecadal differences in *Sargassum* biomass might be due to seasonal variations or to long-term shifts of current boundaries (Butler & Stoner 1984). Howard & Menzies

Table 7 Estimates of the abundance of floating substrata from different regions of the world

Substratum	Region	Abundance		Method	Reference
		Items km ⁻²	kg km ⁻²		
Macroalgae	Scotia Arc	0.2–5.0		VSS	Helmuth et al. 1994a
Macroalgae	NE Pacific (>40°N, coastal)	1.1		VSS	Matsumura & Nasu 1997
Macroalgae	NW Pacific (>40°N, coastal)	0.2		VSS	Matsumura & Nasu 1997
Macroalgae	NE Pacific (20–40°N, coastal)	1.0		VSS	Matsumura & Nasu 1997
Macroalgae	NW Pacific (20–40°N, coastal)	0.8		VSS	Matsumura & Nasu 1997
Macroalgae	Japan		0.3–114	VAS	Mitani 1965
Macroalgae	Japan		3000 (WW)	VSS	Segawa et al. 1960
Macroalgae	Japan		600–1700 (WW)	VSS	Segawa et al. 1961b
Macroalgae	NE Pacific (California)	~3.0	39–1044 (WW)	VSS	Hobday 2000c
Macroalgae	NE Pacific (California)	1–1100	>1500 (WW)	VAS	Kingsford 1995
Macroalgae	NE Pacific (California)	70		VSS	Shumway 1953
Macroalgae	NE Pacific (<20°N, coastal)	1.9		VSS	Matsumura & Nasu 1997
Macroalgae	NW Pacific (<20°N, coastal)	0.3		VSS	Matsumura & Nasu 1997
Macroalgae	North Pacific (central)	0.0		VSS	Matsumura & Nasu 1997
Macroalgae	New Zealand	~2000 (0–12,000)	210 (WW)	VSS	Kingsford 1992
Macroalgae	New Zealand		2–1000 (WW)	VSS	Kingsford 1993
Macroalgae	New Zealand	35–4000	2–270 (WW)	VSS	Kingsford & Choat 1986
Macroalgae	Southern Ocean	3.7		VSS	Smith 2002
Macroalgae	SE Pacific (20–40°N, coastal)	~180 (1–1200)		VSS	Thiel et al. (unpublished data)
Macroalgae	SE Pacific (>40°N, coastal)	~190 (60–300)		VSS	Thiel et al. (unpublished data)
Macroalgae	Bahamas		300 (WW)	Neuston net	Butler & Stoner 1984
Macroalgae	Carribean		20–37 (WW)	Neuston net	Parr 1939
Macroalgae	Gulf of Mexico		300 (WW)	Neuston net	Parr 1939
Macroalgae	North Atlantic		525 (WW)	Neuston net	Niermann et al. 1986
Macroalgae	Sargasso Sea		100 (WW)	Neuston net	Butler & Stoner 1984
Macroalgae	Sargasso Sea		580–1570 (WW)	Neuston net	Parr 1939
Macroalgae	Sargasso Sea		240 (WW)	VSS	Howard & Menzies 1969
Macroalgae	Gulf Stream		500 (WW)	Neuston net	Butler & Stoner 1984

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Table 7 (continued) Estimates of the abundance of floating substrata from different regions of the world

Substratum	Region	Abundance		Method	Reference
		Items km ⁻²	kg km ⁻²		
Macroalgae	Gulf Stream		520 (WW)	VSS	Howard & Menzies 1969
Macroalgae	North Atlantic (near Bermuda)		~100 (DW)	Neuston net	Butler & Morris 1974
Macroalgae	North Atlantic (U.S. coast)		15 (WW)	VSS	Howard & Menzies 1969
Wood (logs)	NE Pacific (>40°N, coastal)	0.3		VSS	Matsumura & Nasu 1997
Wood (logs)	NW Pacific (>40°N, coastal)	0.2		VSS	Matsumura & Nasu 1997
Wood (logs)	NE Pacific (20–40°N, coastal)	0.1		VSS	Matsumura & Nasu 1997
Wood (logs)	NW Pacific (20–40°N, coastal)	0.3		VSS	Matsumura & Nasu 1997
Wood (logs)	NE Pacific (<20°N, coastal)	0.7		VSS	Matsumura & Nasu 1997
Wood (logs)	NW Pacific (<20°N, coastal)	0.1		VSS	Matsumura & Nasu 1997
Wood (logs)	North Pacific (central)	0.0		VSS	Matsumura & Nasu 1997
Pumice	Kuroshio Current	550–270,000		Neuston net	Fushimi et al. 1991
Macrolitter	Bering Sea	0.23		VSS	Day & Shaw 1987
Macrolitter	North Pacific (subarctic)	0.94		VSS	Day & Shaw 1987
Macrolitter	North Pacific (subarctic)	0.15		VSS	Dahlberg & Day 1985
Macrolitter	NE Pacific (>40°N, coastal)	1.0		VSS	Matsumura & Nasu 1997
Macrolitter	NW Pacific (>40°N, coastal)	0.2		VSS	Matsumura & Nasu 1997
Macrolitter	NE Pacific (20–40°N, coastal)	1.0		VSS	Matsumura & Nasu 1997
Macrolitter	NW Pacific (20–40°N, coastal)	0.8		VSS	Matsumura & Nasu 1997
Macrolitter	NE Pacific (<20°N, coastal)	1.8		VSS	Matsumura & Nasu 1997
Macrolitter	NW Pacific (<20°N, coastal)	0.25		VSS	Matsumura & Nasu 1997
Macrolitter	North Pacific (central)	2.2		VSS	Venrick et al. 1973
Macrolitter (bottles)	North Pacific (central)	0.5		VSS	Venrick et al. 1973
Macrolitter	North Pacific (central)	0.01		VSS	Matsumura & Nasu 1997
Macrolitter	North Pacific (subtropical)	3.15		VSS	Dahlberg & Day 1985

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Table 7 (continued) Estimates of the abundance of floating substrata from different regions of the world

Substratum	Region	Abundance		Method	Reference
		Items km ⁻²	kg km ⁻²		
Macrolitter	North Pacific (subtropical)	1.83		VSS	Day & Shaw 1987
Macrolitter	South Pacific (<40°S)	<20		VSS	Gregory 1991
Macrolitter	South Pacific (20–40°S, coastal)	1–36		VSS	Thiel et al. 2003a
Macrolitter	South Pacific (>40°S, coastal)	<1		VSS	Thiel et al. 2003a
Macrolitter	South Pacific (subantarctic)	1–2		VSS	Gregory 1991
Macrolitter	Indonesia	>4000		VSS	Uneputtu & Evans 1997b
Macrolitter	South Atlantic (~30°S, coastal)	19.6		VAS	Ryan 1988
Macrolitter	South Atlantic (~30°S)	1.6		VAS	Ryan 1988
Macrolitter	Gulf of Mexico	0.2– 2.4		VAS	Lecke-Mitchell & Mullin 1992, 1997
Macrolitter	Mediterranean	~2000		VSS	Morris 1980a
Macrolitter	Mediterranean	14–25		VSS	Aliani et al. 2003
Macrolitter	North Sea	1 to >3		VSS	Dixon & Dixon 1983
Microlitter	Bering Sea	80	0.003	Neuston net	Day & Shaw 1987
Microlitter	North Pacific (subarctic)	3370	0.046	Neuston net	Day & Shaw 1987
Microlitter	North Pacific (along 158°W)		0–0.4	Neuston net	Shaw & Mapes 1979
Microlitter	North Pacific (North Pacific Current)	Up to 34,000	0.3	Neuston net	Wong et al. 1974
Microlitter	North Pacific (central)	>300,000	5.1	Neuston net	Moore et al. 2001
Microlitter	North Pacific (subtropical)	96,100	1.21	Neuston net	Day & Shaw 1987
Microlitter	South Atlantic (West Wind Drift)	1300–3600		Neuston net	Morris 1980b
Microlitter	Bahamas	148.4	0.02	Neuston net	Colton et al. 1974
Microlitter	Caribbean	8300	0.08	Neuston net	Colton et al. 1974
Microlitter	South Atlantic	3640	0.04	Neuston net	Ryan 1988
Microlitter	Sargasso Sea	3500	0.29	Neuston net	Carpenter & Smith 1972
Microlitter	Gulf Stream	60	0.01	Neuston net	Colton et al. 1974
Microlitter	Gulf Stream		0.03–0.08	Neuston net	van Dolah et al. 1980
Microlitter	Mediterranean		0.119	Neuston net	Kornilios et al. 1998
Tar lumps	Bering Sea	0	0	Neuston net	Day & Shaw 1987
Tar lumps	North Pacific (subarctic)	1800	0.007 (DW)	Neuston net	Day & Shaw 1987
Tar lumps	North Pacific (along 158°N)		0–1.2 (WW)	Neuston net	Shaw & Mapes 1979

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Table 7 (continued) Estimates of the abundance of floating substrata from different regions of the world

Substratum	Region	Abundance		Method	Reference
		Items km ⁻²	kg km ⁻²		
Tar lumps	North Pacific		3.8 (WW)	Neuston net	Wong et al. 1974
Tar lumps	NE Pacific		0.03 (WW)	Neuston net	Wong et al. 1976
Tar lumps	NW Pacific (outside Kuroshio area)		0.4 (WW)	Neuston net	Wong et al. 1976
Tar lumps	NW Pacific (Kuroshio area)		2.1 (WW)	Neuston net	Wong et al. 1976
Tar lumps	North Pacific (central)	1714		Neuston net	Moore et al. 2001
Tar lumps	North Pacific (subtropical)	1710	0.022 (DW)	Neuston net	Day & Shaw 1987
Tar lumps	Equatorial Pacific (5°N–5°S)		0.03 (WW)	Neuston net	Holdway 1986
Tar lumps	South Pacific		0.0003 (WW)	Neuston net	Wong et al. 1976
Tar lumps	SW Pacific		<0.01 (DW)	Neuston net	Butler et al. 1973 (private communication of J.N. Butler with R.F. Lee)
Tar lumps	Australasia (5–10°S)		0.08 (WW)	Neuston net	Holdway 1986
Tar lumps	Central Indian Ocean (5–10°S)		0.01 (WW)	Neuston net	Holdway 1986
Tar lumps	Northern Arabian Sea		0.21 (DW)	Neuston net	Sen Gupta et al. 1993
Tar lumps	Red Sea		2.45 (WW)	Neuston net	Holdway 1986
Tar lumps	South Atlantic (West Wind Drift)		0.02–0.6 (WW)	Neuston net	Morris 1980b
Tar lumps	South Atlantic (2–6°N)		0.11 (WW)	Neuston net	Sleeter et al. 1976
Tar lumps	Atlantic (4°N–6°S)		0.02 (WW)	Neuston net	Sleeter et al. 1976
Tar lumps	North Atlantic (10–4°N)		0.02 (WW)	Neuston net	Sleeter et al. 1976
Tar lumps	North Atlantic (15–10°N)		0.16 (WW)	Neuston net	Sleeter et al. 1976
Tar lumps	NW Atlantic (20–10°N)		1.12 (WW)	Neuston net	Sleeter et al. 1976
Tar lumps	NE Atlantic		0.007–20.5 (DW)	Neuston net	Ehrhardt & Derenbach 1977
Tar lumps	Bahamas		0.93 (WW)	Neuston net	Joyce 1998
Tar lumps	Caribbean		1.62 (WW)	Neuston net	Sleeter et al. 1976
Tar lumps	Caribbean		0.56 (WW)	Neuston net	Joyce 1998
Tar lumps	Caribbean, Gulf of Mexico		0 to <10	Neuston net	Atwood et al. 1987
Tar lumps	Gulf of Mexico		1.12 (WW)	Neuston net	Sleeter et al. 1976
Tar lumps	Gulf of Mexico		0.82 (DW)	Neuston net	Cordes et al. 1980
Tar lumps	Gulf of Mexico		1.66 (DW)	Neuston net	Pequegnat 1979
Tar lumps	Southern Sargasso Sea		1.37 (WW)	Neuston net	Joyce 1998
Tar lumps	North Atlantic		1.16 (DW)	Neuston net	Levy & Walton 1976
Tar lumps	North Atlantic (U.S. coast)		0.3–2.0 (DW)	Neuston net	van Dolah et al. 1980
Tar lumps	U.S. slope waters		0.55 (WW)	Neuston net	Joyce 1998
Tar lumps	U.S. shelf waters		0.23 (WW)	Neuston net	Joyce 1998

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Table 7 (continued) Estimates of the abundance of floating substrata from different regions of the world

Substratum	Region	Abundance		Method	Reference
		Items km ⁻²	kg km ⁻²		
Tar lumps	NW Atlantic		0.93 (WW)	Neuston net	Morris 1971
Tar lumps	Gulf Stream		0.87 (WW)	Neuston net	Joyce 1998
Tar lumps	Northern Sargasso Sea		1.88 (WW)	Neuston net	Joyce 1998
Tar lumps	Central North Atlantic (15–10°N)		0.03 (WW)	Neuston net	Holdway 1986
Tar lumps	North Atlantic (30–15°N)		2.02 (WW)	Neuston net	Sleeter et al. 1976
Tar lumps	North Atlantic (near Bermuda)		~5 (DW)	Neuston net	Butler & Morris 1974
Tar lumps	East Atlantic		0.03 (WW)	Neuston net	Holdway 1986
Tar lumps	Mediterranean		5.52 (WW)	Neuston net	Holdway 1986
Tar lumps	Mediterranean		0.7–10.0	Neuston net	Morris 1974
Tar lumps	Mediterranean		0.318 (DW)	Neuston net	Kornilios et al. 1998
Tar lumps	NE Mediterranean (off Turkey)		1.9	Neuston net	Golik et al. 1988
Tar lumps	NE Mediterranean (off Libya)		6.9	Neuston net	Golik et al. 1988
Tar lumps	Western Mediterranean		0.2	Neuston net	Golik et al. 1988
Tar lumps	Central Mediterranean (Ionian Sea)		0.2	Neuston net	Golik et al. 1988
Tar lumps	Eastern North Atlantic (50–15°N)		0.86 (WW)	Neuston net	Holdway 1986
Tar lumps	Skagerrak		0.32 (WW)	Neuston net	Smith 1976
Tar lumps	Northern North Sea		0.02 (WW)	Neuston net	Smith 1976
Tar lumps	Norwegian Shelf		0.04 (WW)	Neuston net	Smith 1976
Tar lumps	Barents Sea		0.15 (WW)	Neuston net	Smith 1976

Note: VSS = visual ship-based survey; VAS = visual aerial survey; DW = dry weight; WW = wet weight.

(1969), who distinguished between the Sargasso Sea proper, the westerly adjacent Gulf Stream, and the U.S. coastal shelf water, found the highest mass of floating *Sargassum* in the Gulf Stream (520 kg WW km⁻²), intermediate values in the Sargasso Sea proper (240 kg WW km⁻²), and low values on the continental shelf (15 kg WW km⁻²). In summary, the spatial variability of weight estimates for floating macroalgae reported here corresponds to that of abundance estimates. In general, it can be said that the mass of floating macroalgae ranges between 1 and 500 kg WW km⁻², with maximum values of up to 3000 kg WW km⁻² (Table 7).

As a general trend, floating macroalgae are more abundant in coastal areas than in the open ocean. Furthermore, they are most common at mid-latitudes, but they appear to be largely absent in tropical and polar waters. Floating macroalgae appear to be restricted to waters with temperatures ranging from 5–20°C (Figure 7). Thus, the distribution of floating macroalgae on a global scale largely coincides with the geographic distribution of large macroalgae in general (Lüning 1990).

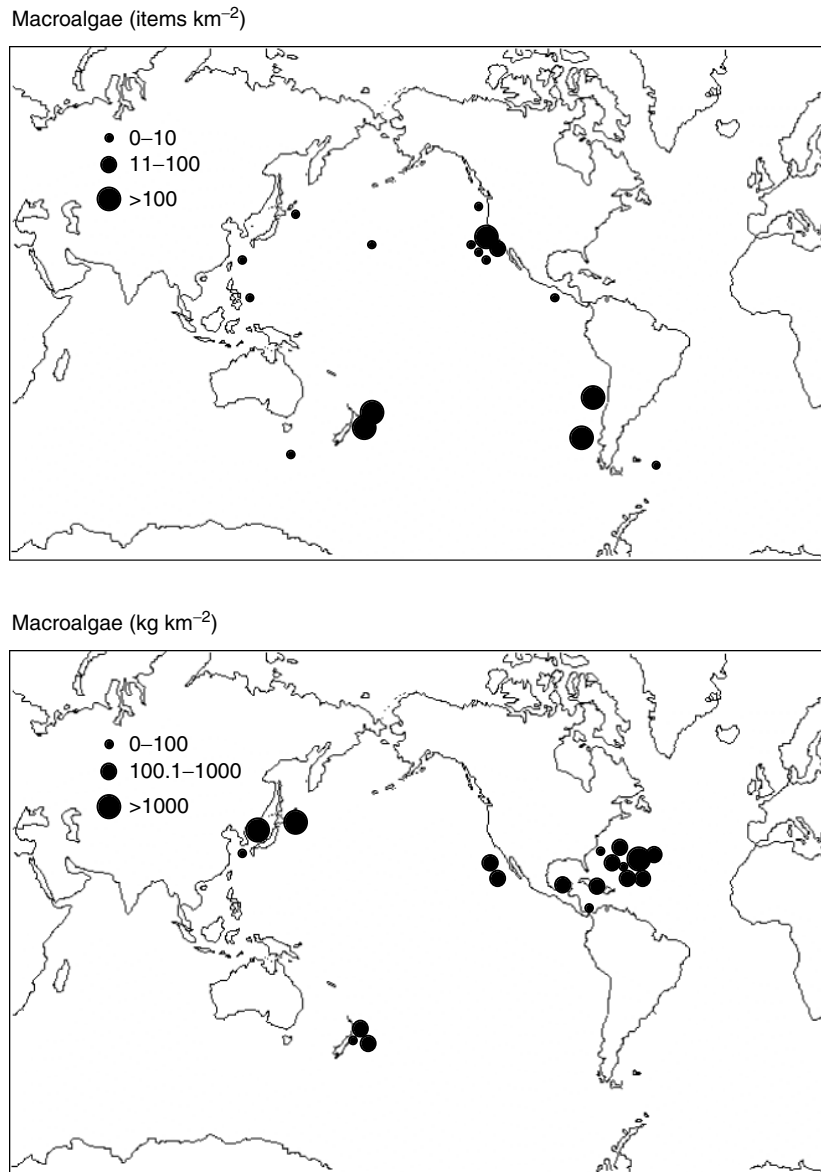


Figure 7 Estimates of abundance (items km⁻²) and mass (kg WW km⁻²) of floating macroalgae from different regions of the world.

Vascular plants

Little information is available about the abundances of vascular plants. Many authors report floating sea grasses from coastal environments such as lagoons, estuaries, and semienclosed bays (e.g., Worcester 1994), but to our knowledge no abundance estimates are available. The situation is similar for terrestrial and freshwater plants, which have been reported from coastal environments by numerous authors (Barbour 1916, King 1962, Shaffer et al. 1995), but their abundance has not been quantified. Some authors provide abundance estimates for wood. For the North Pacific, Matsumura & Nasu (1997) reported abundances of wood logs ranging from 0.1–0.7 items km⁻². Their results show that abundances were highest in the NW Pacific, which had also been suggested

by high densities of driftwood on Hawaiian beaches (Strong & Skolmen 1963). Enormous amounts of driftwood had been reported from beaches along the NW coast of North America (Maser & Sedell 1994). In some regions of Washington State, the number of floating logs battering the rocky shore is so high that this process has a strong impact on the dynamics of intertidal communities (Dayton 1971). Reports of large accumulations of driftwood along shores of northern Canada and NW Europe (Dyke et al. 1997, Johansen 1999) suggest that wood is an important floating item at high latitudes of the Northern Hemisphere. However, accumulations of driftwood or entire floating trees have also been reported from mid- and low latitudes (Abe 1984, Corbin & Singh 1993, Solana-Sansores 2001, Donlan & Nelson 2003). Caddy & Majkowski (1996) provided a map with the main areas for log fishing (i.e., for tuna fish in their proximity), which are located in waters close to the major watersheds of tropical regions, suggesting that most logs have their origin in tropical rivers. The survey of floating wood logs conducted by Matsumura & Nasu (1997) also shows that these are substantially more abundant in coastal waters than in the open ocean. Bark of trees (e.g., cork) may also be locally abundant (Guppy 1917). Intense logging and wood-processing activities during the past century may have contributed to an increase in bark and branches in coastal waters.

Floating seeds of high longevity appear to be primarily abundant at low latitudes, as had already been revealed by Guppy (1906, 1917). However, the apparently lower abundance of floating seeds from beaches at mid-latitudes may be because they are often covered by other items on the beaches of these regions. For the Chilean coast, Guppy (1917) remarked that it is difficult to find seeds among the vast amounts of other materials stranded on local beaches. Since sea beans are not easily detected on beaches, their abundance in the marine environment is probably underestimated. Hewett C. Watson remarked in a letter to Charles Darwin that “millions upon millions of seeds are carried to the sea yearly” (Burkhardt & Smith 1990, cited in Nelson 2000).

Animal remains

No abundance estimates are available for floating parts or bodies of animal origin. Baduini et al. (2001) reported large numbers of floating carcasses of seabirds during summer 1997 in the Bering Sea region. There are anecdotal reports that suggest that local concentrations of cuttlefish shells may occur occasionally (Deraniyagala 1951, cited in Deraniyagala 1960). These episodic and apparently highly localised mass appearances of skeletal remains from cephalopods might occur after spawning events of semelparous species. Occasionally large amounts of skeletal remains can be found on beaches along the North Atlantic (personal observations) and probably of other regions. Floating corals have occasionally been reported from tropical and subtropical regions (Kornicker & Squires 1962, DeVantier 1992), but nothing is known about their abundance at sea.

Volcanic pumice

Little information is available about abundances of floating pumice in the oceans. Using a neuston net, Fushimi et al. (1991) estimated abundances of volcanic pumice of up to 270,000 items km⁻² in the NW Pacific in the waters south of Japan. These authors reported that highest abundances were found in the Kuroshio Current and in the Kuroshio Counter Current, but low abundances were found in oceanic waters. Descriptions by other authors also suggest that floating pumice appears in dense patches with very high abundances locally (Sutherland 1965). Large aggregations of floating pumice have been documented from all latitudes in the Pacific Ocean (Richards 1958, Coombs & Landis 1966, Jokiel 1989, 1990, Fushimi et al. 1991). Volcanic pumice has also been found in the Atlantic Ocean, but abundances appear to be lower than in the Pacific, from where most floating pumice originates (Frick & Kent 1984).

Floating marine debris (macrolitter)

Abundances of floating marine debris consisting mainly of plastics have been estimated in many parts of the world's oceans. Day & Shaw (1987) counted between 0.2 and 1.8 items km^{-2} in the North Pacific, with densities increasing from the Bering Sea to the subtropics. They found the highest abundances in waters just east of Japan, amounting to about 24 items km^{-2} . Venrick et al. (1973) gave an estimate of 0.5 plastic bottles km^{-2} for the North Pacific. In coastal waters of the South Pacific off the Chilean coast densities of floating debris ranged from 1–36 items km^{-2} (Thiel et al. 2003a). Debris was most abundant in coastal waters, especially near major port cities, but in some regions the highest densities were found in offshore waters (Thiel et al. 2003a). In regions south of 40°S abundances of macrolitter were less than 1 item km^{-2} . These results confirm the pattern revealed by Gregory (1991), who reported abundances of 1 or 2 items km^{-2} in the subantarctic Pacific, whereas at latitudes north of 40°S the abundance of macroplastics significantly increased to more than 20 items km^{-2} . For the South Atlantic, Ryan (1988) presented similar results from a visual aerial survey conducted off the southwestern Cape Province of South Africa. Densities of plastics increased from 1.6 items km^{-2} in offshore waters (50 km) to 19.6 items km^{-2} near the coast (<10 km). In the north-central Gulf of Mexico off the coast of Louisiana, large macrolitter was recorded throughout the year (Lecke-Mitchell & Mullin 1992). Abundances were higher in offshore than in inshore waters and ranged from 0.2–0.8 large items km^{-2} . In the North Sea marine litter was present at all stations visited by Dixon & Dixon (1983). Particularly in coastal waters and in the central North Sea, plastic materials were the litter types with the most widespread distributions and highest densities, varying from 1 to >3 items km^{-2} . In the Mediterranean Sea, Morris (1980a) found very high abundances of floating debris. He visually monitored pieces of >1.5 cm and provided estimates of approximately 2000 items km^{-2} , 60–70% of which were plastics. Even higher values have been reported by Uneputtu & Evans (1997b) from a semienclosed bay in an urbanised area in Indonesia, who found abundances of >4000 items km^{-2} .

In summary, densities of floating macrolitter are highest in coastal waters and at mid- and low latitudes (50°N to 40°S) (Figure 8). Typical abundances range from 0.01–25 items km^{-2} , but exceptionally high values of >1000 items km^{-2} can be reached in highly populated regions.

Floating marine debris (microlitter)

The vast majority of plastic items in the oceans consists of small particles (<10 mm in diameter) that are easily overlooked in visual surveys. These small items usually are quantified using a neuston net. For the North Pacific, the highest abundances of plastic microlitter were recorded by Moore et al. (2001) from the North Pacific Central Gyre with more than 330,000 items km^{-2} (Table 7). For the coastal waters of South California, Moore & Allen (2000) reported the enormous quantity of up to 60 million items km^{-3} , but it is not known how many items per square kilometre this value represents. Along 35°N the abundance of plastics increased from west to east with a maximum of 34,000 items km^{-2} (Wong et al. 1974). From north to south the amount of plastic microlitter increased from 80 items km^{-2} in the Bering Sea to 96,000 items km^{-2} in the subtropical North Pacific (Day & Shaw 1987). In the North Atlantic, plastics are widespread and unevenly distributed with abundances varying in the Sargasso Sea from 50–12,000 items km^{-2} with a mean value of 3500 items km^{-2} (Carpenter & Smith 1972). Similar but much more variable densities were found in waters bordering the Sargasso Sea (i.e., Caribbean, Antilles, U.S. continental shelf). Mean values from different surveys, summarised by Colton et al. (1974), ranged from about 60–8300 items km^{-2} , with a maximum of about 250,000 items km^{-2} . In the South Atlantic off South Africa, Ryan (1988) counted an average of 3640 items km^{-2} .

Because samples taken with a neuston net usually are processed in the laboratory, many authors provide weight estimates. The average mass of floating plastics (microlitter) in the North Pacific was estimated by Wong et al. (1974) to be 0.3 kg WW km^{-2} . These values are similar to those

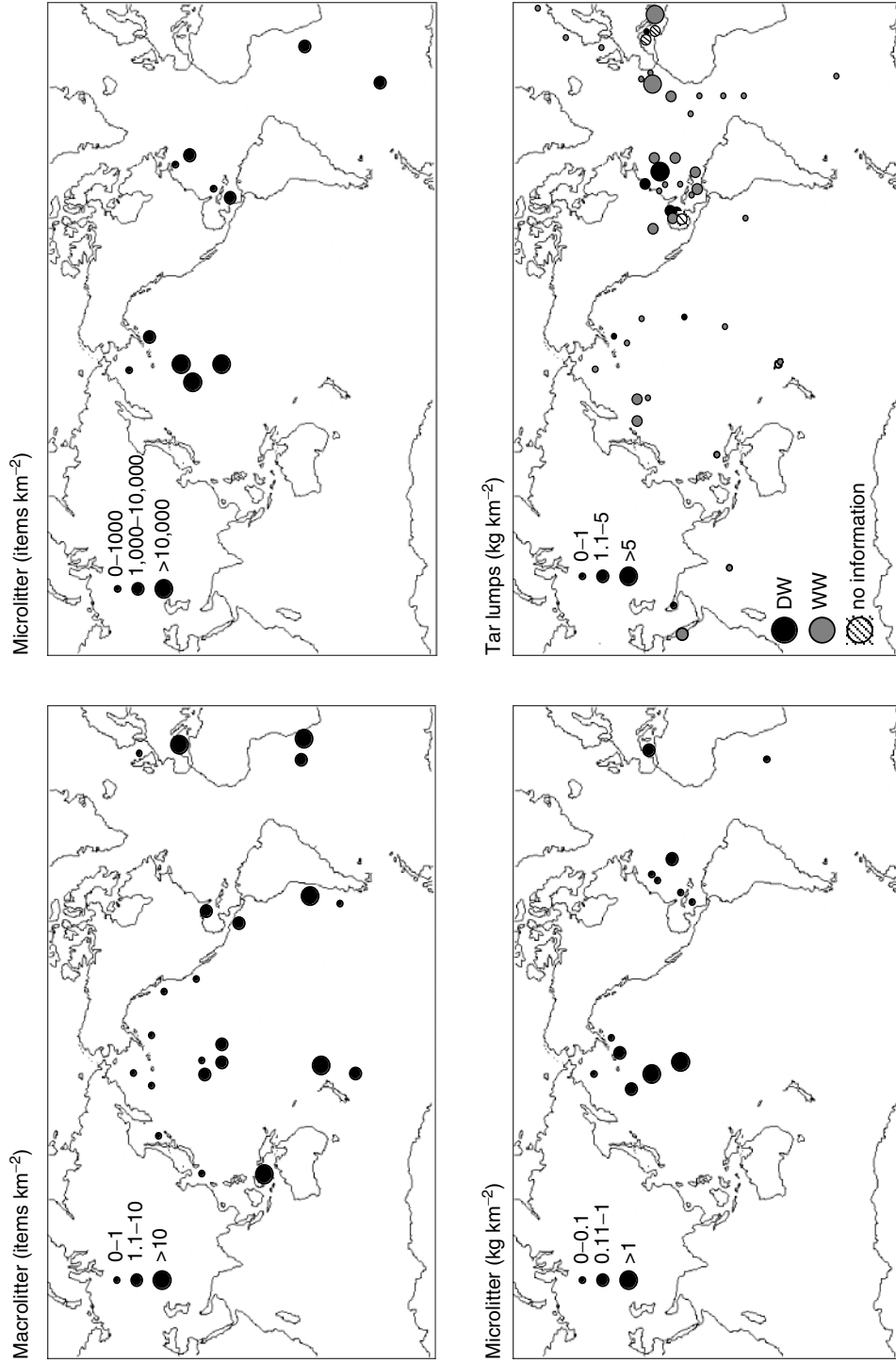


Figure 8 Estimates of abundance (items km⁻²) and mass (kg km⁻²) of macro- and micro-litter and tar lumps from different regions of the world.

reported by Shaw & Mapes (1979), who collected up to 0.4 kg WW km⁻². In the centre of the North Pacific Central Gyre the mass of plastic items increased to an average of 5 kg km⁻², with high variations ranging from 0.06–30.0 kg dry weight (DW) km⁻² (Moore et al. 2001). Day & Shaw (1987) found that the dry weight of small plastic items increased from the Bering Sea (0.003 kg km⁻²) to subtropical waters (1.2 kg km⁻²). The mass of floating plastics in the Atlantic Ocean appears to be lower than in the Pacific. In the western North Atlantic mass estimates ranged from 0.03–0.08 kg km⁻² (van Dolah et al. 1980). Colton et al. (1974) found very similar results from the U.S. continental shelf between approximately 30 and 40°N, but maximum values reached up to 1.4 kg km⁻². In the Sargasso Sea the average mass of plastic microlitter was an order of magnitude higher (0.29 kg km⁻², Carpenter & Smith 1972). Mean values from different surveys varied between 0.01 and 0.08 kg DW km⁻². Mass estimates from the SE Atlantic were very similar, reaching up to 0.04 kg DW km⁻², but a high variability over small spatial scales was found (Ryan 1988).

In summary, the average mass of plastic microlitter in the world's oceans appears to vary from insignificant amounts up to 0.1 kg DW km⁻², with maximum values exceeding 1 kg DW km⁻². The high mass of plastic microlitter is usually reported from coastal waters (Moore et al. 2002), but in the open ocean, in the centres of the gyres, large amounts of plastic microlitter can also be found (Figure 8).

Pelagic tar

The abundance of tar lumps in the marine environment has been the subject of numerous investigations. Butler et al. (1973) calculated a total amount of about 2 million tons of floating tar in the world's oceans. On a transect from Japan to the Californian coast, Wong et al. (1974) collected tar in the Pacific. Along 35°N, tar densities decreased from west to east, with highest abundances of up to 14 kg WW km⁻² occurring in waters between Tokyo and north of Hawaii (Table 7). The average mass of tar lumps amounted to 3.8 kg WW km⁻². During their cruise along 158°W in the North Pacific, Shaw & Mapes (1979) found tar to be absent in waters north of 43°N. They observed a high degree of patchiness in the tar distribution with values ranging from 0–1.2 kg WW km⁻². The absence of tar in the northern North Pacific (Bering Sea) was confirmed by Day & Shaw (1987). Farther south the mass increased from 0.01 kg km⁻² in subpolar waters to 0.02 kg DW km⁻² in the subtropical North Pacific, which corresponds to about 1700 tar lumps km⁻². With less than 0.01 kg km⁻², the mean mass of floating tar in the South Pacific appears to be lower than in the North Pacific (Butler et al. 1973). As in the northern North Pacific, the North Atlantic has also been found to be essentially free of floating tar at latitudes north of 45°N, whereas in regions south of 45°N the mass of tar in the North Atlantic increases up to a mean of 1.16 kg DW km⁻² (Levy & Walton 1976). Only in the coastal regions of NW Europe have substantial amounts of floating tar been detected (Smith 1976). In the northwestern North Atlantic (off Nova Scotia), average mass amounts to 0.93 kg WW km⁻² (Morris 1971). In the Sargasso Sea region and east thereof, values often exceed 1 kg WW km⁻² (Sleeter et al. 1976, Joyce 1998). In continental shelf waters of the U.S. from Florida to North Carolina, only very few stations were heavily contaminated with floating tar lumps. Van Dolah et al. (1980) could not detect any seasonal pattern in the distribution of tar, but higher incidences were observed in offshore than in inshore waters. Average densities varied from 0.3–2.0 kg DW km⁻², with a maximum concentration of >10.0 kg DW km⁻². Surprisingly, Cordes et al. (1980) detected no significant increase in tar abundance in the same region after an oil spill in the Gulf of Mexico. About 6 months after an oil rig blowout in June 1979, the average mass of tar found off the coasts of Florida and Georgia was about 0.8 kg km⁻². The total mass varied between 0.01 and 5.6 kg DW km⁻², which was similar to the values recorded by van Dolah et al. (1980) over a 2-yr period, 1973–75. They also found tar to be mainly absent within 40 km of the shore. The waters in the Gulf of Mexico exhibited densities that were about twice as high as those along the Atlantic coast of the U.S. A mean concentration of 1.66 kg km⁻² included high variations ranging from 0–31.9 kg DW km⁻² (Pequegnat 1979), similar to that reported by Sleeter et al. (1976) for the

same region. No pattern of seasonality and no clear inshore–offshore trend were detectable. The high mass of floating tar in the Gulf of Mexico might be due to the high density of oil rigs in that region. The major currents transport floating tar to the Strait of Florida, the Gulf Stream, and the Sargasso Sea. Butler (1975) often observed tar in the Sargasso Sea and the adjacent Gulf Stream to be associated with floating *Sargassum*. With values of 0.02–0.6 kg WW km⁻² tar mass was lower in the South Atlantic than in the North Atlantic (Morris 1980b). High masses of tar were also detected in the Mediterranean Sea where densities varied from 0.7–10.0 kg km⁻² (Morris 1974).

In summary, the average mass of floating tar varied from 0 to about 4 kg km⁻², with peak abundances of up to 10 or more kg km⁻² off Japan and in the Mediterranean. In general, tar lumps appear to be more abundant in the Northern than in the Southern Hemisphere (Figure 8). High latitudes (>45°) appear to be essentially free of floating tar lumps, but occasionally large numbers of tar lumps are washed ashore on the coasts of NW Europe at latitudes greater than 50°N (Minchin 1996). A clear inshore–offshore trend is not generally evident.

In general, the abundance of floating items decreases with distance from source regions. Floating macroalgae and sea grasses have been found to be substantially more abundant in coastal waters than in the open ocean (the Sargasso Sea being an exception), i.e., close to the sites where these plants grow in benthic habitats (e.g., Lüning 1990). Most other floating items show similar patterns. Tar and plastics are found predominantly along shipping routes with heavy oil transport (Shaw & Mapes 1979, Holdway 1986) and close to areas associated with petroleum industries such as major ports and oil rigs (Levy & Walton 1976, Cordes et al. 1980). Wong et al. (1974), however, reported that the distribution of tar in the North Pacific along 35°N was not consistent with main tanker routes. They found tar mainly accumulated in regions of low wind stress. Other observations also suggest that some items that have a high longevity at the sea surface may be transported over long distances and accumulate temporarily in eddies or in front systems (Owen 1981, Shanks 2002), and finally end up on the seafloor or on beaches. For example, Acha et al. (2003) found high abundances of plastic debris on the seafloor near an estuarine front. Similarly, Ebbesmeyer & Ingraham (1992) reported that plastic shoes accidentally released in the northern North Pacific accumulated on beaches of the NE Pacific.

Temporal variations in abundance of floating items

On the local scale, floating items may appear in large quantities during some periods and at other times they may be virtually absent from the surface of the sea. In some regions, the presence of floating plants seems to be closely linked to seasonal growth cycles. For example, in Japanese waters many authors reported the highest abundances of floating macroalgae (*Sargassum* spp.) during the spring and summer months (Segawa et al. 1960, Hirosaki 1963, Ida et al. 1967, Ohno 1984a, Ikehara & Sano 1986, Hirata et al. 2001). Similar observations have been made on European coasts following the introduction of *S. muticum* (Critchley et al. 1987). On the Swedish west coast, Karlsson & Loo (1999) reported massive floating events over a few days in summer. Toward the end of the annual growth season *Sargassum* plants fragment easily (Norton 1976, 1977, Deysher & Norton 1982), and this process may contribute to the high abundances of floating macroalgae reported during the summer months. The succession of different *Sargassum* species in the neuston (Figure 9) might be a reflection of the growth cycles of individual algal species (Ohno 1984a, Hirata et al. 2003).

Seasonal variations have also been revealed by Kingsford (1992) for coastal waters of north-eastern New Zealand, where he observed very high densities of floating macroalgae (including *S. sinclairii*) during austral spring and summer. No seasonal variations were observed for large rafts of *Macrocystis pyrifera* in Californian waters by Hobday (2000c) who discussed that the absence of seasonal patterns might be due to either methodological limitations or environmental conditions that affect supply and residence of floating macroalgae in a given area. In this context, Kingsford (1992) mentioned that the general seasonal pattern with low abundances during the winter months

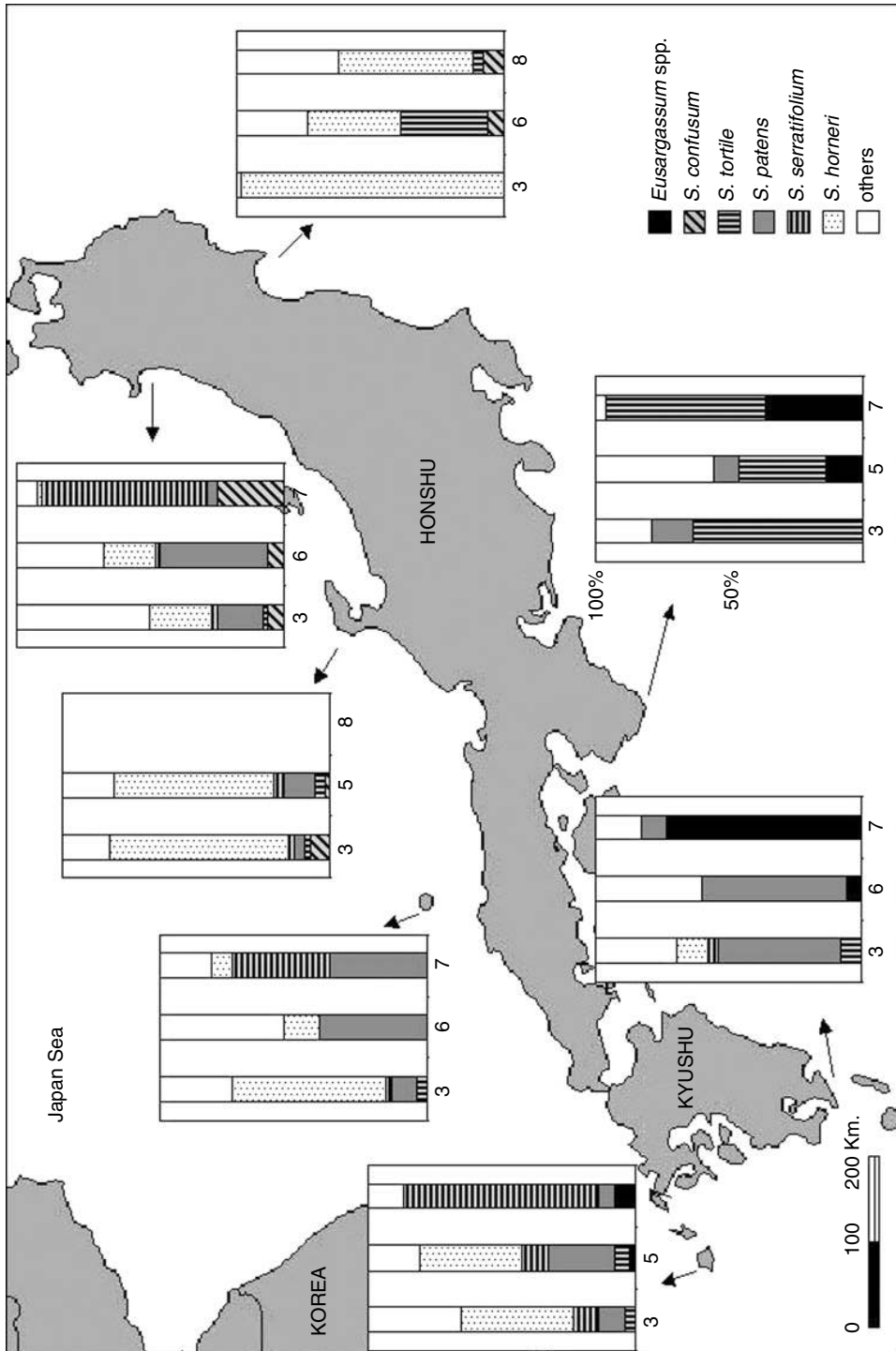


Figure 9 Seasonal variation in the distribution of the main species of *Sargassum* and *Eusargassum* floating in the waters around Japan; numbers indicate months. (Modified after Segawa et al. 1964.)

occasionally was disrupted by storms, after which abundances of floating algae reached high values. Highest abundances of *M. pyrifera* have been observed in Californian waters during the winter storm season when detachment rates were high (Kim 1992, Seymour et al. 1989). These observations are supported by reports of large amounts of stranded macroalgae on Californian beaches during the winter months (ZoBell 1971). For New Zealand, Marsden (1991) reported large amounts of stranded macroalgae during austral summer. The abundance of floating sea grasses shows seasonal patterns similar to those of floating macroalgae. In many temperate regions, the shoots of plants die back and leaves may float away, and large quantities of stranded sea grass leaves during specific seasons give testimony to this process (Ochieng & Erftemeijer 1999).

Besides seasonal variations there may also be interannual variations in the amounts of floating macroalgae and sea grasses. Parr (1939) reported a high temporal variability in abundance of *Sargassum* in the Sargasso Sea. The annual biomass estimated by Parr (1939) varied by an order of magnitude from one year to the next (see also Deacon 1942). Interannual variation in biomass of floating macroalgae is also reflected in the highly variable amounts of algae that are cast ashore during subsequent years (ZoBell 1971, Kirkman & Kendrick 1997). The main causes for interannual changes in the amounts of floating macroalgae might be found in variations of (1) productivity or (2) supply due to storm-induced detachment of benthic macroalgae. During El Niño Southern Oscillation (ENSO) events, both of these causes might coincide, resulting in extensive loss of benthic macroalgae (Ladah et al. 1999). Besides these causes, shifting current regimes may also be responsible for variable abundances of floating macroalgae (or other floating items) in specific regions (Butler & Stoner 1984).

The abundances of terrestrial plants, in particular in temperate regions, can also be expected to follow seasonal patterns that are influenced by seasonal growth cycles and by seasonally varying volumes of river runoff. Solana-Sansores (2001) and Castro et al. (2002) remarked on the importance of rivers for the delivery of floating objects of terrestrial origin (mainly wood). They also noted that abundances vary according to seasonally changing river runoff. Gomes et al. (1998) reported that log fishing in the SE Caribbean is related to seasonal supply of driftwood logs from riverine input. King (1962) monitored the rafts passing from a small river in Costa Rica to the open sea and remarked that the abundance of rafts regularly increased after rainfalls. Similar observations have been made for other plant materials of terrestrial origin (see, e.g., Rouch 1954, Heatwole & Levins 1972, Zarate-Villafranco & Ortega-García 2000). After an intensive rainstorm, Moore et al. (2002) observed substantially higher abundances of floating plastics in Californian coastal waters than before the storm. They emphasised that most of the microlitter collected in their study had a terrestrial origin. Variations in river runoff between years (e.g., as a result of large-scale climatic variations such as ENSO) may also lead to interannual variability in the supply of floating items of terrestrial origin, as has also been suggested by Zarate-Villafranco & Ortega-García (2000).

In northern Norway the abundance of driftwood reaching beaches increases strongly during April and May each year, most likely because during the spring these items become released from the ice (Johansen 1999). A similar seasonal pattern had been revealed for sediments transported by ice (Hebbeln 2000).

Many studies revealed the connection between storms and the appearance of large amounts of floating items on local beaches. In the case of macroalgae and sea grasses this appearance may be caused by storm-induced detachment from benthic habitats (Witman 1987, Seymour et al. 1989) and in the case of floating items of terrestrial origin might be due to runoff carrying these items to the sea. Thus, wave action and runoff during storms lead to increased supplies of floating materials to coastal waters. However, items found after storms on local beaches often are heavily fouled by rafting organisms, which suggests that these items must have been afloat for a long time before the storm. Following several days of strong onshore winds, Winston (1982) collected plastic materials from Florida beaches, many of which were heavily fouled with large bryozoan colonies. Similarly, Teichert (1970) reported abundant strandings of heavily fouled *Nautilus* shells in the Bay of Bengal and noted that their appearance is linked to the monsoon season in May and June.

Johansen (1999) also remarked on the importance of strong winds: he suggested that strong northerly winds may push wood from the Barents Sea across the Atlantic Current to reach northern Norway. Aliani et al. (2003) also suggested that variations in the abundance of floating marine debris in a certain area may be caused by wind-induced changes in residence time of floating items. During periods with strong winds, many items may be cast ashore, resulting in low abundances of floating items (Aliani et al. 2003). Regardless of the causes, strong temporal variations of the abundance of floating items have been observed in many different regions. Most of these variations are due to seasonal or climatic variations in wind, waves, and terrestrial runoff.

Besides weather, volcanic activity also affects the temporal distribution of floating items. Goda & Nishinokubi (1997) noted that avalanches caused by a volcanic eruption carried many trees into a bay in Japan, from where the trees then floated off into coastal waters. Besides these indirect effects on the abundance of floating items, volcanic activity directly affects the presence and abundance of floating pumice. Most recent reports of volcanic pumice can relatively safely be linked to specific events occurring in particular regions (e.g., Richards 1958, Sutherland 1965, Frick & Kent 1984). Following such events large fields of floating pumice may occur in certain areas.

For floating items of anthropogenic origin long-term changes can be expected. Increases in the amounts of floating plastic litter and tar lumps have occurred during the past century. With increasing environmental awareness and improved legislation during the last quarter of the past century, some reduction of floating items related to human activities has been observed. Incidence of plastic litter in stomachs of seabirds has slightly diminished over the past two decades (Vlietstra & Parga 2002 and citations therein), suggesting that improving legislation slowly leads to lower abundances of floating plastics in the sea. Similarly, various authors have reported a decrease in the abundance of floating tar over the past three decades in many regions (Holdway 1986, Golik et al. 1988, Joyce 1998). Beach surveys also revealed decreasing amounts of anthropogenic litter in some regions (Golik 1989, Ribic et al. 1997), but trends showed an increasing tendency in other regions (Walker et al. 1997). Regardless of these temporal trends, floating items of anthropogenic origin are still highly abundant in most parts of the world's oceans (see above).

In summary, some floating items such as macroalgae and sea grasses exhibit consistent patterns and their presence in certain regions appears to be relatively predictable. For example, during summer months large amounts of floating macroalgae are present in coastal waters of mid-latitudes such as Japan, New Zealand, Iceland, the California Current, and the Gulf Stream. Similarly, large quantities of floating plastics can be found consistently in coastal waters of low and mid-latitudes. In contrast, the temporal distribution of other floating items, such as terrestrial plants and volcanic pumice, and their presence in certain regions are highly unpredictable. The most important conclusion appears to be that many floating items are delivered to the world's oceans in pulses that are related to seasonal growth season, storms, terrestrial runoff, or volcanic eruptions.

Floating velocities and trajectories

Floating items are transported across the world's oceans by the major current systems. While long-term movements are primarily driven by oceanic currents, short-term dispersal may also be strongly influenced by winds (see above). The importance of currents for the transport of floating items is supported by (1) floating velocities and (2) floating trajectories.

Typical floating velocities reported for floating items correspond largely to the velocities of the major oceanic currents. Most velocities range between 0.5 and 1.0 km h⁻¹, regardless of the shape and size of the substratum (Table 8). Similar velocities had already been reported by Guppy (1906, 1917) for various regions throughout the world's oceans. The strong similarity in floating velocities is even more surprising because very different methods were employed to obtain these estimates. For example, Segawa et al. (1962) used mark-recapture experiments to determine floating velocities and trajectories of floating macroalgae in the coastal waters of Japan, and based on recovery of the marked patches on the shore, they estimated that algal patches had moved at velocities of 0.5–0.85

Table 8 Velocities of floating objects estimated by different methods

Type of substratum	Velocity (km h ⁻¹)	Region	Current system	Method	Reference
Macroalgae	0.2–0.5	California	Coastal currents	Direct measurement	Kingsford 1995
Macroalgae	0.75–1.3	Scotia Arc	West Wind Drift	Velocity estimates based on oceanographic current velocities	Helmuth et al. 1994a
Macroalgae	0.2–2.3	California	Coastal currents	Radio tracking	Harrold & Lisin 1989
Macroalgae	0.4	California	Coastal currents	Satellite tracking	Hobday 2000c
Macroalgae	0.9–5.5	SE Japan	Kuroshio Current	Inferred from velocity of experimental drifters	Nakata et al. 1988
Macroalgae	0.5–0.85	Kyushu, South Japan	Tsushima Current	Mark and recapture	Segawa et al. 1962
Macroalgae	0.8	Japan	Tsushima Current	Mark and recapture	Yoshida 1963
Macroalgae	0.03–0.2	Japan	Kuroshio Current	Mark and recapture	Ida et al. 1967
Wood (frozen into ice)	<0.1	Arctic	Transpolar Drift	Inferred from ice movement	Dyke et al. 1997
Wood	3.5–7.0	Ariake Sea (Japan)	Kuroshio Current	Satellite tracking	Goda & Nishinokubi 1997
Wood	0.6	Southern Ocean	West Wind Drift	Estimated from drift period	Deacon 1960
Wood	0.5–0.8	West of Costa Rica	North Equatorial Counter Current	Mark and recapture	Hunter & Mitchell 1967
<i>Nautilus</i> shell	0.3	Philippines	North Equatorial Current	Mark and recapture	Saunders & Spinoso 1979
Whale carcass	1.0	Off South Africa	Coastal currents	Direct measurement	Dudley et al. 2000
Pumice	0.6–1.0	New Zealand	West Wind Drift	Estimated from drift period	Coombs & Landis 1966
Pumice	0.7	Off Mexico (Pacific)	North Equatorial Current	Estimated from drift period	Richards 1958

Pumice	0.8	Krakatoa	South Equatorial Current	Estimated from drift period	Richards 1958
Pumice	0.9	North Pacific	Kuroshio, North Equatorial, Subtropical Counter Current	Velocity estimates based on oceanographic current velocities	Fushimi et al. 1991
Pumice	1.2	Southern Ocean	West Wind Drift	Estimated from drift period	Sutherland 1965
Artificial rafts (plastic, drift bottles, etc.)	3.5-5.5	Equatorial Pacific	Equatorial Current	Visual tracking	Gooding & Magnuson 1967
Artificial rafts (plastic, drift bottles, etc.)	0.6	NE Pacific (45-50°N)	North Pacific Current	Estimated from drift period	Ebbesmeyer & Ingraham 1992
Drift bottles	0.8	North Atlantic	Gulf Stream	Estimated from drift period	Guppy 1917

km h⁻¹. In contrast, Harrold & Lisin (1989) equipped macroalgal patches with radio transmitters and regularly tracked their movements at sea. Using this method, they revealed that patches occasionally may move very fast, but at other times advance slowly (0.2–2.3 km h⁻¹). Hobday (2000c) used patch mimics (satellite drifters) to obtain estimates of the movement patterns of macroalgal patches in the Southern California Bight and revealed average velocities of approximately 0.4 km h⁻¹. Numerous estimates are available for volcanic pumice because the site and date of volcanic eruptions are typically well known. This information, together with the first arrival date of a piece of pumice at a given site, allows for relatively reliable estimates of floating velocities. Typical floating velocities for volcanic pumice range from 0.6–1.2 km h⁻¹, similar to those reported for plastic shoes (Ebbesmeyer & Ingraham 1992).

Floating velocities above 2 km h⁻¹ have been reported for the Equatorial Pacific and for the region around Japan (Table 8). Two independent studies from the Kuroshio Current region estimated these high floating velocities, which correspond closely to current velocities measured for this region (Pickard & Emery 1990), and suggest that floating items indeed can be transported very rapidly in these western boundary currents. Similarly, the floating velocities estimated for floating items in the West Wind Drift (Table 8) are also in the same range as typical current velocities in surface waters of the Southern Ocean (Daly et al. 2001). All these observations strongly suggest that oceanic currents have a strong influence on the velocities of floating items.

Trajectories reported for floating items also correspond closely to the directions of the major oceanic currents. In the following paragraphs some trajectories of floating items reported in the scientific literature are briefly summarised. This geographic account will follow the direction of the surface layer of the global conveyor belt (Broecker 1991).

In the northern North Pacific an accidental experiment, during which large quantities of floating plastic shoes were released, demonstrated in an impressive manner that between 45 and 50°N these items were transported in an eastward direction toward the NW coast of North America (Ebbesmeyer & Ingraham 1992). Following the same system toward the south, floating items are transported in a westward direction with the North Equatorial Current (Figure 10). This trajectory is supported by observations from Strong & Skolmen (1963), who found that most drift logs that stranded on Hawaii had their origin in Washington State and Oregon. Guppy (1906) had already reported on the large abundance of driftwood in that region. Some of the driftwood logs found on Hawaii had their origin in SE Asia, suggesting that they were transported with the Kuroshio and North Pacific Currents halfway around the North Pacific Gyre.

Within the California Current, floating items are generally transported to the south, but northward movements are also observed during certain seasons (Hobday 2000c). In this context, Bushing (1994) found floating macroalgae *Nereocystis luetkeana* near Santa Catalina Island off southern California, i.e., substantially to the south of its distributional range. This observation confirms that floating macroalgae may be transported over large distances by oceanic currents.

Fushimi et al. (1991) noted that volcanic pumice was transported toward Japan by the northern extension of the North Equatorial Current. Hirosaki (1965) suggested that the appearance of *Eusargassum* spp. in coastal waters of northern Japan indicates that these macroalgae have been transported northward by the Kuroshio Current. Various other authors have reported on the north-easterly transport of floating macroalgae in Japanese waters (e.g., Segawa et al. 1962).

In the Pacific Equatorial Current, Gooding & Magnuson (1967) followed an artificial float that moved rapidly toward the west. These observations coincide with those of Emery (1955), who suggested that wood logs may reach the Tuomoto Islands in the equatorial West Pacific from South America, basically following the same route taken by Thor Heyerdahl (1947) and Vidal Alsar (1973). Most logs arriving at Tuomoto Islands were so intensively colonised by boring organisms that they were of little value for local people (Emery 1955), indicating that they had been floating for a long time, possibly arriving from South America.

Chirat (2000) described a strong correlation between drift patterns of dead *Nautilus* and *Allonautilus* and the main oceanic currents in the Indian and Pacific Oceans. Teichert (1970) also

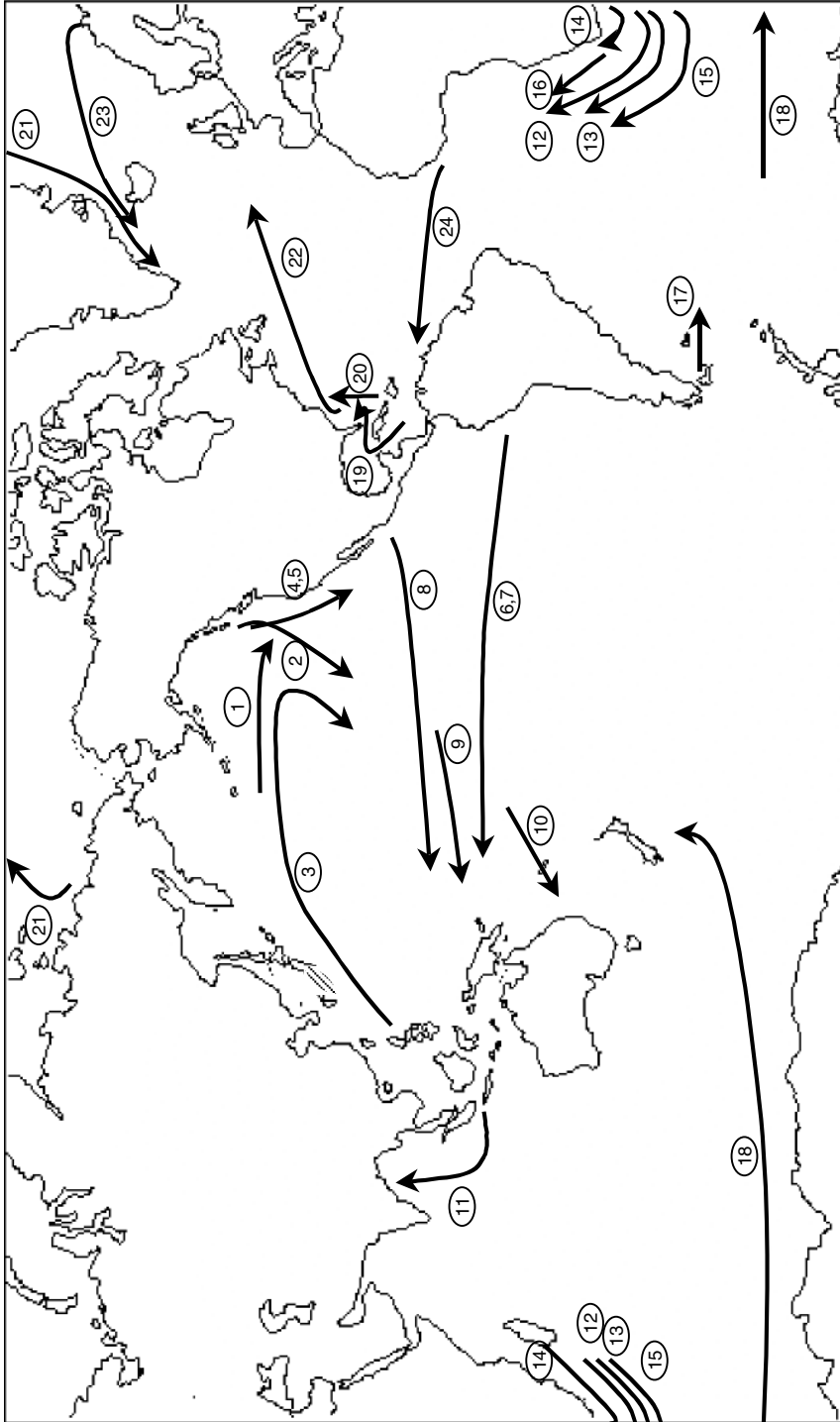


Figure 10 Trajectories of different floating substrata reported from different regions of the world; selected examples of trajectories for major current systems: 1 P, Ebbesmeyer & Ingraham 1992; 2 W, Strong & Skolmen 1963; 3 W, Guppy 1906; 4 M, Hobday 2000c; 5 M, Bushing 1994; 6 W, Emery 1955; 7 n.i., Guppy 1906; 8 V, Richards 1958; 9 V, Jokiel 1984; 10 V, Jokiel 1990; 11, *Nautilus* shells, Teichert 1970; 12 V, Walker 1950; 13 V, Walker 1950; 14 S, Frick & Kent 1984; 14 S, Muir 1934; 15 V, Walker 1950; 16 M, Arnaud et al. 1976; 17 M, Helmuth et al. 1994a; 18 V, Coombs & Landis 1966; 19 P, Winston 1982; 20, floating corals, Kornicker & Squires 1962; 21 W, Dyke et al. 1997; 22 S, Guppy 1917; 23 n.i., Ingólfsson 1992; 24 W, Guppy 1917. P, plastic litter; W, wood; M, macroalgae; S, seeds; V, volcanic pumice; n.i., no information.

suggested that shells of *Nautilus pompilius* found in the Bay of Bengal must have their origin somewhere near Indonesia. For the SW Pacific Jokiel (1989), based on an extensive discussion, suggested arrival of floating items from eastern source regions. Early studies by Guppy (1906) had already indicated that floating items may become dispersed efficiently in that region.

Some of the first reports from the Southern Ocean had already established the main trajectory direction of floating items in the West Wind Drift. Guppy (1917) reported that several drift bottles had been recovered thousands of kilometres east of their release sites. Underlining the importance of this current, Smith (2002) estimated that the western shores of Macquarie Island (54° 38'S, 73° 30'E) located in the centre of the West Wind Drift would receive on average 2500 rafts of *Durvillaea antarctica* each day. Currents in the West Wind Drift are predominantly in the eastward direction, as has been noted by Helmuth et al. (1994a,b). This route has also been reported for volcanic pumice, the track of which could be relatively safely established for the Southern Ocean (Frick & Kent 1984). These and other authors had also remarked on the influx of volcanic pumice into the Indian Ocean and the Australian and New Zealand region (Sutherland 1965, Coombs & Landis 1966).

In the western Indian Ocean, currents flow toward the south and the Agulhas Current connects to the Benguela Current (Pickard & Emery 1990). This is the route that, according to Walker (1950) and Frick & Kent (1984), is most likely to be the path of volcanic pumice found along the western coast of South Africa.

The trajectories of floating items in the South Atlantic have received relatively little attention. In contrast, intensive research has been conducted in the North Atlantic. Early on, watchful observers had already recognised that floating materials reaching the western shores of Europe came from source regions to the west, but it was not until Columbus that the origin of some of these items was identified. Using his knowledge of source regions of sea beans and the sites where these had stranded, Guppy (1917) provided a very detailed account on the trajectories of floating items in the North Atlantic. Based on his data he could show that sea beans (and other items) were frequently transported by the Gulf Stream from the East Coast of North America toward Europe. Some of these items are transported toward the Azores and southern Europe, whereas others are transported toward NW Europe. Using a similar approach, Guppy (1917) also showed that floating items that have their origin on the coast of Africa were occasionally transported toward the Caribbean Sea by the Equatorial Current. Since then, many different authors have reported on the importance of the Gulf Stream in transporting floating items toward NW Europe. Hentschel (1922) mentioned that he found a plant of *Sargassum* on a beach at Wangerooge (North Sea). Originating from the North American Atlantic coast, the obligatory rafting isopod *Idotea metallica* is thought to be introduced to NW European waters by the Gulf Stream (Naylor 1957), and it has been found as far north as the Norwegian coast (Pethon 1970). Minchin (1996) mentioned stranded drift on the western shores of Great Britain with clear signs of having originated from the Gulf Stream region. Guppy (1917) reported that on the southern shores of Iceland many trees are found, which hint toward their origin in the Caribbean or south thereof. He names mahogany logs and also seeds of *Mimosa* spp. that can be found on the shores of Norway, the Faroes, Iceland, and even Greenland. These reports indicate that these floating items may be carried toward high latitudes in the North Atlantic with the Gulf Stream and the Norway Current. Smith (1976) reported that tar lumps in the Barents Sea show indication of weathering suggesting that they had come from upcurrent sources (North Sea) in the Norway Coastal Current.

Within the Arctic Sea, floating items (sea ice and driftwood) are transported with the Beaufort Gyre in a clockwise circulation. The Transpolar Drift, which exits through the Fram Strait, transports floating items out of the Arctic Sea. The origin of driftwood and distributional evidence from some vascular plants have been used to infer that floating items with their origin in Siberia and NW Russia may be transported via the Transpolar Drift toward East Greenland (Johansen 1999, Johansen & Hytteborn 2001). Distributional evidence from rocky shore fauna has also been used to infer that these organisms may have been dispersed on floating substrata from northern Norway toward



Figure 11 Drift line of floating macroalgae in southern Chile. Seabirds (here black-browed albatross, *Thalassarche melanophris*) often gather along these drift lines.

Iceland, and then farther to Greenland and NE America (Ingólfsson 1992). This is supported by reports on driftwood being transported with the East Greenland Current into Baffin Bay (Dyke et al. 1997).

The oceanic currents that drive the above-described trajectories of floating items are relatively consistent and stable large-scale features. Other consistent oceanographic features such as fronts or eddies may also influence the dispersal and distribution of floating items at smaller scales (Figure 11). One important reason for the patchiness of floating items such as macroalgae as well as any other floating objects (Bourne & Clarke 1984, Witherington 2002) is the accumulation at fronts between two different water masses (Acha et al. 2003). Coastal fronts may be generated in waters streaming around geological formations such as islands, reefs, and peninsulas (Wolanski & Hamner 1988). Parker & Tunnicliffe (1994) reported frequent observations of floating macroalgae above Cobb Seamount approximately 500 km west to the coast of Oregon. Possibly, these algae become entrapped in the eddies developing above these seamounts, similar to what has been reported for oceanographic buoys (Richardson 1980). Other authors have reported large amounts of diverse floating items accumulating in oceanic fronts (Bourne & Clarke 1984, Flament & Armi 2000, Witherington 2002). Within these fronts, floating items may move very fast along the frontal axis (Flament & Armi 2000).

Internal waves and surface slicks produced by these fronts typically move in an onshore direction (Kingsford & Choat 1986, Shanks 2002). During these movements at velocities of approximately 1 km h^{-1} (Kingsford & Choat 1986), the slicks transport accumulated floating items in the same direction, i.e., toward the shore. Carr (1986) remarks that *Sargassum* algae are concentrated in large lines extending over “100 miles or more.” He also reports the observation of a

30-mile drift line in the Gulf of Mexico. Wind-induced formation of rows of *Sargassum* or other floating items has also been described by Faller & Woodcock (1964) and Hamner & Schneider (1986). Langmuir circulations develop at a minimum windspeed of about 3 m s^{-1} , and there is no evidence that windrows exist in strong winds when surface waters are heavily disturbed by waves (Barstow 1983). Distances between parallel windrows determine the catchment area of the front and can amount to up to 300 m (Barstow 1983). The accumulation of floating algae in fronts leads to entanglement of the plants and the formation of large patches or mats. Pelagic tar often co-occurs with *Sargassum* because both are caught in fronts where tar easily sticks to the plants (Butler 1975, Cordes et al. 1980).

Besides affecting the trajectory of floating items via wind-induced circulation, wind may also have a more direct effect on some floating items. Goda & Nishinokubi (1997) observed that wind speed and direction affected the trajectory of mimic driftwood in the Ariake Sea (Japan). Sutherland (1965) attributed the high velocity of floating pumice from the Sandwich Island eruption to the fact that large pumice pieces lying high in the water were pushed by wind and currents in the same direction. Observations by Segawa et al. (1962) on floating macroalgae labelled with postcards revealed that trajectory and velocity are strongly influenced by the prevailing winds (Figure 12). Deysher & Norton (1982) also suggested that the velocity of floating *Sargassum* plants off the California coast can be accelerated by strong winds.

Transport directions may also change over time. In some regions there are seasonal changes in current directions (e.g., Morton & Britton 2000). For example, Green (1999) pointed out that current patterns in the NW Indian Ocean may change between the winter and summer monsoons. On the southern coast of Java, floating objects may be transported in an eastward direction during the summer monsoon and in a westward direction during the winter monsoon. Changes in the intensity or direction of current-mediated transport may also occur between years or even over larger temporal scales. Butler & Stoner (1984) suggested that changes in the local abundance of floating *Sargassum* may be due to interannual variations in currents. Based on driftwood samples, Dyke et al. (1997) have suggested that during the Holocene period there was a change in the direction of the Transpolar Drift in the Arctic Ocean. At present, part of the wood originating from sources in northern Siberia (Johansen 2001) is transported along the east coast of Greenland and then around the southern tip of Greenland into Baffin Bay (Dyke et al. 1997).

It is evident that surface currents have the potential to transport floating items together with the associated rafting biota toward new shores. Velocities and directions are occasionally highly favourable for long-distance transport, underlining the potential importance of floating items in the dispersal of rafting organisms. Several zoogeographic studies have already hinted at the linkage between downcurrent sinks and upcurrent source regions (e.g., Jokiel 1989, Ingólfsson 1992, Ó Foighil et al. 2001), and in future studies, it appears a promising enterprise to examine the relationship between the trajectories of floating items and the biogeography of coastal organisms.

Historical changes in occurrence of floating items

Floating items have also travelled the world's oceans during evolutionary history. The common occurrence of erratic rocks in coal reservoirs has been used to infer that these were transported with driftwood (Emery 1955). Marine organisms on or in fossilised driftwood (e.g., Simms 1986, Arua 1991) suggest that rafting may also have been an important dispersal process in palaeo-oceans. The palaeobiogeographic distribution of nautiloid shells is most likely based on the fact that shell remains have floated over long distances after the death of the animals (Chirat 2000). The palaeobiogeography of some gastropod species with direct development has also been used to infer that these (or their egg masses) may have rafted on floating plants (Givens 1991). Remains of Holocene seaweed (most likely *Sargassum*) with attached calcareous polychaetes have been found in anoxic deep-sea sediments, suggesting that the floating algae may have sunk rapidly to the sediment after becoming negatively buoyant (Kennett & Penrose 1978). The abundant presence of sea-rafted

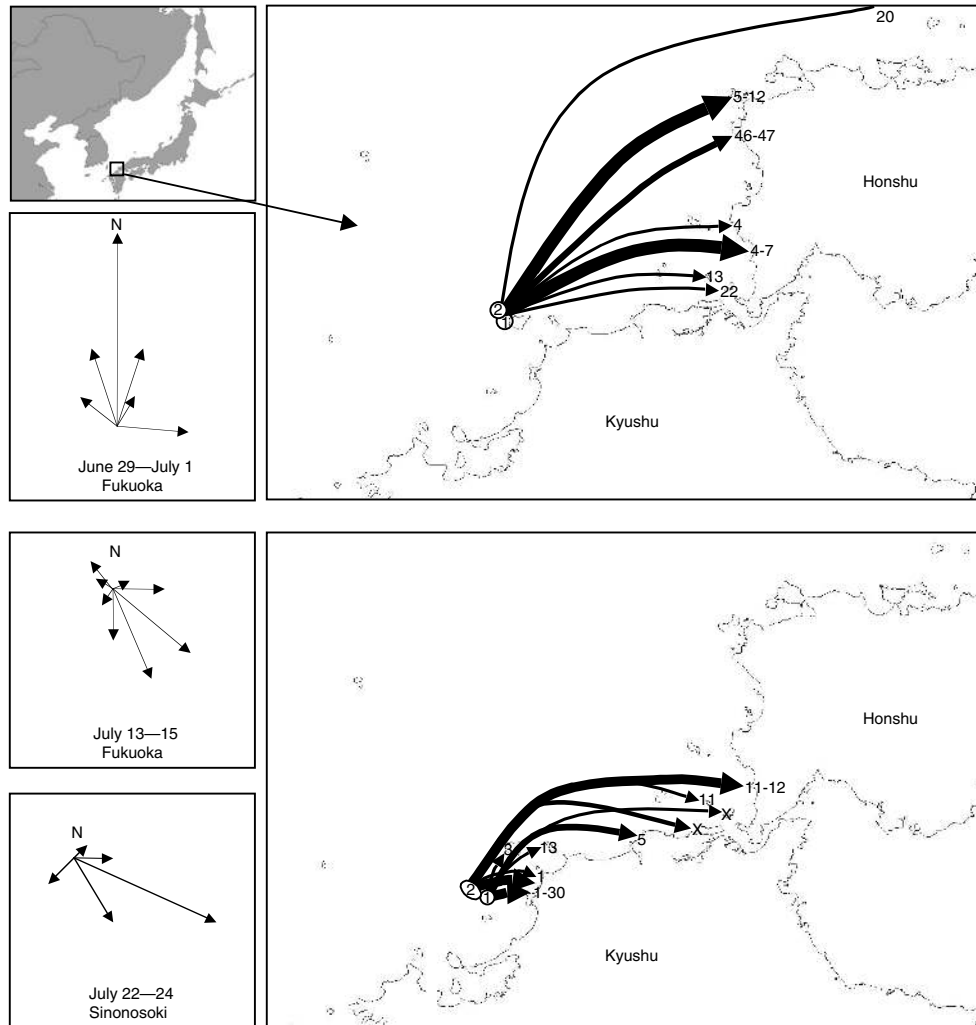


Figure 12 Trajectories of postcard-labelled floating macroalgae released in summer 1960 off SW Japan. Numbers indicate the length of the drift period in days, thickness of arrows indicate numbers of floating items recovered, and inserts on the left of each drift map show the prevailing wind directions during the drift period. (Modified after Segawa et al. 1962.)

pumice of Holocene origin on some coasts (Ward & Little 2000) also hints at the importance of floating pumice during recent history. Whereas these reports indicate the presence of floating items in palaeo-oceans, little is known about their abundance and trajectories. Similarly, few reports on historic changes in abundance and composition of floating items are available. Dramatic changes, though, have taken place following the increase of the human population during the past centuries. Logging activities have contributed to changing supplies of floating wood (Maser & Sedell 1994). Whereas the amount of driftwood in the world's oceans may have increased during the initial stages of large-scale logging in the past century, efficient retention of driftwood in rivers and estuaries has led to diminished supplies in recent years. Similarly, the regulation of river runoff and the construction of dams have contributed to dramatic changes in supply of driftwood and other floating items of terrestrial origin in many regions of the world. Canalisation of rivers and straightening of coastlines may also have changed local current regimes and the trapping and retention efficiency of coastal habitats.

In the 19th century, large amounts of coal slag from furnaces were dumped in the sea, as can be inferred from the large quantities found in the flotsam of northwest European shores during that time (Bäckström 1890). These slags may have had longevity and characteristics similar to those of floating pumice. With the advent of the plastic age, the abundance of floating items of high longevity has dramatically increased throughout the world's oceans (e.g., Barnes 2002). Floating items of anthropogenic origin can now be found in regions where few floating items were present previously. For example, Guppy (1906) remarked that the Mediterranean Sea was poor in floating items, whereas present-day authors have repeatedly revealed very high amounts of floating plastics (Morris 1980a) and tar lumps (Morris 1974). These changes have led to substantial changes in rafting opportunities in many regions of the world. Today, floating items of anthropogenic origin are still very abundant in the world's oceans, even though improved legislation has led to slight decreases in some regions. Some authors suggest that the abundant presence of anthropogenic items may have contributed to the high number of species introductions in coastal habitats (Barnes 2002, Aliani & Molcard 2003).

Floating substrata as dispersal agents

This review shows that floating substrata in the world's oceans differ strongly in their suitability and availability for potential rafting organisms. This has important implications for rafting as an ecological process. In the following section an attempt is made to synthesise the main information in order to reach general conclusions about the importance of floating substrata as dispersal agents.

The resource value of floating substrata depends on whether they are of biotic or abiotic origin. The food value and longevity of floating items exhibit an inverse relationship where biotic substrata feature relatively high food value but limited longevity and abiotic substrata are of little or no food value but are highly resistant to degradation (Figure 13). The longevity of biotic substrata is often limited because biological processes contribute to their degradation. Macroalgae are consumed by a wide diversity of grazing organisms but may continue to grow while afloat and thereby extend their longevity. Several studies suggest a delicate balance between degradation and growth in floating macroalgae, which appears to be mediated largely by temperature (Hobday 2000b). Apparently, consumption increases at high temperatures, exceeding the growth potential of floating macroalgae, thereby leading to rapid disintegration. This may be the main reason for the minor importance of macroalgae as floating substrata at low latitudes where water temperatures are high. Floating wood does not grow during the voyage at the sea surface, but is less susceptible than macroalgae to degradation by consumers and, consequently, may have a comparatively high longevity. The longevity of animal carcasses is primarily limited by the fact that these are highly attractive to consumers and therefore degrade relatively rapidly. Most abiotic substrata are of little or no food value for rafting organisms. The high longevity of animal skeletons, volcanic pumice, plastic litter, and tar balls at the sea surface might be largely due to the fact that these items are unattractive to secondary consumers.

The size of floating substrata has a strong influence on the number of organisms that can colonise them. Both biotic and abiotic substrata are prone to become fouled by rafting organisms. During growth these fouling organisms may lead to an increase in specific gravity of the floating assemblage and cause it to become negatively buoyant. Substratum size, structure, and surface area may affect the total biomass of the attached epibiota. For substrata of given physical and chemical characteristics a simple relationship between size and epibiont-induced loss of buoyancy can be proposed (Figure 14). At a small size (<1 cm in diameter), only very small organisms are able to colonise substrata, and these may not be able to cause a strong decrease in buoyancy. Intermediate-size substrata may harbour many different organisms, which during growth may cause items to sink. On very large floating items the volume-to-surface ratio may be sufficiently large to minimise the effects of a dense fouling community. Loss of buoyancy caused by fouling organisms can be expected to be less likely in simple and voluminous items than in complex and less voluminous

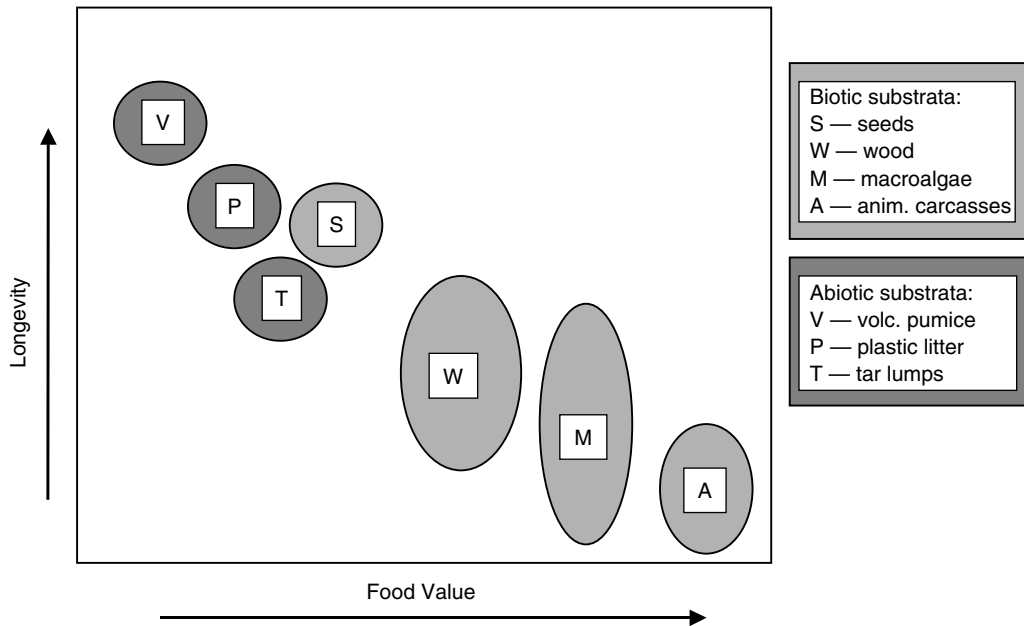


Figure 13 Hypothetical relationship between food value and longevity of biotic and abiotic floating substrata.

items. Voluminous and compact items such as driftwood, sea beans, pumice, plastic spherules, bottles, and buoys thus should be less susceptible to sinking as a result of fouling than complex and flat items such as macroalgae and plastic sheets (Figure 14). In summary, rafting organisms may contribute to the demise of their rafting substrata by consumption (leading to degradation) and increase of specific gravity (leading to loss of buoyancy). Biotic and complex intermediate-size substrata (1–100 cm in diameter) appear to be most susceptible to these destructive processes.

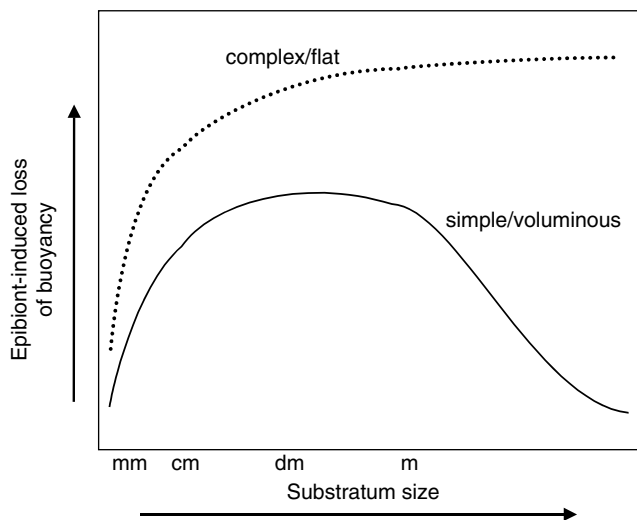


Figure 14 Hypothetical relationship between substratum size and epibiont-induced loss of buoyancy for two categories of floating substrata; categories considered comprise those of (1) complex structure or large flat surfaces and (2) simple structure or voluminous.

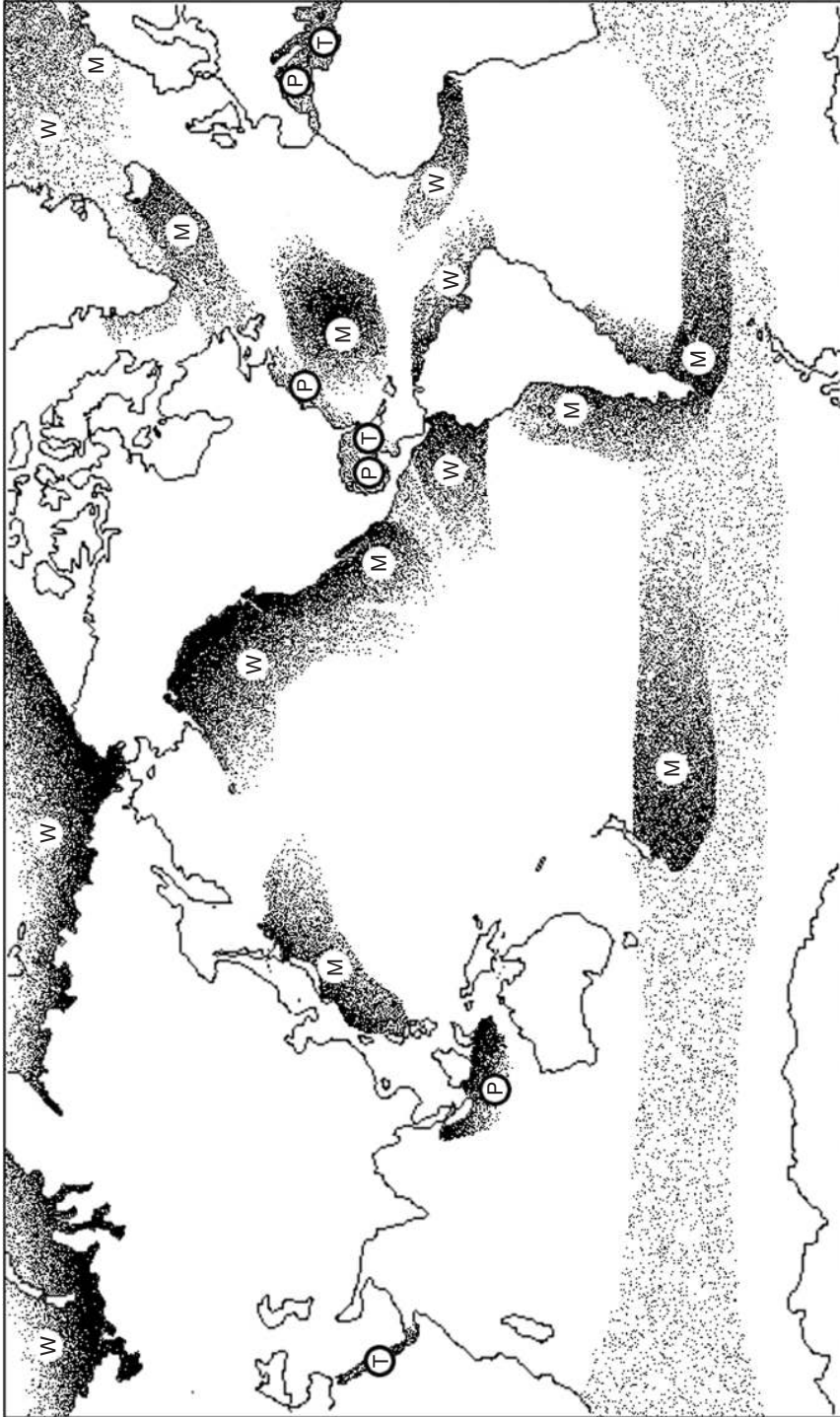


Figure 15 World map showing the regions where different floating substrata are of major importance; letters indicate substratum type: M, macroalgae; W, wood; P, plastic litter; T, tar lumps. Substrata can be found throughout the world's oceans but are less predictable or of minor abundance than in the regions shown; for some regions information is lacking (e.g., Indic Ocean). Density of shading indicates abundance of floating substratum type.

The importance of rafting in different regions will strongly depend on the abundance of floating items. The availability of floating items is determined by (1) supply and (2) sinks. Herein it became evident that supply of different substrata may show strong spatial and temporal variations. The majority of floating items have their origin in coastal regions (Figure 15). Floating macroalgae and sea grasses are abundant near coastal habitats with extensive kelp forests and sea grass beds, from which they are detached primarily at the end of the annual growth season. Wood is delivered to the northern oceans (Arctic, northern North Pacific, and northern North Atlantic) from the extensive forested areas in that region. Driftwood appears to be of less importance in the Southern Ocean but is abundant off the major rivers at low latitudes. A temporal supply of driftwood is related to ice melting at high latitudes and the rainy season at low latitudes. Volcanic pumice may be introduced at all latitudes but appears to be most common in the Pacific Ocean. A temporal supply of pumice is strongly correlated with volcanic activity, when over a short period large quantities of floating pumice may become available. Anthropogenic litter is introduced in large quantities at mid- and low latitudes near the major centres of human population, but it can also be found at high latitudes near sites of temporary human activities (e.g., shipping and fishing). There appears to be no distinct seasonal trend in the supply of anthropogenic floating items, but varying terrestrial runoff may affect delivery to regional seas.

The sinks of floating items are determined by their longevity at the sea surface, wind, and oceanic currents. Due to their limited longevity, floating macroalgae and sea grasses usually may not be transported far beyond the regions of supply. However, in regions where degradation processes are slowed or counteracted by growth, floating macroalgae might travel over long distances, as had been suggested for the Southern Ocean (e.g., Helmuth et al. 1994a, Smith 2002). Driftwood, as a result of relatively high longevity, may be transported far from the regions of origin, and some large items, resistant to sinking, may cross entire ocean basins. Volcanic pumice apparently rarely sinks to the seafloor and may become dispersed throughout the world's oceans at very long distances from their origin, which is also true for some plastic items. Onshore winds and currents push vast amounts of floating items toward coastal habitats and onto ocean shores worldwide, underlining the importance of oceanic currents and winds in their transport. The geomorphology of the shoreline may affect the probability of floating items to be trapped in nearshore habitats. Rugged shorelines with many inlets and bays may represent efficient and final traps for floating items. Here, floating items may be held back in shallow waters or stranding on beaches and in salt marshes. This may not only be negative but also present an opportunity for rafting organisms to colonise nearshore habitats in calm shallow waters.

Some of the sinks may be final, but others may only present a resting station for floating items. Biotic substrata degrading on the shore or sunk to the deep sea will most likely lose any rafting organisms due to death, even though some of the animals shipwrecked at sea may actively swim and potentially find other floating items (e.g., Hobday 2000a, Castro et al. 2002). Other items that have been trapped in coastal bays, in salt marshes, or on beaches may return to the sea during strong high tides or storms. Depending on the conditions during these resting stops on the shore or in nearshore habitats, some of the rafting organisms may survive and continue their voyage after such a stopover. Many authors have also reported that floating items are concentrated in certain areas, e.g., eddies and frontal systems. Here, different items may come into direct contact with each other, allowing rafting organisms to change between substrata. Floating items may also entangle in these areas and continue their voyage as patches of substrata of diverse characteristics and origin. These processes are expected to affect the composition of the rafting community on the resulting heterogeneous patches.

The fact that floating items are usually carried in the predominant downcurrent direction may have strong implications for the transport of rafting organisms from upstream sources to downstream sinks. Many different studies revealed the link between source regions and coastal sinks. For example, Guppy (1917) remarked that sea beans, driftwood, and other items are transported via the Gulf Stream from the Caribbean to NW Europe where they can frequently be found on local

beaches. He also found driftwood from Africa on Caribbean shores. Ingólfsson (1992) suggested that floating macroalgae from northern Europe may have travelled to Iceland and Greenland and from there even farther to NE America, carrying with it members of the rocky shore fauna from NW Europe. Helmuth et al. (1994a) revealed that floating macroalgae collected between the Falkland Islands and South Georgia had their origin in Tierra del Fuego (South America). Several authors suggested downcurrent transport of volcanic pumice or floating corals together with attached organisms (Jokiel 1990, DeVantier 1992). Similar downcurrent transport has been reported for many other floating items and regions of the world. In some regions where potential coastal sinks are far from source regions, floating items may end their voyage at sea. This might be the case for many floating macroalgae in Japan that are transported with the Kuroshio Current into the open North Pacific (e.g., Safran & Omori 1990). However, some long-living substrata may cross long distances, permitting transport of rafting organisms between distant shores. Because abiotic substrata are more likely to travel for longer periods and over wider distances than biotic substrata, organisms capable of surviving on abiotic substrata may have a higher likelihood of becoming dispersed via rafting than organisms that require biotic substrata.

One of the most interesting results of this review in the context of rafting is the fact that the temporal supply of many floating items is highly variable on both annual and interannual scales. Periods of abundant supply alternate with periods when almost no new items are delivered to the sea. For some items (e.g., macroalgae and plants) supply may vary on a regular, seasonal basis, but for other items supply may be less predictable and less frequent (driftwood, pumice, and animal remains). Floating items of anthropogenic origin are delivered to the world's oceans on a much more regular basis than most natural floating items. The temporal variability in supply of floating items will have strong implications for rafting as an ecological process. Dispersal via rafting on floating items of natural origin may be a rather sporadic event.

Outlook

The main questions of interest in the context of rafting as a dispersal mechanism are: (1) Which organisms are dispersed via rafting? (2) Over what distances is rafting effective? The answers to these questions depend on the characteristics of the floating substrata. Herein we synthesise some information that will help to answer these questions. However, there are still many questions left that require better answers in the future in order to evaluate the importance of floating substrata as dispersal vectors. There are strong indications that macroalgae are abundant at mid-latitudes and that driftwood is of major importance in the arctic region and at low latitudes, but for many regions no quantitative information about the spatial and temporal distribution of floating items is available. We suggest the use of ship surveys to obtain quantitative estimates from different regions. No sophisticated equipment is necessary for such surveys and studies could be conducted from ships of opportunity, similar to what is done with the Continuous Plankton Recorder Surveys (Warner & Hays 1994). Presently, there is good evidence that some abiotic substrata (volcanic pumice, plastic litter) have a very high longevity, but there is still a research need for information on biotic substrata under different conditions. In particular, it appears to be promising to study the longevity of floating macroalgae in regions differing in nutrient concentrations and water temperature because these factors may influence growth and degradation of macroalgae. In this context the interactions between rafting organisms and their floating substrata are of major interest because these will have an influence on degradation and loss of buoyancy. These studies should be conducted over a wide range of substratum sizes because the colonisable space on a floating item may have a strong influence on the outcome of these interactions. Finally, the trajectories and velocities of floating substrata require further attention. Estimates summarised herein suggest that most substrata are transported at average velocities of 0.5–1 km h⁻¹, but there is also a strong indication that floating substrata occasionally may travel at much faster speeds. The main trajectories of floating substrata appear to coincide with the major oceanographic currents, but sometimes substrata seem to take

unexpected turns. To our knowledge, common floating substrata have only been tracked at sea in coastal waters of Japan (Segawa et al. 1962) and California (Harrold & Lisin 1989, Hobday 2000c). We propose tracking floating items at sea in other regions of the world's oceans to obtain better estimates of the velocities and trajectories of the different types of substrata. During their voyage, floating items often are concentrated in convergence zones (fronts) and eddies, which may result in formation of large, heterogeneous patches and in transfer of rafting organisms between substrata. These processes should be examined because, in these areas of accumulation of floating items, rafting organisms arriving on unsuitable substrata may find more suitable transport vehicles. The appearance of large numbers of specific floating items at sea seems to be sporadic and unpredictable, yet these events may be of major importance since during these periods many individuals of a rafting species may travel together, thereby increasing the chances of successful establishment in new habitats. Therefore, every effort should be made to study rafting during these sporadic events (e.g., floating pumice after volcanic eruptions or driftwood following river floods). Rafting can only result in successful dispersal if the floating assemblage reaches new coastal habitats. Most shore surveys of floating items have been conducted on sandy beaches, which are a hostile environment for most rafting organisms. We propose to examine arrival rates of floating items in a wide variety of coastal environments that could be potential habitats for coastal organisms, including rocky shores, boulder beaches, estuaries, mangrove and kelp forests, and sea grass beds.

It is evident that floating substrata are of major importance for potential rafters, but the capabilities and requirements of the rafting organisms themselves will be critical in determining whether rafting can result in successful dispersal. The capacity to survive on a floating item and to colonise new habitats is most important in this context. In a future contribution we will examine which organisms are commonly reported as rafters and whether these organisms show any particular adaptations to life on a pelagic raft. Furthermore, we will critically illuminate the different steps and scales involved in the rafting process in order to evaluate the role of rafting as an important dispersal mechanism in present-day oceans.

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