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THE ECOLOGY OF RAFTING IN THE MARINE ENVIRONMENT. III. BIOGEOGRAPHICAL AND EVOLUTIONARY CONSEQUENCES

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Abstract Rafting of marine and terrestrial organisms has important ecological, biogeographical and evolutionary implications. Herein the general principles of rafting are described and how they contribute to population connectivity. Rafting dispersal has particular characteristics, which may differ substantially from those of species with planktonic larval dispersal. Dispersal distances achieved via rafting can vary considerably: journeys may be very short or in some cases extremely long, depending on currents and wind. Accumulation of rafts in convergence zones facilitates cohesion of travelling groups, possibly reducing the risk of founder populations being very small. This becomes particularly important over long distances where singular founder events could provoke strong reduction of the genetic variability in the founded population. The frequency of transport affects the degree of connectivity between local populations. Three important rafting routes are distinguished: frequent, intermittent and episodic. Frequent rafting routes are found in bays, lagoons and estuaries, and they are typically facilitated by substrata of biotic origin (seagrass, saltmarsh vegetation, intermediate-sized algae and mangroves). Intermittent rafting routes are found along temperate continental shores where they are facilitated primarily by giant kelps. In the subtropics and the Arctic intermittent rafting routes facilitated by wood are particularly important. Episodic rafting routes, which often cross vast areas of open ocean (biogeographic barriers), are facilitated by volcanic pumice, floating trees and occasionally by giant kelps when these are pushed beyond intermittent routes by strong winds or currents. Dispersal events occur in a highly sporadic manner in this latter category of rafting route, but when they happen, large amounts of floating substrata and rafters may be dispersed simultaneously. Intervals between events can be decades, centuries or even millennia, and consequently populations resulting from these events may be isolated from each other for long time periods. Population connectivity on frequent, intermittent and episodic rafting routes is high, intermediate and low, respectively. Genetic studies support these predictions, and furthermore underline that rafting may contribute to population connectivity over a wide range of geographic scales, from <100 km up to >5000 km. Rafting also has a strong effect on evolutionary processes of the organisms dispersed by this means. It is suggested that local recruitment (consequence of direct development) contributes to enhanced rates of population divergence among local populations of common rafters, but occasionally high genetic diversity may result from secondary admixture. Isolation of colonisers after singular episodic rafting events facilitates allopatric speciation. Through these processes rafting dispersal may support local species richness and thus have an influence on local biogeography and biodiversity. Human activities affect rafting connections in the oceans either by reducing or enhancing the possibility of transport and

landfall. In many cases it cannot be safely decided whether the appearance of a species in a new habitat is due to rafting or to other transport mechanisms, and genetic studies can help to identify the most likely causes. Future field and laboratory studies on the ecology of potential rafters in combination with genetic studies on different spatial and temporal scales will contribute to a better understanding of the mechanisms of rafting dispersal, consideration of which is crucial in developing efficient conservation measures in the marine environment.

Introduction

> *The existence of the* Plagusia tomentosa *[=*P. chabrus *Linnaeus 1758] at the southern extremity of Africa, in New Zealand, and on the Chilian coasts, may perhaps be due to migration, and especially as it is a southern species, and each of these localities is within the subtemperate region. We are not ready however to assert, that such journeys as this range of migration implies are possible. The oceanic currents of this region are in the right direction to carry the species eastward, except that there is no passage into this western current from Cape Horn, through the Lagulhas current, which flows the other way. It appears to be rather a violent assumption, that an individual or more of this species could reach the western current from the coast on which it might have lived; or could have survived the boisterous passage, and finally have had a safe landing on the foreign shore. The distance from New Zealand to South America is five thousand miles, and there is at present not an island between.*
>
> **Dana (1856) reporting on the geographical distribution of Crustacea**

The riddle of *Plagusia chabrus* still is not resolved. It is well known that this species is widely distributed in the southern oceans, but it is not clear whether the individuals from New Zealand, South America and South Africa indeed represent the same species or not (C. Schubart, personal communication). Most likely it will be necessary to await molecular studies to show whether the populations from those distant regions were separated a long time ago, or whether exchange between them still exists. In case these studies show actual gene flow, Dana (1856) already offered a possible explanation of how this could be achieved over such long distances: “They may cling to any floating log and range the seas wherever the currents drift the rude craft”. While he did not have the insights of post-Darwinian biologists and the tools of modern science, Dana (1856) had already recognised the importance of the interaction between dispersal and allopatric speciation. The questions that fascinated Dana and his contemporaries 150 years ago continue to move scientists today. However, despite the enormous scientific progress since then, dispersal remains an important incognitum to biologists. In particular, marine biologists are faced with the problem that many of the species of interest are difficult or impossible to track during their boisterous journeys in the oceans. Many marine organisms are small, and following them in the vast realms of open water is unfeasible. This is especially true for those species that have planktonic larvae. Yet scientists have managed with admirable effort to follow tiny larvae during their planktonic journey and to obtain reliable estimates of effective dispersal distances (e.g., Young 1986; Stoner 1990, 1992), but only for short-lived larvae (a few hours). For most species with longer-lived larval stages no or only approximate estimates are available. This is even more true for invertebrate species without larval stages. Many of these latter species rely on other dispersal mechanisms (e.g., rafting) but very little is known about the distances they may achieve during these voyages, let alone actual exchange between distant populations.

In general, it had been assumed for a long time that the dispersal potential of species with planktonic larvae would be relatively high while that of species without planktonic larvae would be limited. Results that did not coincide with this general perception have increasingly puzzled marine biologists during the past 20 years. When Johannesson (1988) found abundant populations of the directly developing gastropod *Littorina saxatilis* but not of *L. littorea*, a species with a planktonic larva, on a remote island in the North Atlantic she formulated the 'Paradox of Rockall'. More recently, Colson & Hughes (2004) observed fast recolonisation of remote sites by another directly developing gastropod, *Nucella lapillus*, and furthermore they revealed continuous genetic population structure across the British Isles. The authors of these (and other) studies inferred that, in the absence of pelagic larvae, dispersal could be achieved via rafting on floating substrata (Edmands & Potts 1997, Hoskin 1997, Arndt & Smith 1998, De Matthaeis et al. 2000, Collin 2001, Porter et al. 2002, Sponer & Roy 2002, Colson & Hughes 2004, Waters & Roy 2004a, Baratti et al. 2005, Lourie et al. 2005). Indication that rafting dispersal may be important for a wide diversity of species is continuously increasing with evidence coming from small unicellular organisms, invertebrates and even large terrestrial invertebrates (Masó et al. 2003, Waters & Roy 2004a, Glor et al. 2005). Thus, it appears that the wide distribution of some species with direct development is no longer a paradox; dispersal of these species may be much more efficient and common than previously assumed. Rafting can thus transport organisms to distant habitats, but how much exchange is there between populations and what does it depend on?

Exchange processes between habitats and populations occur over many different scales in the marine environment (Carr et al. 2003). For example, ecologists recognised early on that high temporal and spatial variability in recruitment intensity often depends on supply and exchange between neighbouring populations. Important trophic fluxes between habitats further underline the fact that many marine systems exchange biomass (and living organisms) with neighbouring systems. With the advent of molecular techniques an increasing number of genetic studies offered important insights into the connectivity (extent to which populations are linked by exchange of propagules, i.e., dispersing eggs, larvae, recruits, juveniles or adults) of local populations of marine organisms. In some cases these studies have revealed high connectivity between distant local populations (e.g., Johnson & Black 1984a,b; Hellberg 1996; Ayre & Hughes 2000; Kyle & Boulding 2000; Lessios et al. 2001; Pfeiler et al. 2005), while in others they have identified almost complete lack of exchange between neighbouring populations (e.g., Ayre & Dufty 1994, McFadden 1997, Ayre & Hughes 2000). Conservation biologists are keenly aware of the fact that population connectivity is a crucial variable when designing networks of marine-protected areas (see Palumbi 2003, Grantham et al. 2003, Baums et al. 2005, Kinlan et al. 2005).

The degree of population connectivity depends on (i) the distances between habitats, (ii) the prevalent current patterns, (iii) supply of propagules, (iv) the dispersal capability and (v) the colonisation potential of the organisms under consideration. Dispersal capabilities of marine organisms vary substantially depending on their sizes, morphology, behaviour and life histories. Dispersal can be achieved by planktonic larvae or swimming adult stages that are capable of maintaining themselves in the water column, thereby facilitating transport via currents. In this case, dispersal distances are largely determined by currents and by the swimming ability of the respective organisms (either larvae or swimming adults) (e.g., Shanks et al. 2003). Estimates of potential dispersal distances can be obtained by combining current velocities and larval life span for species with planktonic larvae (Siegel et al. 2003, Kinlan et al. 2005). Species without planktonic larvae or with adults that lack efficient swimming capability depend on other dispersal mechanisms, usually aided by a dispersal agent, for example birds (Green & Figuerola 2005), fish (Domaneschi et al. 2002), humans (Wonham & Carlton 2005) or floating substrata (Thiel & Gutow 2005a,b). In general, distances between habitats, currents and propagule supply are the main factors that influence the degree of population connectivity in species with autonomous dispersal stages and those dependent on dispersal agents. However, population connectivity potential differs between these two groups in that the latter additionally depends on the characteristics of the dispersal agent, here floating substrata.

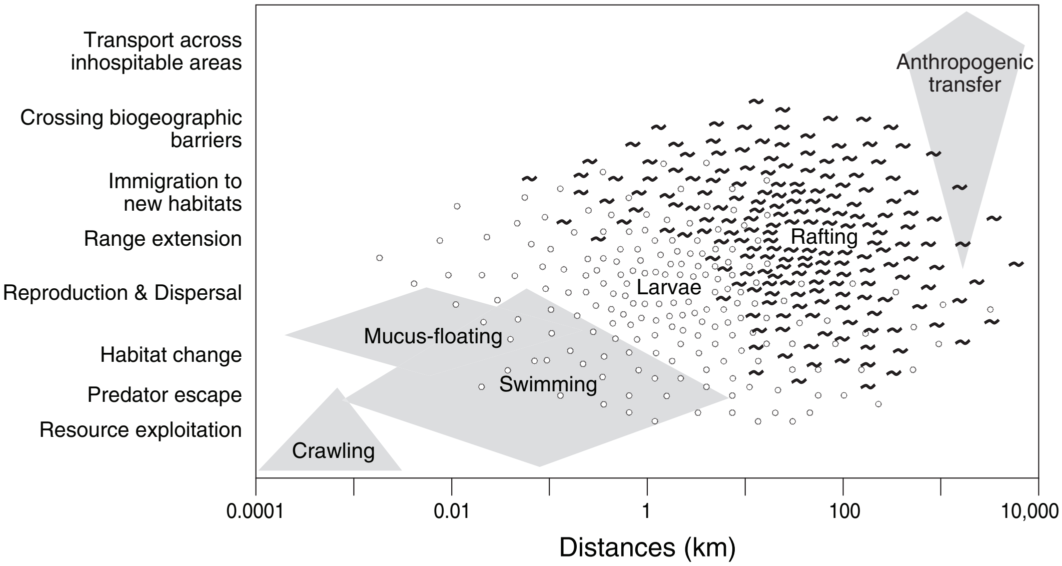

Figure 1 Schematic relationship between geographical distance and biologically relevant movements indicating the principal dispersal mechanisms on each scale.

A diverse armada of floating objects is continuously underway in the world's oceans, the most important being macroalgae, wood, volcanic pumice and increasing amounts of plastics (Thiel & Gutow 2005a). These floating objects differ substantially in their suitability for rafting organisms, in particular in food value and longevity. In addition, in most regions the abundance, drift direction and velocity of floating objects depend on unpredictable events (for example storms), thereby introducing additional uncertainty when estimating population connectivity via rafting dispersal. Perhaps it is due to the stochastic nature of rafting dispersal that most recent efforts in estimating population connectivity in the marine realm have focused on organisms with autonomous dispersal stages (Gerber et al. 2005), even though there are many reported cases of organisms without pelagic larval stages, which depend on rafting (or other mechanisms) for dispersal (Thiel & Gutow 2005b).

While it is increasingly known and widely accepted among ecologists that rafting dispersal occurs, relatively little is known about its significance in marine (and terrestrial) communities. Organisms are dispersed via diverse mechanisms in the sea (Figure 1). Most of these mechanisms are of great importance at certain life history stages and are most effective over a particular range of distances. For example, walking and crawling may be important on the scale of cm or several m, depending on the size and characteristics of a species. Swimming organisms may move over hundreds of metres up to several kilometres. Planktonic larvae are dispersed over a wide range of distances from a few metres up to hundreds of kilometres. Rafting is effective over similar distances but there is indication that some rafters may be carried over thousands of kilometres, distances rarely achieved by planktonic larvae. Anthropogenic transport of marine organisms (for example through ballast waters) extends over similar distances as rafting. However, unlike rafting dispersal, human activities may carry marine organisms over very large distances, across regions that exceed the physiological limits of many organisms (Carlton & Geller 1993). This can occur when organisms are enclosed in spaces maintaining favourable environmental conditions during transport (ballast water tanks in ships, or coolers for aquaculture purposes). Thus, as a natural process, rafting operates at spatial scales also covered by other dispersal mechanisms in the sea. However, it appears to be particularly effective over distances where other mechanisms lose importance (Figure 1).

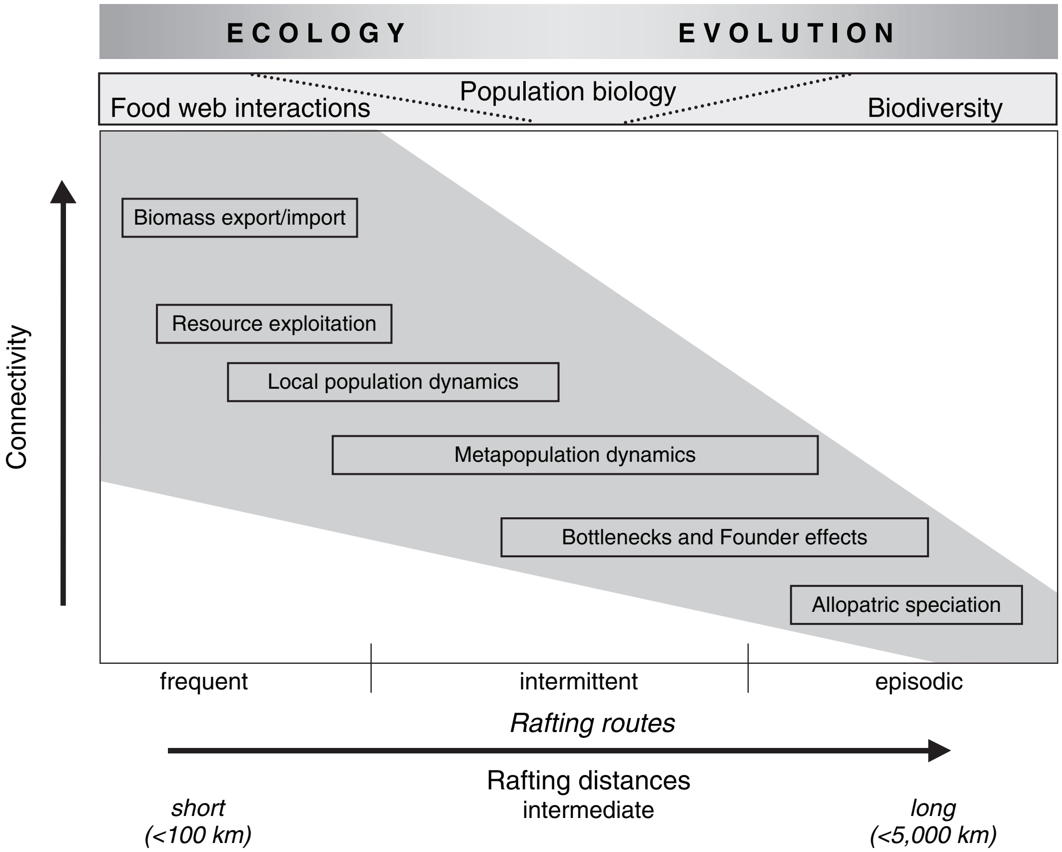

Figure 2 Schematic relationship between frequency/distance of rafting events/routes and the degree of connectivity between local populations. Important ecological and evolutionary processes affected by this relationship are also indicated. The shaded area indicates that the number of species and individuals expected to successfully disperse by rafting decreases with increasing rafting distances.

Rafting may transport a wide variety of organisms (Thiel & Gutow 2005b) but this process is only of evolutionary or ecological significance if the journey leads them to sites beyond their neighbourhood area and if rafters can disembark and establish in coastal marine or terrestrial habitats. Depending on the frequency and intensity of transport, one can hypothesise that there should be three principal temporal and spatial scales over which rafting acts (Figure 2). Frequency of transport is also related to transport distances since many of the most common floating substrata persist only for limited time periods at the sea surface (non-lignified vascular plants, seagrasses, small algae), while substrata that become available less frequently (large trees, calcareous skeletons, volcanic pumice) have a very high longevity (Thiel & Gutow 2005a). At very high rafting frequencies, organisms utilise rafting to reach resource patches within habitats, and abundant rafting events also facilitate export and import of organisms to and from neighbouring habitats. This will also lead to effective mixing of individuals between resource patches, thereby reducing the probability of deme formation. At intermediate rafting frequencies, rafting events are sufficiently common to permit efficient exchange between and within local populations, affecting the dynamics of metapopulations and local populations. Depending on the frequency and intensity of the connectivity, local populations will display varying degrees of genetic relatedness. At low rafting frequency, dispersal events are so rare that a species (group) that is successfully transported will not experience the arrival of additional conspecifics over many generations, allowing for genetic differentiation and eventually even allopatric speciation. It is important to keep in mind that these categories are arbitrary, but that they reflect the three principal temporal and spatial scales over which rafting dispersal operates.

In general, it can be hypothesised that at high rafting frequencies, ecological and microevolutionary processes should be dominating, while at low rafting frequencies cladogenetic events (e.g., allopatric speciation) will gain importance. Given the fact that rafting frequency depends, among other things, on the availability and longevity of floating substrata, and that not all organisms are adapted to survive for long time periods as rafters, it can furthermore be expected that different taxa are differentially adapted to be dispersed via rafting. For example, few organisms may be able to survive long-lasting journeys, and consequently only a specific subset of organisms may experience long-distance dispersal via rafting permitting colonisation of new habitats. Likewise, only some organisms are capable of using rafts as short-term floats, allowing them to move between local habitats or exploit ephemeral resource patches.

In this review, the ecological, biogeographical and evolutionary implications of rafting dispersal in the marine environment will be addressed. The review is concerned with the consequences of rafting on a variety of scales. Based on published case studies, the account will explore whether predictions based on longstanding assumptions of marine dispersal are valid, and if so, for which organisms. Furthermore, future study topics will be suggested, addressing important questions that need to be answered in order to better understand rafting dispersal. Finally, it will be pointed out where, why and how rafting-mediated connectivity needs to be considered in the design of areas protecting coastal marine environments.

Dispersal in the sea

General considerations

In general, dispersal is what maintains and expands the geographic range of species and as such it determines the degree of genetic connectivity between local populations of a species (Palumbi 2003). Dispersal can be active (autochrony: swimming, crawling) or passive (rafting, human-mediated) and it may be by diffusion from the home range or by long-distance dispersal (also called jump dispersal). Long-distance dispersal (LDD) can be defined relative to some ecologically significant scale that sets the limits of the local population or the mean dispersal distance for the metapopulation (Kinlan et al. 2005). It is important to consider that LDD and the absence of dispersal represent extremes along a dispersal scale continuum (Bradbury & Snelgrove 2001, Mora & Sale 2002, Kinlan & Gaines 2003, Shanks et al. 2003, Kinlan et al. 2005). Both organisms with a planktonic larva and organisms with direct development (brooders) may have high potential for LDD. For brooders, LDD is probably achieved via rafting of non-larval individuals (Highsmith 1985, Jackson 1986, Johannesson 1988, Ó Foighil 1989, Ó Foighil et al. 1999, Helmuth et al. 1994). In the context of the present review, it will be examined under which conditions rafting can be an effective dispersal mechanism resulting in successful LDD and colonisation of new habitats or to the maintenance of population connectivity over time.

Many biotic and abiotic factors determine the potential for dispersal of a species, and the effects of these factors are variable among taxonomic groups and localities (Scheltema 1988, Shanks et al. 2003, Kinlan et al. 2005). Effective marine dispersal distances are distributed over a wide continuum of spatial scales (Underwood & Chapman 1996, Bradbury & Snelgrove 2001, Mora & Sale 2002, Kinlan & Gaines 2003, Shanks et al. 2003, Kinlan et al. 2005), and even within a species it may vary at different locations in space and time (Cowen et al. 2003, Sotka et al. 2004). At one extreme of this continuum, populations are considered closed because local recruitment is the result of local propagule production (e.g., Taylor & Hellberg 2003). At the other extreme, open populations are broadly connected at larger spatial scales and the arrival of propagules to the population contributes substantially to local recruitment (Caley et al. 1996). Thus, depending on the spatial scale considered, species differ in the extent to which local recruitment depends on local propagule production (Kinlan et al. 2005). Even though most marine systems are thought to be more open than terrestrial systems (Roughgarden et al. 1988, Underwood & Fairweather 1989, Gaines & Bertness 1992, Caley et al. 1996, Carr et al. 2003), there is accumulated evidence from plankton distribution (Grantham 1997), local larval retention (Swearer et al. 1999) and genetic connectivity (Palumbi 2003), among others, that many marine species have restricted dispersal, suggesting that their populations might not be demographically open or that dispersal distances of many marine organisms may be shorter than expected (Jones et al. 1999; Swearer et al. 1999, 2002; Palumbi 2004; Sotka et al. 2004, Baums et al. 2005). On the other hand, there is a growing number of reports of species with a much wider geographic distribution than can be explained by their autonomous dispersal capabilities (Johannesson 1989, Castilla & Guiñez 2000).

These considerations underline the importance of taking a close look at all aspects of the dispersal behaviour of the species under consideration. For marine organisms, life history traits, habitat and oceanographic conditions are the most important factors affecting their dispersal potential (Mileikovsky 1971, Jablonski 1986, Scheltema 1986, Strathmann 1987, Sponaugle et al. 2002, Grantham et al. 2003, Muñiz-Salazar et al. 2005). Marine communities contain taxa with varying reproductive patterns (Thorson 1950, Levin 1984, Strathmann 1987, Pechenik 1999, Grantham et al. 2003) that are thought to influence their dispersal potential (Mileikovsky 1971, Jablonski 1986). While for many species larval dispersal together with biotic and abiotic factors determines their geographic range (Thorson 1950, Mileikovsky 1971, Strathmann 1974, Jablonski & Lutz 1983, Scheltema 1986, Díaz 1995, Underwood & Chapman 1996, Watts et al. 1998), several observations have supported a more open view of marine dispersal that examines dispersal potential beyond the presence of a larval stage (Levin & Bridges 1995, Palumbi 1995, Ayre & Hughes 2000, Grantham et al. 2003). Larval dispersal is often considered as active dispersal since some larvae are known to have specific active behaviours that enhance the probabilities of either being transported by currents or of being retained in certain regions (Havenhand 1995, Shanks 1995).

Larvae, juveniles and adults may accomplish dispersal by active behaviours such as swimming and crawling. For many benthic marine invertebrates, though, these latter mechanisms only account for movement within the local range (local movement) and not for diffusion or LDD. The dispersal mode of marine species may also be passive (such as rafting) and may happen at one or more of the above life stages. Rafting differs from larval dispersal in not (in most cases) being restricted to a particular life stage, and not being limited by the duration of a stage (as it does not depend on it) but rather on external factors such as raft availability, the capability of organisms to persist on the raft during the journey and colonisation success (Thiel & Gutow 2005b). Even though there is a general lack of direct evidence for rafting dispersal occurring in benthic marine invertebrates (but see Worcester 1994), there has been increasing awareness that rafting might be an important dispersal mechanism that plays a significant role in determining the geographic range of distribution of many species (Sterrer 1973; Johannesson 1988; Ó Foighil 1989; Ó Foighil et al. 1999; Castilla & Guiñez 2000; Sponer & Roy 2002; Waters & Roy 2003, 2004a; de Queiroz 2005; Kinlan et al. 2005). This is also supported by the fact that many species with direct development have wider geographic distributions than congeners with a planktonic larval stage (e.g., Johannesson 1988, Ó Foighil 1989).

Rafting dispersal

Many organisms (even those with pelagic larvae) can potentially accomplish connectivity among localities through rafting. Species that usually inhabit benthic coastal habitats are often found on

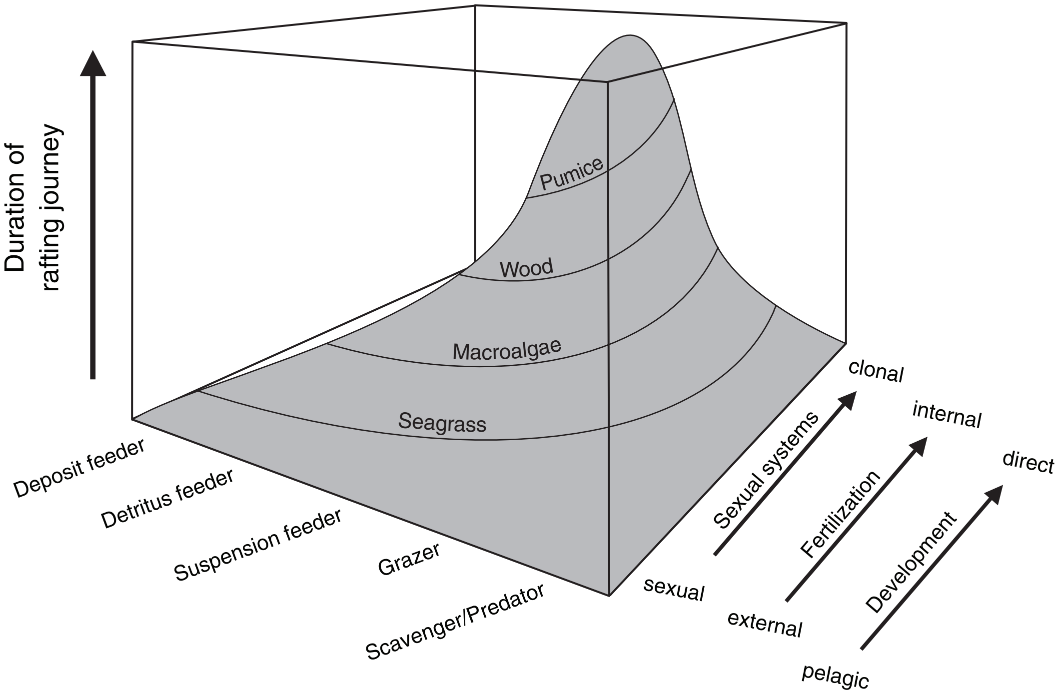

Figure 3 Schematic relationship between feeding and reproductive biology of rafters and duration of rafting journeys. The number of rafting species decreases with length of the journey and only selected groups achieve very long journeys. Main substrata and their relative importance are also indicated.

rafts. Based on an extensive review, it has been argued that rafting is very common in certain regions and that some organisms are well adapted for rafting (Thiel & Gutow 2005b). The rafting voyage is a selective process that favours travellers with certain adaptations. Organisms need to maintain themselves on the raft, feed (depending on the length of the voyage), grow and reproduce. The most important selective pressure that rafters experience during the voyage depends on the floating substrata (Figure 3). These not only differ in their availability but also in their quality as a raft for associated organisms (Thiel & Gutow 2005a). Substrata of biotic origin (floating animal and plant material) have a high food value for organisms but their longevity generally is limited (e.g., Hobday 2000a), while substrata of abiotic origin (volcanic pumice and plastics) have no food value but float for long time periods, often >1 yr (Jokiel 1989, Bryan et al. 2004, Barnes & Milner 2005). Since raft longevity in combination with current velocities and/or prevailing winds determine dispersal distances, organisms that live on biotic substrata have a lower dispersal potential than organisms that can settle and survive on abiotic substrata.

In general, suspension feeders abound among the rafting fauna because they do not depend on the raft for nourishment. On biotic substrata a high diversity of grazers and predators/scavengers is also frequently found. Differences in species composition between rafts may also be due to competitive interactions that are commonly reported from rafting communities (Thiel & Gutow 2005b). Interspecific competition may lead to the eradication of inferior species (Gutow & Franke 2003). Dominant competitors capable of proliferating during rafting journeys will slowly but steadily monopolise resources on a raft (Stevens et al. 1996, Tsikhon-Lukanina et al. 2001). Rafting communities that are underway for long time periods may therefore be impoverished in species. If organisms reproduce during the voyage, individuals that reach new habitats may be offspring of original travellers. Intraspecific competition, strong selective processes and genetic drift may thus lead to proliferation of particular lineages within a species during long-lasting rafting journeys.

Successful dispersal not only depends on the transport direction and velocity of floating items, but also on their total abundance in a particular region. In contrast to organisms that are dispersing in the water column (larvae), rafting organisms are being dispersed in a two-dimensional space (sea surface). Additionally, floating items are not homogeneously or randomly distributed on the sea surface, but rather clumped due to accumulation in convergence zones. Occasionally strong wind and waves may disperse floating items, but during calm weather they will be accumulated in convergence zones again. This facilitates interactions (positive: reproduction and protection; negative: competition and predation) among rafters from different floating items. If many floating items are underway in the same current system, mobile organisms may switch between rafts to avoid drowning on deteriorating rafts, escape from dominant competitors or predators, or associate with conspecifics for the purpose of reproduction.

A comparatively large proportion of successful rafters are hermaphrodites or proliferate asexually (Thiel & Gutow 2005b). There are also many gonochoric and sexually reproducing species with a very short planktonic larval stage or which lack a planktonic larva. The latter species produce fully developed offspring that may recruit directly on the maternal raft, thereby allowing the persistence of a species during prolonged journeys (Figure 3). Initially, any organism that can hold onto a floating substratum may be dispersed over short distances, but LDD is only achieved by species capable of feeding and reproducing during the journey. In consequence, suspension feeders and organisms with local recruitment are favoured for LDD via rafting. In summary, the quality of floating substrata exerts a strong selection on the pool of potential rafting organisms, and selective pressures increase during prolonged journeys (Figure 3). These processes (selection, local recruitment, inbreeding and genetic drift) may also have important consequences for the genetic structure of rafting demes.

Colonisation and establishment of local populations

When dense assemblages of floating items are transported together in nearshore convergence zones, there is a high probability that many rafting conspecifics will get ashore simultaneously. Clearly, arrival of many floating items with an armada of conspecific rafters increases the probability of successful reproduction in new habitats. Additionally, the number of conspecifics that arrive simultaneously has important effects on the potential persistence of a new population, because if too few individuals colonise, founder effects can be drastic and the genetic variability may be imperilled. This, of course, is less important if rafting is frequent, and multiple colonisers arrive during repeated arrival events.

Since dispersal stages of many marine organisms have only limited autonomous swimming capabilities, they must be delivered directly to benthic habitats in order to settle successfully. Larvae of many marine invertebrates have evolved diverse behaviours that ensure delivery to suitable habitats (see, e.g., contributions in McEdward 1995). For example, many species exhibit vertical migrations in the water column in order to enter favourable currents to reach open water for larval development or to return to benthic habitats for settlement (Young 1995). Floating substrata remain at the water surface where they are at the mercy of wind and surface currents. Thus, in contrast to many species with pelagic larvae, rafting organisms have little or no chance of influencing the direction of transport during the journey. However, being limited to a two-dimensional space also presents advantages because it facilitates cohesion of propagule clouds (see above).

Once arriving near potential new habitats, rafting organisms face the problem of moving from the raft to benthic habitats. While final stages of many planktonic larvae are adapted to actively select settlement substratum, most rafting organisms have little opportunity for selection. In many cases, arrival appears to be a chance process. When reaching coastal habitats, sessile organisms may either grow over onto benthic substrata (Worcester 1994), be scraped off by hard-bottom substrata (Jokiel 1989), or they may release spores or larvae (Keough & Chernoff 1987). Semisessile and mobile organisms such as gastropods, crustaceans and echinoderms, can also actively abandon rafts and reattach or crawl over to benthic substrata (Thiel & Gutow 2005b). It is during arrival that floating substrata exert a final selective influence on rafting organisms. Complex floating items (seagrass shoots, macroalgae, trees) may entangle in benthic habitats such as rocky shores, seagrass beds, kelp or mangrove forests. It can be hypothesised that mobile organisms that raft on these substrata, have higher probabilities of going ashore successfully than other organisms.

Following arrival in a new habitat, successful colonisation can occur only if species reproduce effectively. Here the reproductive biology of an organism gains extraordinary importance. In particular when few individuals arrive in new habitats, similar reproductive traits as those selected for during long rafting journeys are advantageous (i.e., capability of establishing local populations). Species with asexual reproduction or self-fertilising hermaphrodites are favoured since they do not depend on the presence of conspecifics — at least in some taxa the consequences of reduced genetic diversity do not appear to impede establishment (e.g., Jackson 1986). In species that require cross-fertilisation, the presence and abundance of mating partners is crucial. At low densities of potential mates, the species with internal fertilisation may be favoured over external fertilisers, which usually form aggregations or spawn synchronously in order to achieve high concentrations of gametes. When few conspecifics are present, gamete concentrations may be too low for successful fertilisation in broadcast spawners. In species with internal fertilisation, efficient searching or courtship behaviours may facilitate association of mating partners in benthic habitats, thereby ensuring successful fertilisation. Once fertilisation has happened, the developmental mode of species furthermore becomes critical. Williams & Reid (2004) discussed this for littorinid snails: “establishment of a self-sustaining population at such a distance [1400 km] must be very much rarer, because the founding population should be of sufficient density to ensure that mates can be found and to overcome the dilution of the resulting progeny during their own pelagic phase”. It is here that direct developers are at an advantage, because in many cases their offspring are retained in close vicinity, facilitating coherence of the founder population and future reproduction. In particular, when propagules are transported over long distances and few individuals arrive in new habitats, rafting organisms have a higher probability of successfully colonising than species with planktonic larvae because in the former reproductive traits have been selected that favour colonisation (Figure 4).

The positive relationship between raft size and number of travellers (Thiel & Gutow 2005b) may not only have effects on the persistence of a species on the raft (reproduction during the journey) but also on the colonisation success after arrival (reproduction in new habitats). Single travellers (on small rafts) may have a lower likelihood of finding mates, impeding successful establishment in new habitats, and even if they reproduce and form small populations, their sustainability may be limited due to the fitness consequences resulting from strong founder effects. If competent and sufficient individuals arrive, rafting may lead to founding of a new population (Johannesson 1988, Castilla & Guiñez 2000, Colson & Hughes 2004) or be a means that contributes to connectivity among populations (Grosberg & Cunningham 2001, Hellberg et al. 2002, Palumbi 2003), but its importance in population maintenance remains unexplored (Martel & Chia 1991, Grantham et al. 2003). Dispersal sets a tradeoff between the probability of extinction and local adaptation (Jablonski & Lutz 1983) that is likely to impact the evolution of dispersal patterns (Grantham et al. 2003).

The reproductive traits that are selected during prolonged rafting journeys and at establishment in new coastal habitats (asexual reproduction, internal fertilisation and direct development) will have important consequences for local population structure. While these traits favour cohesion and sustainability of founding groups, they also result in a high degree of inbreeding and genetic relatedness.

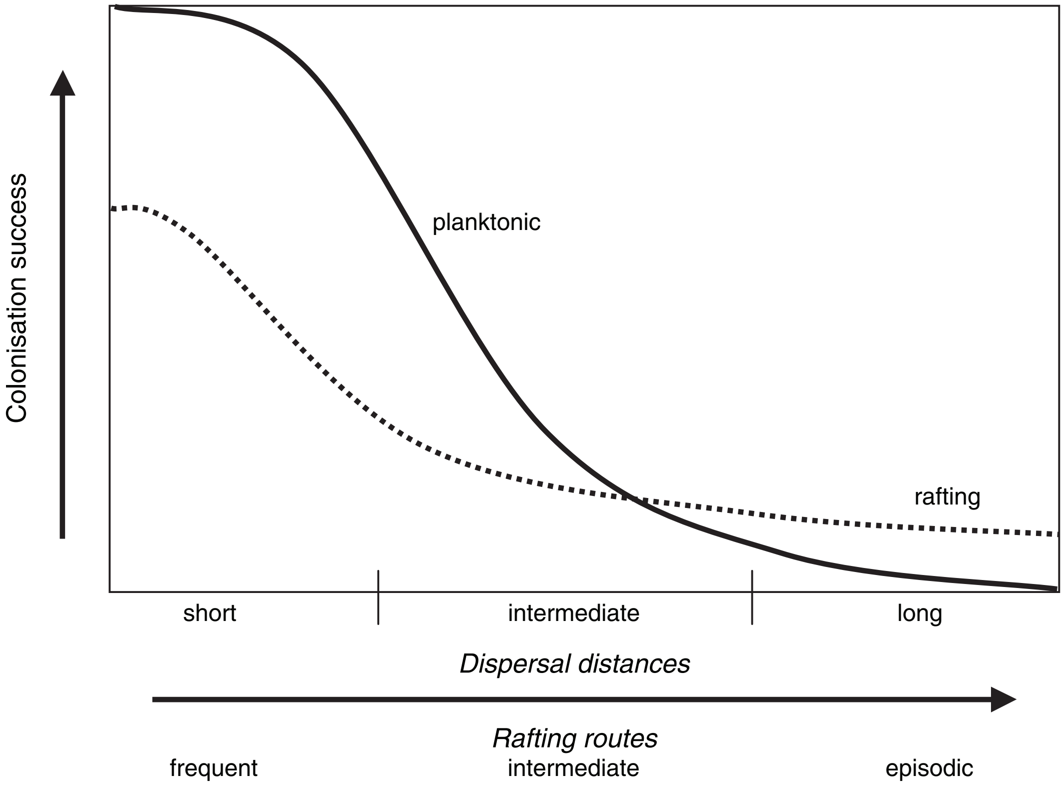

Figure 4 Schematic relationship between rafting routes (distances) and the colonisation success of rafting organisms, compared with that of planktonic organisms. At very long dispersal distances, rafting organisms have a higher likelihood of successful colonisation (due to their reproductive biology) than planktonic organisms.

Rafters achieving LDD may be pre-adapted to establish local populations, but these will be at a high risk of extinction. Rafting can thus be considered a selective process that has strong implications for the biogeography and evolution of marine species, in particular for the many marine benthic invertebrate species that lack a planktonic dispersal stage and thus depend on rafting for dispersal.

Since rafting organisms have no influence on the direction and velocity of transport they may frequently be carried to marginal or even inhospitable environments. A patch of floating algae (originally growing in hard-bottom habitats) thrown onto a sandy beach is a vivid example for the latter (inset in Figure 5). It can be expected that the probabilities of reaching suitable habitats depend on transport distances (Figure 5). Rafts travelling over short distances may have a high likelihood of intercepting habitat patches similar to those where travellers went onboard. For example, most seagrass shoots or mangroves detached from their native habitat in a bay or estuary may be retained in adjacent seagrass or mangrove patches. In contrast, rafts carried out of a bay and travelling over farther distances will have a low probability of reconnecting with habitats sharing the characteristics of their sites of origin.

The distributional range of marine organisms depends on a variety of factors, the most important being the availability of suitable habitat (including abiotic factors such as temperature, salinity, light and oxygen), food supply and biotic interactions. Outside the physiological limits of a species, metabolic costs of individuals are too high for these species to persist or to reproduce successfully (Pörtner 2002). Establishment or maintenance of viable populations within the ecological range of a species is only possible if production and survival of propagules is assured. When organisms are

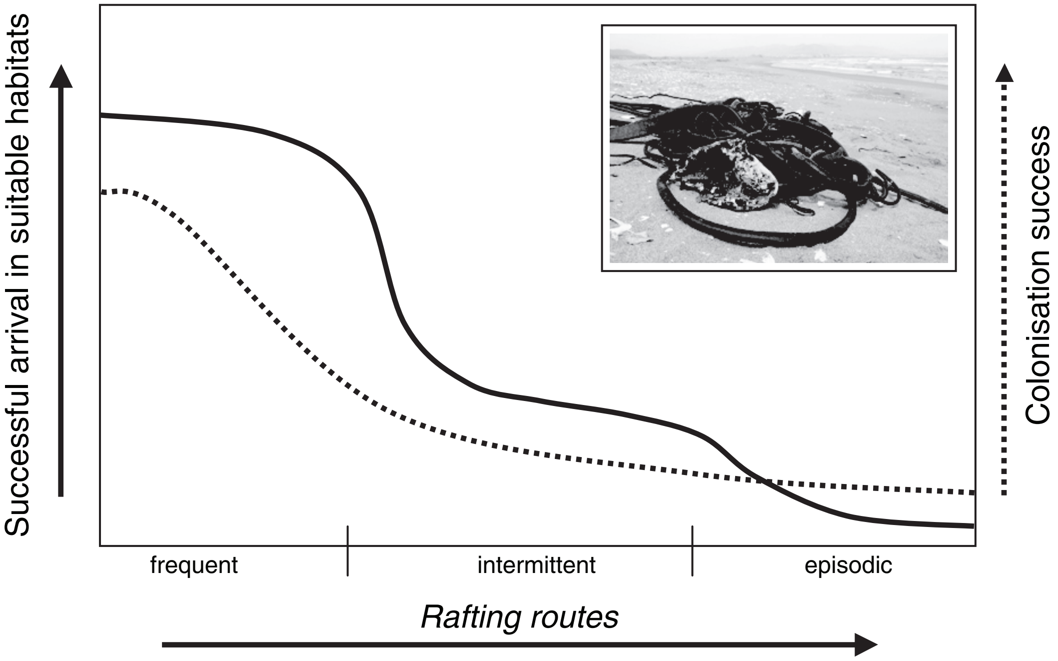

Figure 5 Schematic relationship between rafting routes and the probability of successful arrival in suitable habitats. Between categories of rafting routes the probabilities decrease in a stepwise manner. For example, organisms travelling on frequent rafting routes within bays or estuaries may have a high probability of reconnecting with suitable habitats within bays, but once flushed out to the outer coast, the probability of returning to a bay with suitable habitats diminishes substantially. Insert shows an individual of the floating kelp *Durvillaea antarctica*, commonly growing on exposed hard bottoms, washed up on a sandy beach (reaching unsuitable habitat for most species that live and raft on this macroalga).

carried into regions that are close or even outside their ecological range their reproductive potential may be strongly reduced (due to physiological constraints and low densities), and local populations may not be self-sustainable, endangering their persistence. Individuals may temporarily survive and even reproduce successfully, but local populations might rapidly disappear, for example during seasonal changes. Local populations may be exposed to recurrent colonisation and extinction events (Marko 2005). This appears to be the case in the obligate rafter *Idotea metallica*, which regularly is transported into the North Sea, but apparently is eradicated in this region during harsh winter conditions (Gutow & Franke 2001). Castilla & Guiñez (2000) discussed the case of a local population of the gastropod species *Concholepas concholepas* (native to the Pacific coast of South America) in South Africa, which established and became extinct during the Pliocene/Holocene. They suggested that this population might have arrived via rafting, but reasons for extinction are not known. Since the environmental conditions in the Benguela Current are similar to those in the Humboldt Current region, extinction may not have been due to physiological reasons but was possibly caused by limited reproductive potential of a small local population or by the negative consequences of a strong founder effect.

Metapopulation structure and processes

Floating substrata can transport rafting organisms to new habitats and may allow their immigration to other populations of conspecifics. The frequency of rafting events along a route affects the possibility of successful colonisation or the degree of connectivity between local populations. Colonisation and connectivity achieved via these rafting routes maintains uni- or bidirectional migration among local populations. This kind of population structure (i.e., with many local populations that interact through gene flow) is referred to as a metapopulation. Grimm et al. (2003) identified the characteristics of a metapopulation as: (a) a system of local populations having their own dynamics, (b) some local populations are so small that they face risk of extinction, (c) local populations interact via propagules and (d) dispersers are able to establish new local populations in empty patches. Local populations occupy an area that reflects the mobility and habitat requirements of the organisms (Camus & Lima 2002). Many marine benthic invertebrates, in particular those dispersed by rafting, seem to fit a metapopulation model, particularly because of the fragmented nature of marine benthic environments. Strong gene flow among populations prevents differentiation of local populations by mixing gene pools and preventing local effects of genetic drift. Conversely, restricted gene flow among local populations reduces the effective population size, leading to decreased genetic variability within local populations. The effects of genetic drift and localised selection are stronger for populations with restricted gene flow. The gene flow patterns of marine metapopulations are not straightforward. Most populations are not characterised by constant and bidirectional gene flow among all local populations, suggesting that more complex patterns of dispersal are imposed by the intrinsic characteristics of marine environments and species.

The direction of exchange between local populations will have important consequences for the dynamics of the metapopulation of a species. Cook & Crisp (2005) emphasised, albeit not in the context of rafting, that increasing strength in directionality of dispersal increases the frequency of multiple dispersal events in one direction relative to the other. In the case of rafting, the main source population of a rafting species may be a single interbreeding population that changes over time and produces enough propagules for their own persistence as well as for export to other sink areas. Over time there may be multiple colonisations in a sink area due to settlement and establishment of propagules that reach the area by directional rafting on an intermittent or frequent rafting route. Metapopulation structure changes with the number of local populations and the degree and direction of gene flow among them.

Different degrees of connectivity lead to variable genetic differentiation between the populations of a species that are connected by a rafting route, and thus differing metapopulation structures (see how metapopulation dynamics span across all rafting frequencies in Figure 2). It has been argued that a single migrant per generation is sufficient to prevent genetic differentiation of populations (Wright 1951). When levels of gene flow are lower, populations may share many alleles due to common ancestry, but their frequencies will change due to genetic drift and local selective pressures, leading populations to genetically differentiate over time. Gene flow is a force that acts against the development of new lineages as it prevents differentiation and speciation. Consequently, if populations are isolated, for example after being established from a single rafting colonisation event, they will accumulate genetic differences over time. In contrast, populations that are connected by frequent rafting events (and thus maintaining high gene flow with source population) will tend toward homogenisation over time.

Just as the theory of island biogeography of MacArthur & Wilson (1967) predicts that species diversity is a balance between arrival of species through migration and the loss through extinction, the genetic diversity of a population is a balance between the arrival of new alleles (gene flow) and the loss of alleles due to genetic drift (island model of genetic diversity of Wright 1940; see also Vellend 2003). Genetic drift is mostly the product of the random sampling of gametes that occurs in every generation and causes a change in the allelic frequencies of the population from one generation to the next. Genetic drift usually has no detectable effect on populations that are large enough such that the sampling of gametes does not change the frequency of alleles in the population. However, if populations are small, like the ones found on a raft or those originating from rafting-mediated colonisation events, genetic drift may cause perceptible changes in allele frequencies or cause some alleles to completely disappear and the population will lose genetic variation.

Two highly documented genetic drift events are bottlenecks and founder effects. These two events have identical genetic architecture as they result from evolution in small populations, but their originating mechanisms differ. Bottlenecks are drastic reductions in population size (and genetic variability), triggered by a change in the biotic or abiotic conditions, while founder effects refer to the result of the founding of a new population by only a few individuals. Because the founding population is small (for example, the colonisers that arrive on a raft), it contains only part of the genetic diversity present in the source population. The population starts with the little genetic diversity present in the founder population, and over time may gain new genetic diversity. If the new diversity arises solely by mutation, then the differences between source and founded populations will be detectable with genetic markers. But if the new diversity were to arise by continual migration from the source population, then it would not be detectable, especially if gene flow is high. An episodic rafting route (less frequent and with long-distance trajectories) may result in a founder effect if few individuals of a species colonise the arrival area. Frequent and intermittent routes have relatively high connectivity between localities, decreasing the probability of a single founder effect and leading to multiple ones that, depending on the amount of source populations, will have varying effects on the genetic structure of the populations. Chambers et al. (1998) explained that low levels of gene flow in combination with direct development cause small-scale founder effects in subpopulations that increase the overall genetic diversity of the whole metapopulation. This latter scenario of genetic structure may prove common in brooders that disperse via rafting.

Connectivity is a measure of the strength of the connections between local populations. It depends mainly on the dispersal of individuals (carriers of genes) and in particular on the number and origin of immigrants to local populations, and has important consequences for the genetic structure of metapopulations. Gene flow estimates are quantifications of the connections in terms of amounts of individuals that migrate (and effectively reproduce) in each generation. Gene flow is often reported as Nm, a measure that is based on both effective population size (N) and migration rate (m). Depending on the levels of relatedness among populations, inferences can be made about the realised dispersal of propagules over time. Genetic data allow for inferences of real rather than potential dispersal distances (Hunt 1993). Realised dispersal is determined by many parameters, including mode of development, oceanographic conditions, history of populations and others that may influence the pattern of migration among populations. For many species, rafting must be assumed to increase their dispersal potential (even enabling them to achieve LDD) and the connectivity between local populations.

Dispersal patterns

Gene flow patterns among local populations may resemble more or less the proposed models of dispersal. The basic dispersal model that is the underlying model assumed in many commonly used analytical tools is the island model of Wright (1931), in which several local populations are connected by random migration from a common pool, and mating is more frequent within than between populations. In this case, the metapopulation will eventually reach genetic drift/migration equilibrium. This model is appropriate for two-population cases or for equally spaced oceanic islands, but may not accurately describe the structure of marine species distributed along a coastline (Hellberg et al. 2002). Slatkin (1977) proposed the propagule- and migrant-pool models. The propagule-pool model is like the island model as there is only one population that serves as the source of migrants. In the migrant-pool model, instead, migration is random and gene flow occurs among all local populations. An alternative metapopulation model is the stepping-stone model (Kimura & Weiss 1964, Maruyama & Kimura 1980) that has been increasingly applied to examine the structure of marine metapopulations (Slatkin 1993, Hellberg et al. 2002). Under this model, population differentiation increases with increasing geographic distance between local populations. The resulting pattern is known as isolation by distance (IBD) (Wright 1943, Slatkin 1993). In the stepping-stone model, gene flow occurs among local neighbours in a continuously distributed population (i.e., no extreme LDD). For a population to be continuously distributed the habitat has to be continuous and a series of conditions need to be met (e.g., oceanographic conditions do not isolate populations, selection does not interfere with the pattern, populations are not at genetic equilibrium). Many studies have concluded that marine populations conform with IBD patterns, while other studies have found that other more general metapopulation models are more accurate.

Even though many marine populations show a pattern of IBD, high dispersal potential (e.g., through larvae or rafting) sometimes leads to genetic homogenisation of populations or to a population differentiation not following a distance pattern. Rafting may have a strong effect on the local dynamics by providing a means of propagule input to a local population. Additionally, it may have a strong impact on the migration patterns among local populations, especially for organisms that lack other means of dispersal.

The frequency of dispersal opportunities over variable spatial scales leads to different dispersal scenarios. At a micro- to mesogeographic scale (i.e., within a patch of habitat, for example, a bay) frequent rafting opportunities are more common and could lead to genetic homogenisation if exchange is abundant and follows a migrant-pool model. Less frequent or restricted gene flow among local subpopulations within the patch of habitat will lead to genetic differentiation at a microspatial scale, leading to high population fragmentation and extinction risk. At a broader geographic scale, local populations may be more or less connected by a rafting route (e.g., with populations outside of a bay). If propagules come from one or few source populations, small founder effects will accelerate genetic drift and reduce the genetic variation within and among populations (Harrison & Hastings 1996, but see Wares et al. 2005). Instead, if propagules come from many sources, small founder effects may increase local genetic diversity. Thus, the genetic structure will depend on both the local gene flow dynamics and on the connectivity with populations outside of the patch.

The genetic differentiation of populations from different habitat patches may follow contrasting patterns depending on the kind of rafting route and its characteristics. For example, a rafting route with regular supply of floating substrata (= dispersal opportunities) following a unidirectional current could lead to a pattern of IBD along the coast. However, this is only likely if the rafting route links a series of local populations that receive propagules only from up-current populations. The stretch over which populations may display IBD will depend on the local hydrography. If the current direction is not strongly defined (i.e., is bi- or multidirectional) or when it is not temporally stable, so that it sometimes reverses, there will be no IBD pattern and instead the population may present a migrant-pool model of colonisation. There may be areas where currents converge and redirect offshore posing a gene-flow barrier to many rafters. At either side of the barrier the populations may be structured following an IBD pattern, while being strongly differentiated from the populations from the other side of the barrier. The absence of an IBD pattern of differentiation could be associated with medium-distance or LDD dispersal events, either through larvae or in the case of direct developers, through rafting (e.g., Colson & Hughes 2004). However, both organisms with direct and planktonic larval development can be dispersed over long distances by rafting (see below).

Some studies have shown that dispersal is directional among populations of marine species (Wares et al. 2001, Waters & Roy 2004a). Oceanographic and climatic conditions are probably the main factors determining the directionality of a rafting route in the ocean (Gaines et al. 2003, Muñiz-Salazar et al. 2005). Cook & Crisp (2005) state that successful LDD depends on a number of variables that have a "strong directional component" such as the dispersal ability of the organisms or their propagules, favourable environmental conditions for dispersal (currents, location of raft sources) and a suitable habitat for establishment. If currents are persistent, transport will be highly directional. Dispersal of organisms (gene flow) and oceanic currents match closely in these regions, enabling the persistence of downcurrent populations through metapopulation effects. If a close match is found for species without a pelagic dispersal stage, rafting is often inferred as the most likely dispersal mechanism. An example for this are local populations of terrestrial lizards *Anolis sagrei* on the Bahama Islands, where these lizards are supposed to be dispersed over-water after hurricane events (Calsbeek & Smith 2003): "We found directionality of gene flow that is congruent in all cases with the prevailing direction of ocean currents, including the exceptional case in which currents adjacent to Florida drive gene flow south from Bimini to Andros Islands". Similar directional source-sink connections are hypothesised for many other organisms and regions. For the North Atlantic, Wares & Cunningham (2001) inferred that recent (re)colonisation of areas in the northwest Atlantic has occurred from source populations in the northeast Atlantic. They based this suggestion on the higher genetic diversity in European compared with North American populations, making it most likely that the direction of colonisation was from east to west. In the southern oceans, many authors have suggested that transport of propagules follows the direction of the West Wind Drift (e.g., Ó Foighil et al. 1999, Donald et al. 2005). Waters & Roy 2004a observed paraphyletic lineages of a brooding seastar (*Patiriella exigua*) in South Africa while they found monophyletic lineages in the Australian region (i.e., in down-current direction in the West Wind Drift). Based on these results, they inferred that the populations in the Australian region had developed from a singular dispersal event, most likely via rafting.

It is not always easy to identify the direction of connectivity between local populations, mostly because methodologies like *F*-statistics do not account for directionality (for alternative approach see Wares et al. 2001). Knowledge of the prevailing current regime in a region may also help to interpret phylogenetic trees by aiding in the identification of the gene flow direction (see e.g., Carranza et al. 2000).

Rafting dispersal pathways

Rafting, as most other dispersal mechanisms, occurs over a wide variety of temporal and spatial scales. Terrestrial biogeographers commonly distinguish three types of dispersal pathways that connect two (or more) localities: corridor, filter and sweepstake routes. A corridor is a route that is defined as part of the same landmass with a similar habitat to the two localities being connected, and that allows most organisms to cross it. A filter or filter bridge is an interconnecting region that has more restrictive habitat characteristics than a corridor, and only some organisms are capable of crossing it. Finally, a sweepstakes route has completely different habitat characteristics than the areas it is connecting such that dispersal events are rare across the barrier, most of them being considered to be accidental. The biota found on a sweepstakes route is considered disharmonic, as it is not a representative sample of the ecologically integrated and balanced biota that is being connected by the route (Cox & Moore, 1993). Because the three types of route imply different probabilities of successful dispersal, they result in different degrees of similarity (community and lineage composition) between the biota connected by the route. In the terrestrial environment, corridors are common dispersal routes, while sweepstakes routes, as their name indicates, are rare events or events that rarely result in successful dispersal.

In the sea, the distinction between corridors, filter and sweepstakes routes is also applicable but harder to envision than for terrestrial environments. Herein, three main types of rafting routes (frequent, intermittent and episodic — see also Figure 2) are distinguished, analogous to the dispersal routes described for terrestrial environments. Rafting routes can be classified according to the frequency of rafting events, which depend on environmental conditions favouring availability of floating items, their persistence and the length of the journey. Just as there is a continuum in populations from being demographically open to closed, there is also a continuum in rafting dispersal potential. High frequency rafting routes connecting two or more areas, typically of distances <100 km, will be referred to herein as frequent rafting routes. On these frequent rafting routes, floating substrata are available in large quantities and any organism capable of holding onto the substratum can migrate via rafting. Rafting distances and duration usually are short, and thus there is no need for organisms to feed during transport, similar to the situation in terrestrial corridor routes. Voyages on intermittent rafting routes extend over greater distances (100–5000 km) and last longer, requiring that travellers feed or at least use body reserves during transport. This means that the pool of species capable of travelling on these intermittent routes is more eclectic. Organisms unable to fulfil their metabolic requirements or to survive conditions on a raft will not usually be transported on intermittent rafting routes. Dispersal on frequent and intermittent rafting routes commonly occurs on substrata derived from the natural habitats of rafting organisms, thus resembling a dispersal corridor in terrestrial environments. However, the duration of the voyage and the need to satisfy metabolic requirements on intermittent rafting routes produces a filter effect, only permitting successful dispersal of certain organisms. If rafting is extremely rare, so that it does not represent a permanent or semipermanent connection between populations or regions, it will be considered an episodic rafting route. Episodic routes result from random and independent events that for a short ecological timescale provide abundant floating substrata, establishing a route of rafting dispersal that allows colonisation of faraway sites. These routes are expected to occur at distances >5000 km and because rafting episodes are so rare it could be predicted that in many cases it results in allopatric speciation.

Examples will be presented from the literature in order to elucidate the processes acting on frequent, intermittent and episodic rafting routes and how these affect ecological, biogeographic and evolutionary consequences. These rafting routes have strong implications for the exchange of rafters and the consequences vary from trophic dynamics (frequent routes), to metapopulations with more or less connectivity among local populations (frequent and intermittent routes) and allopatric speciation (episodic routes) (Figure 2).

The rafting routes

Floating substrata are most abundant in those regions where they are supplied and their routes of dispersion are driven by oceanic currents and wind. There exist important regional differences in abundance and supply of floating substrata, and consequently, rafting opportunities and dynamics are also variable. The three rafting routes identified above can also be distinguished according to the temporal and spatial scales over which rafting opportunities arise (Thiel & Gutow 2005a). Frequent routes are found where substrata are supplied in great quantities and continuously (or at least every year) with a high degree of predictability. They occur in bays, lagoons and estuaries along coastlines of many regions of the world. On intermittent rafting routes, substrata are available on a regular basis, but supply and dispersal scale can vary on an annual basis. Episodic rafting routes only receive a very sporadic input of floating substrata (e.g., following volcanic eruptions, hurricanes or tsunamis). Instantaneous local supply, regardless of the frequency of occurrence (frequent, intermittent or episodic), can be very high on all three rafting routes.

The substratum characteristics also vary in accordance with their frequency of supply. Interestingly, there is a tendency that many of the frequently supplied substrata have a limited longevity. For example, seagrass shoots (occurring on frequent rafting routes) usually float for a few days, and the maximum longevity recorded at the sea surface is 2 weeks (Harwell & Orth 2002). At the other extreme, volcanic pumice is only available very sporadically, but may float for several years (Frick & Kent 1984, Jokiel & Cox 2003, Bryan et al. 2004). These characteristics, in particular supply and longevity, affect the consequences of rafting, in particular the number of rafters and the potential dispersal distances.

Herein, for each rafting route specific predictions will be made with respect to their ecological and evolutionary consequences, and it will then be examined whether or not there is support for these predictions. There are, however, also unpredictable events (storms or intense floods) that change the relatively stable direction and frequency of a dispersal route. These events may interrupt frequent rafting routes (disconnecting areas) or push floating substrata to areas off the trodden paths (episodic rafting route). It should thus always be kept in mind that there is overlap between the three rafting routes.

Many of the dispersal mechanisms and particular floating substrata that will be discussed below are most relevant at one scale of dispersal (i.e., rafting route, but they may also operate across rafting routes). In general, most of the various natural floating substrata appear to fit one of these three scales relatively well (see also below). However, anthropogenic substrata (plastics and tar lumps) are present and potentially important on all three rafting routes. Plastics have caused substantial concern as potential rafting substrata for three main reasons: i) they are ubiquitous and continuously introduced to the oceans, ii) the amounts of plastics have been increasing dramatically during the last century and iii) they have a high longevity, possibly facilitating LDD (Winston et al. 1997, Barnes 2002, Barnes & Milner 2005). These anthropogenic substrata led to new, artificial, rafting routes that are a relatively new phenomenon. Due to their different characteristics and potential impact, these artificial rafting routes will be briefly dealt with in a separate subsection, outlining the temporal and spatial scales covered by these routes.

Frequent natural rafting routes

Continuous supply of floating substrata on frequent rafting routes

In some areas of the world oceans, large quantities of floating materials are continuously supplied, offering abundant possibilities for organisms to be dispersed via rafting. This situation is the case in temperate coastal ecosystems, where every spring and summer large quantities of plants and algae are produced in estuaries, coastal lagoons and shallow waters along the continental shelf. These floating substrata are dispersed by tidal currents and, when carried into offshore waters, by coastal currents. Most of these substrata (seagrasses, marshgrasses, macroalgae, mangrove wood) are already colonised by a diverse biota at the moment of going afloat. Within estuaries, bays or lagoons, these substrata and associated rafters are transported throughout the system leading to efficient exchange between neighbouring habitats. Similarly efficient exchange might also be expected around island shores. If rafting frequencies are very high, some organisms may even utilise this process to exploit resource patches within these ecosystems. Furthermore, at very high frequency of production and transport of floating items, biomass of floating substrata (and associated organisms) can be exported to neighbouring habitats within bays. These exchanges result in very efficient trophic and genetic connections between habitats and local populations. Multiple examples are known for rafting transport on floating plants and macroalgae via these common rafting routes. Here, examples for biomass transport, resource exploitation, and exchange of rafting colonisers within estuaries, lagoons and bays are presented. Since in these systems floating substrata are most abundantly available, it could be expected that frequent rafting routes occur therein. When a raft is carried out of these systems, the probability of reconnecting to suitable habitats decreases (see also Figure 5).

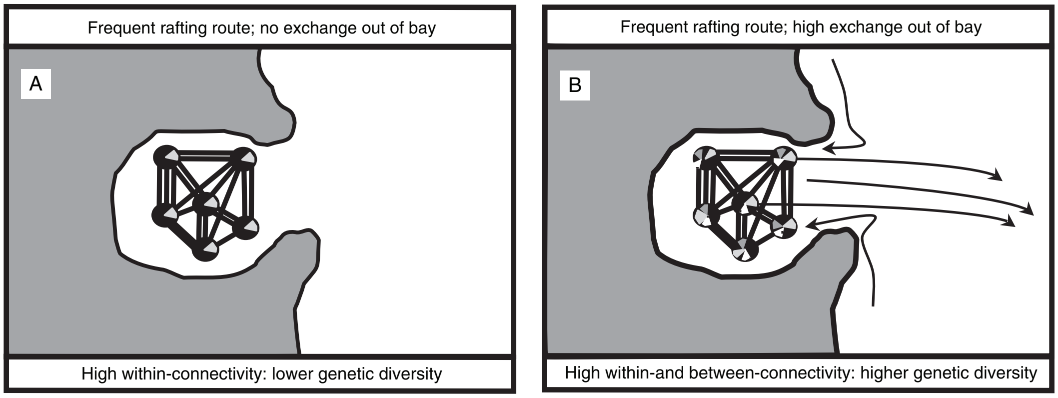

Figure 6 Scheme showing the two extreme situations on frequent rafting routes and the expected genetic consequences. (A) shows a frequent rafting route in a bay without any out-of-bay connection, while (B) shows a frequent rafting route with relatively strong out-of-bay connections. Genetic diversity is expected to be lower in (A) showing a closed metapopulation than in (B) representing an open metapopulation, due to the genetic input from external sources in (B).

On most frequent rafting routes, it is expected that connectivity is high within estuaries, bays or lagoons. This will lead to panmictic populations within these systems. Genetic diversity will depend on the size of populations within bay systems and on the degree of exchange with populations from other bays. If within-bay populations are virtually isolated and receive no immigrants, their genetic diversity is expected to be lower than in situations where bay populations occasionally obtain input from outside sources (Figure 6).

Examples of frequent rafting routes

Seagrass beds During their annual growth season, seagrasses produce large quantities of above-ground biomass (Alongi 1998), parts of which are continuously sloughed off (e.g., Flindt et al. 2004). Large proportions of the above-ground production are prone to be exported from the system (Cebrian & Duarte 2001). Depending on the buoyancy of detached blades and shoots, export occurs via the sea surface or via bedload transport (see also Alongi 1998). The transport mechanism (sea surface or bedload) will have strong effects on export distances, and it can be expected that positively buoyant species are transported substantially farther than negatively buoyant species. Consequently, positively buoyant seagrasses may reach neighbouring seagrass patches and thereby contribute to the connectivity between habitats and populations. However, surprisingly little information is available about the buoyancy properties of seagrasses. There are anecdotal reports that some species are negatively buoyant (*Thalassia testudinum*, Flindt et al. 2004; *Posidonia oceanica*, J. Cebrian, personal communication), while others are known to be positively buoyant (*Zostera marina*, Bach et al. 1986, Harwell & Orth 2002; *Syringodium filiforme*, Flindt et al. 2004; *S. isoetifolium,* Alongi 1998; *Cymodocea nodosa*, J. Cebrian personal communication; *Heterozostera tasmanica*, personal observation). In particular blades and shoots of *Zostera marina* are highly buoyant and may persist for >2 weeks at the sea surface when they can be dispersed considerable distances within bay systems (Harwell & Orth 2002).

Senescent blades of the seagrass *Z. marina* are frequently sloughed off during the growth season, and they are widely transported by currents within an enclosed lagoon (Flindt et al. 2004). Those authors observed that the vast majority of detached blades of *Z. marina* floated at or near the sea surface (Figure 7). They suggested that this transport represents an important component

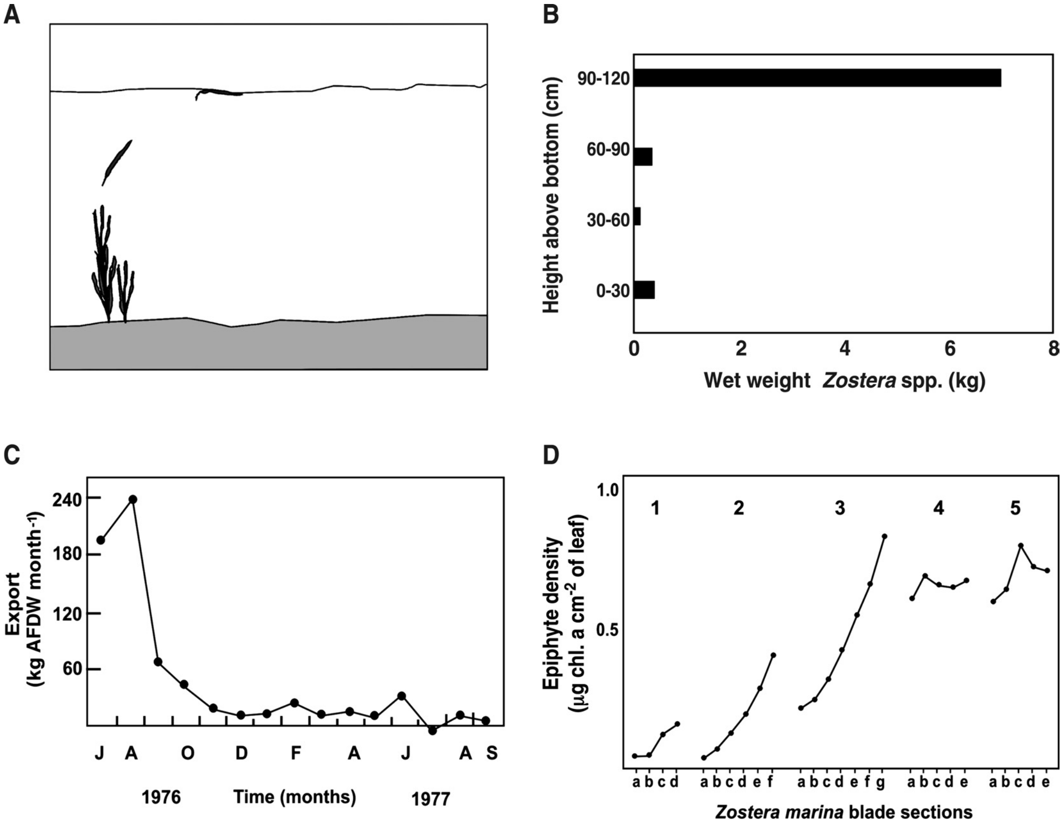

Figure 7 Dynamics on frequent rafting routes supported by seagrass as rafting substrata. (A) Detached blades or shoots float to the sea surface and are dispersed by currents. (B) Export of parts of *Zostera* sp. at different heights above the bottom; upper height represents sea surface; after Flindt et al. (2004). (C) Annual pattern of biomass export (in ash-free dry weight AFDW) from a *Z. marina* bed in North Carolina; after Bach et al. (1986). (D) Density of epiphytes on blades of *Z. marina* in a Danish estuary; Five blades (1–5) are shown with different segments starting at the base (a) and ending at the tip of the blade; after Borum (1985).

of biomass transfer within lagoonal ecosystems. Bach et al. (1986) revealed that export from a seagrass bed in an enclosed estuary reached levels of >20% of the monthly production. They estimated seasonal transport of blades along the sea surface and found that export is highest during late summer, but there may be high interannual variation in production and export (Figure 7). They also reported that floating blades still contained epiphytes, but since their study focused on trophic dynamics, they did not mention the fate of these (and other organisms). It is well known that old seagrass blades usually are overgrown by a diverse biota including algae, hydrozoans, bryozoans, ascidians, and others (e.g., Borum 1985, Borowitzka & Lethbridge 1989) (Figure 7). Since epibionts may constitute a large proportion of total biomass (Borowitzka & Lethbridge 1989), substantial export of associated organisms may occur together with export of floating seagrass blades. These can be deposited in close vicinity of the seagrass beds or at far distances offshore, depending on the buoyancy and longevity of detached seagrass blades or shoots.

High production and export of above-ground biomass along the sea surface will also lead to efficient dispersal of seagrasses and associated organisms within estuaries, lagoons or coastal bays. Evidence for high connectivity between local seagrass populations within bays or lagoons comes from genetic studies of seagrasses themselves. No significant genetic differentiation between populations of *Z. marina* was found at distances of 54 km in the European Wadden Sea and 33 km in the Baltic Sea (Reusch 2002). Similarly, Olsen et al. (2004) found little genetic variation in populations of *Z. marina* within neighbouring bay systems, and they suggested that this might be due to efficient exchange via rafting (see also Figure 8). Examining floating shoots, Reusch (2002) suggested that at least 10% of the shoots arriving at a seagrass bed were immigrants from other populations — to the present authors' knowledge this is the only study investigating the genetic relatedness between benthic and rafting populations. For *Z. noltii*, Coyer et al. (2004) revealed that "substantial gene flow among intertidal and subtidal populations occurs at the level of tens of km", and they emphasised the importance of dispersal of floating shoots along the sea surface.

Serving as floating substrata for other organisms, seagrasses may also facilitate the connectivity between local populations of common seagrass inhabitants. Indication for the relatively short distances covered by floating seagrasses (i.e., within bay systems) comes from a study by Collin (2001) who, referring to a species of *Crepidula*, discussed that "the high levels of population structure in *C. convexa* suggest that rafting on seagrass could only be a significant cause of among-population gene flow over short distances". Direct evidence of dispersal on floating seagrass comes from a study by Worcester (1994) who observed that colonial ascidians *Botrylloides* sp. rafting on blades of *Zostera marina* are efficiently dispersed within an estuary. The high frequency of rafting and successful colonisation observed by the author suggests that benthic populations of this species in that bay are not limited by dispersal. Similar effects can be expected in other estuarine, lagoonal or bay systems with abundant seagrass populations. Boström & Bonsdorff (2000) observed high individual turnover of species inhabiting a seagrass bed in the northern Baltic Sea and they suggested moving algae (albeit benthic drift algae) as a potential dispersal vector (see also Brooks & Bell 2001). Thus, it can be hypothesised that eventual genetic differences between subpopulations within local populations of many seagrass epibionts are not a consequence of restricted dispersal, but rather of environmental factors.

Salt marshes Intertidal salt marshes have a high primary production, generating plant biomass of >1 kg dry weight (DW) m^{-2} y^{-1} (Bouchard & Lefeuvre 2000). Toward the end of the growth season, above-ground parts of many saltmarsh plants die back, and during storms or spring tides, these may be transported away (Figure 9). Export from salt marshes into nearby coastal habitats has been well known for decades (Teal 1962) and a large proportion of this export may be via the sea surface. It has been reported that dead or living parts of some saltmarsh plants are positively buoyant (Thiel & Gutow 2005b) but it is not well known how long these can persist at the sea surface. Dalby (1963) reported that seed-containing fragments of *Salicornia pusilla* may float for up to 3 months. Whole branches with fruits of the coastal plant *Crambe maritima* were found on beaches of the North Sea and it has been estimated that these may have come from source populations at least 7 km upcurrent (Cadée 2005). Most of these floating materials may be washed up in the flotsam in close vicinity of their sites of origin within the salt marsh: "Macrodetritus moved by tides from the production site in the low marsh accumulate in drift lines in the middle and high marshes, which act as sinks of organic matter" (Bouchard & Lefeuvre 2000). However, some of this dead organic matter may also be carried greater distances (Bouchard et al. 1998). Bart & Hartman (2003) suggested that during storm and hurricane events entire patches of saltmarsh vegetation can be eroded. Positively buoyant peat patches containing rhizomes may then be carried to other neighbouring salt marshes in a bay or estuary.

Connectivity between populations of saltmarsh plants themselves is achieved via floating propagules of either vegetative (roots and rhizomes, e.g., Proffitt et al. 2003, Travis et al. 2004) or sexual origin (seeds and fruits, e.g., Huiskes et al. 1995). Potential dispersal distances of roots and rhizomes are not well known, but fruits and seeds have been reported to disperse at least over distances of 60 km via tidal currents (Koutstaal et al. 1987). Few studies are available on rafting

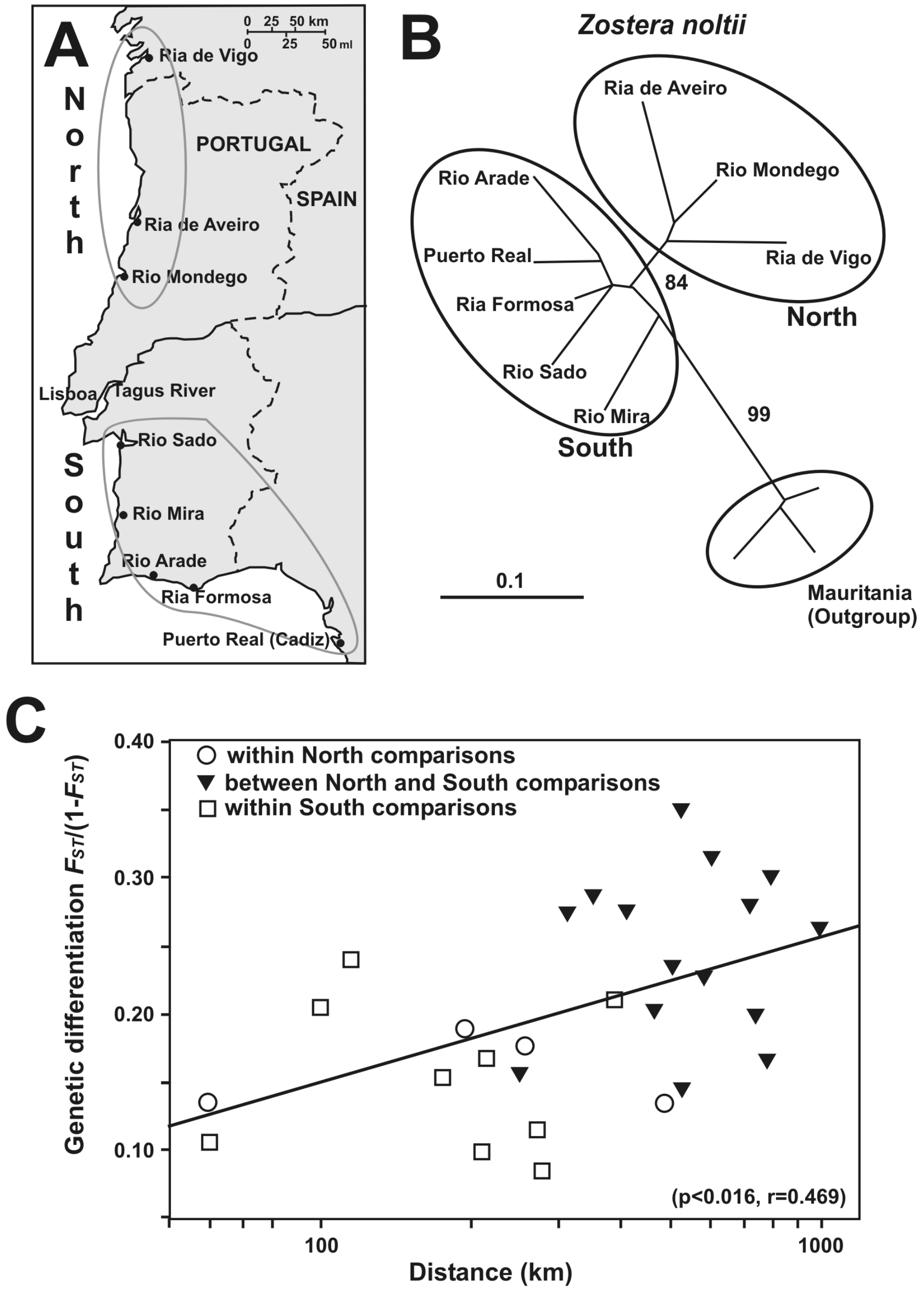

Figure 8 Genetic relationships between populations of *Zostera noltii* from W Iberia. (A) Study sites along the Atlantic coast of Portugal and S Spain. (B) Neighbour-joining tree based on pairwise Reynold's distances (using microsatellites). The northern populations and the southern populations are monophyletic and form sister clades. (C) Isolation by distance based on pairwise comparisons of genetic and geographic distance among eight populations. IBD pattern among all populations was significant (Mantel test, $p < 0.016$), but no significant IBD was found for the southern populations ($p < 0.549$), suggesting a high degree of connectivity between them. Figures modified after Diekmann et al. (2005).

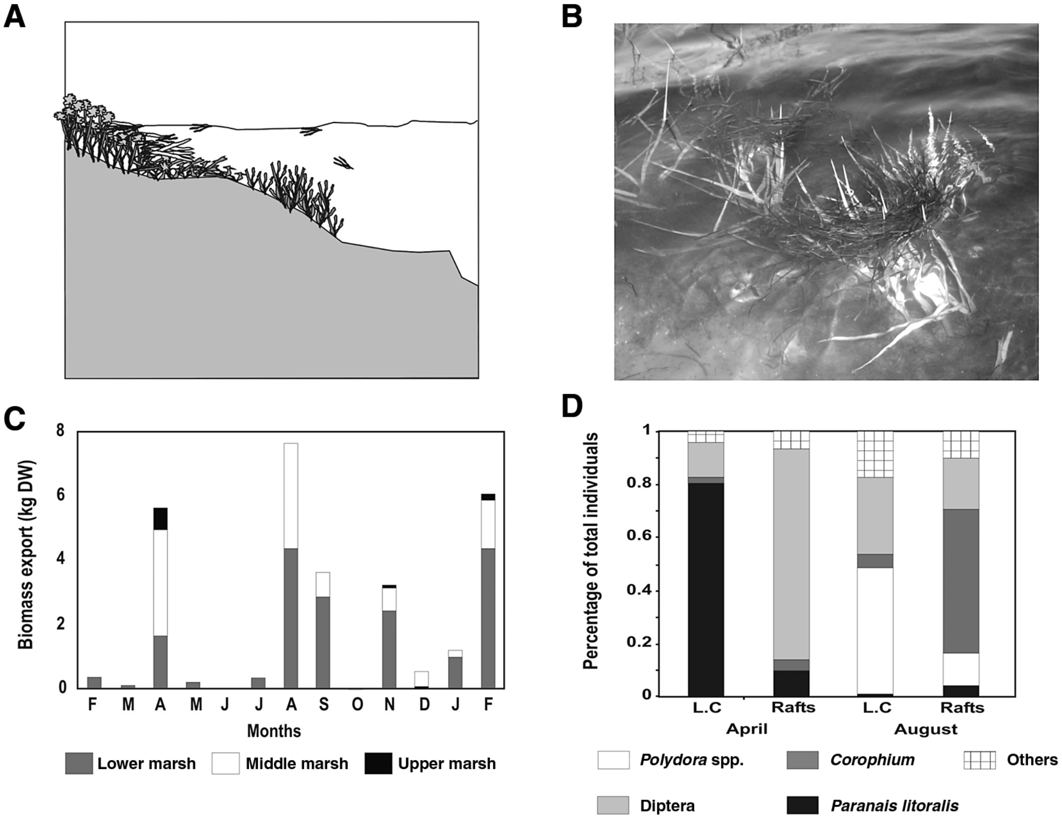

Figure 9 Dynamics on frequent rafting routes supported by saltmarsh vegetation. (A) Detached shoots, senescent plants or patches with rhizomes floating to the sea surface and that are dispersed by currents. (B) Plants of *Spartina* sp. during high tide with entangled seagrass shoots. (C) Annual pattern of biomass export from a salt marsh on the French Atlantic coast; after Bouchard & Lefeuvre (2000). (D) Proportion of macrofaunal groups found in larval collectors (L.C.) and on floating rafts in a restored salt marsh in California; after Moseman et al. (2004).

transport of organisms associated with saltmarsh plants, but it is known that gastropods climb up the stem of marsh grasses and diverse insects feed on and reproduce in saltmarsh plants. A diverse fauna inhabits the rhizome mats of salt marshes, and several recent studies indicate that saltmarsh plants and algae serve as dispersal vectors for these organisms within bay systems. In a restored salt marsh, Moseman et al. (2004) observed diverse organisms, including polychaetes, turbellarians, molluscs, crustaceans and insects arriving on algal rafts (Figure 9), and they concluded that rafting transport contributes large numbers of colonisers to salt marshes. Levin & Talley (2002) made similar observations at another restoration site: all initial colonisers arrived via rafting (on seagrasses, saltmarsh vegetation and macroalgae), and most of them included macrofauna with mobile adults and without planktonic larval stages (for example the amphipods *Hyale frequens*, *Pontogeneia rostrata* and *Jassa falcata*, the tanaid *Leptochelia dubia*, the gastropods *Barleeia subtenuis* and *Cerithidea californica*, and several annelids). Those authors also noticed abundant rafting dispersal in a neighbouring undisturbed salt marsh, emphasising that "rafting of macrofauna is also common in undisturbed settings". They concluded that the high rates of recolonisation are partly made possible by the high degree of connectivity between saltmarsh patches within bay systems.

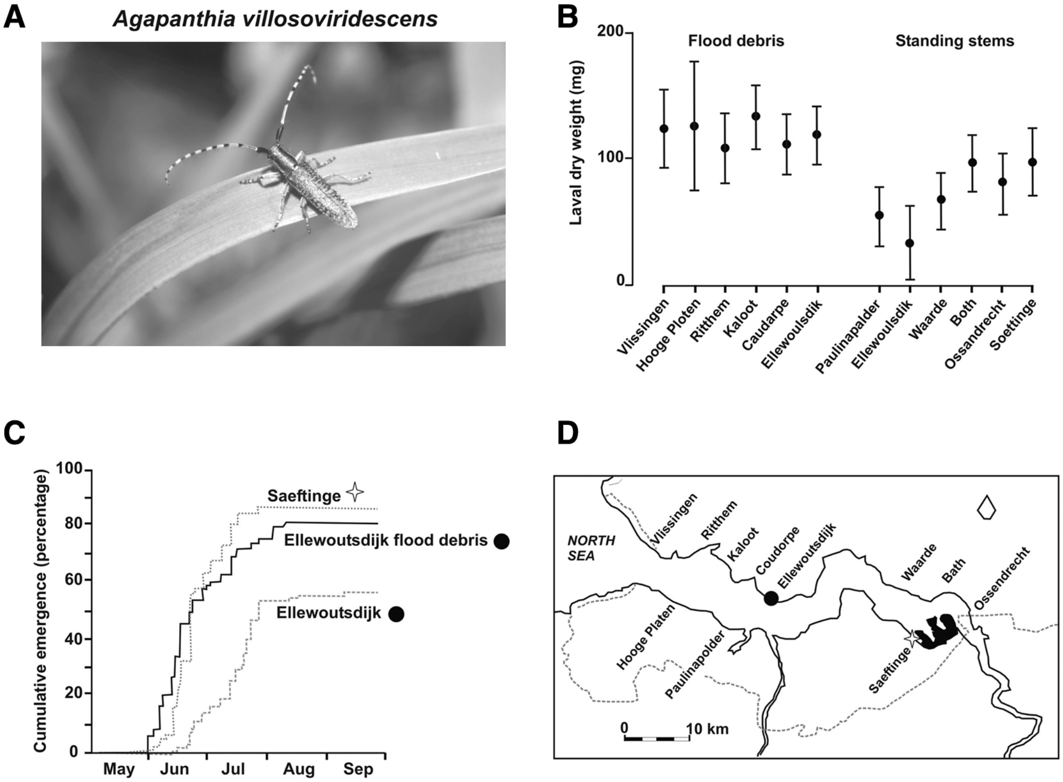

Figure 10 (A) Adult of the beetle *Agapanthia villosoviridescens* (photo courtesy of Per H. Olsen). (B) Dry weight of the larvae of *A. villosoviridescens* collected in flotsam and in standing saltmarsh plants at different sites in the estuary; the large size of larvae found in down-estuary flotsam suggest up-estuary sources. (C) Cumulative emergence of larvae of *A. villosoviridescens* from flotsam, and from standing plants at the presumed site of origin (Soeftinge) and another site (Ellewoutsdijk); the similarity of emergence-pattern between down-estuary flotsam and up-estuary plants suggests up-estuary sources. (D) Sites in the Westerschelde estuary where larvae were collected in flotsam and in standing saltmarsh vegetation. Figures (B–D) modified after Hemminga et al. (1990).

Wilhelmsen (1999) revealed a high degree of connectivity between local populations of *Littorina saxatilis* and she suggested that dispersal may occur via floating marsh grass or seagrass shoots. Strong evidence for efficient dispersal of insects via saltmarsh vegetation comes from a study by Hemminga et al. (1990). Those authors collected large numbers of viable larvae of the beetle (*Agapanthia villosoviridescens*) in dead stems of *Aster tripolium* that had accumulated in flotsam of the Schelde Estuary (NL). Based on morphological evidence and of accompanying saltmarsh vegetation in flotsam, the authors concluded that these larvae had rafted to the collecting sites from upstream source populations (Figure 10). This transport mechanism appears to be important since adults of this beetle "rarely seem to fly". Hemminga et al. (1990) also observed other species in the hollow stems and they suggested that "tidal transport of insects [via rafting] between isolated estuarine salt marshes is an actual process and probably is more common than is apparent until now". Many insects overwinter as larval or pupal stages in senescent saltmarsh vegetation (Denno 1977, Denno et al. 1981), which during winter storms may become detached and dispersed with tidal currents, thereby contributing to connectivity between subpopulations within estuaries. In this context it appears interesting that Peterson et al. (2001) revealed strong gene flow between local populations in a predominantly flightless plant hopper (*Tumidagena minuta*), which lives under the layer of plant debris accumulating in the high salt marsh. Possibly, dispersal of this species is achieved when detritus in the upper marsh goes afloat during strong winter storms.

Shallow-water macroalgal belt The intertidal belt and shallow subtidal waters of temperate regions in both hemispheres are colonised by lush populations of intermediate-sized macroalgae. Many of these algae possess gas-filled structures providing positive buoyancy to these species (e.g., *Ascophyllum* spp., *Fucus* spp., *Sargassum* spp.) (Thiel & Gutow 2005a). Thalli or whole individuals of these algae are frequently detached due to grazer-activity or wave-induced failure and may then float away. There are abundant reports of these algae encountered on sandy beaches (e.g., Stegenga & Mol 1983), yet surprisingly little is known about their arrival on rocky shores or in other subtidal habitats. Also, no data on quantity and direction of export fluxes of these intermediate-sized algae are available. However, based on anecdotal accounts it appears safe to assume that much of the ungrazed annual production of the buoyant algae in these algal belts will be exported via the sea surface to surrounding areas or regions. As a result of their intermediate longevity these algae may be efficiently moved around within estuaries, lagoons or bays, but they may also be frequently exported from these systems (see also below). Dense patches of these algae have been reported from large marine systems such as the North Sea (Franke et al. 1999, Gutow & Franke 2003, Vandendriessche et al. 2006), the Irish Sea (Davenport & Rees 1993), the British Channel and the Baltic Sea (M. Thiel, personal observations), the Gulf of Maine (Locke & Corey 1989), the Strait of Juan de Fuca (Shaffer et al. 1995), and the Japan Sea (Segawa et al. 1964).

Many species of these intermediate-sized algae are colonised by a diverse biota including mobile and sessile species (Mukai 1971, Norton & Benson 1983, Kitching 1987, Ingólfsson 1998, Fredriksen et al. 2005, Buschbaum et al. 2006). Mobile grazers such as isopods from the genus *Idotea* are commonly found on floating *Fucus vesiculosus* and *Ascophyllum nodosum* (Gutow 2003). In laboratory experiments, it could be shown that *Idotea baltica* rapidly consumes its floating substratum (Gutow & Franke 2003). Since this species is restricted to coastal areas, the author suggested that, after exploiting a patch of floating algae, these highly mobile isopods (see Orav-Kotta & Kotta 2004) may return to benthic populations or search for new floating patches (Gutow & Franke 2003). Thus, *I. baltica* appears to be capable of exploiting floating patches as food resources. Similar relationships can be expected for other mobile crustaceans such as palaemonid or hippolytid shrimp. Common decomposers of detached algae such as amphipods from the genus *Orchestia* or isopods from the genus *Ligia* have also been found on floating algae in estuaries (Wildish 1970). Juvenile stages of many fish species associate with floating algae, where they forage on associated rafters (e.g., Shaffer et al. 1995, Ingólfsson & Kristjánsson 2002).

In addition to mobile species, many sessile organisms are found on these algae, including spirorbid polychaetes, hydrozoans, bryozoans and ascidians. Due to the small size of the holdfasts of these intermediate-sized algae, most organisms grow on their blades. The high abundance and intermediate longevity of these floating algae facilitate not only temporary exploitation of these ephemeral habitats, but also efficient dispersal of associated organisms within bays, and occasionally even between bays along the outer coast.

Some indication for connectivity among populations, both within and between bays, on relatively small spatial scales comes from a study by Engelen et al. (2001) on floating algae. They suggested some connectivity between bays via rafting individuals but they also noted local differentiation (Figure 11). For two common epibionts on fucoid algae, rafting has also been inferred to contribute to population connectivity (for the nudibranch *Adalaria proxima* – Todd et al. 1998 and for the bryozoan *Alcyonidium gelatinosum* – Porter et al. 2002). Similarly, the gastropod *Littorina saxatilis* may also be dispersed on floating fucoids (Johannesson & Warmoes 1990).

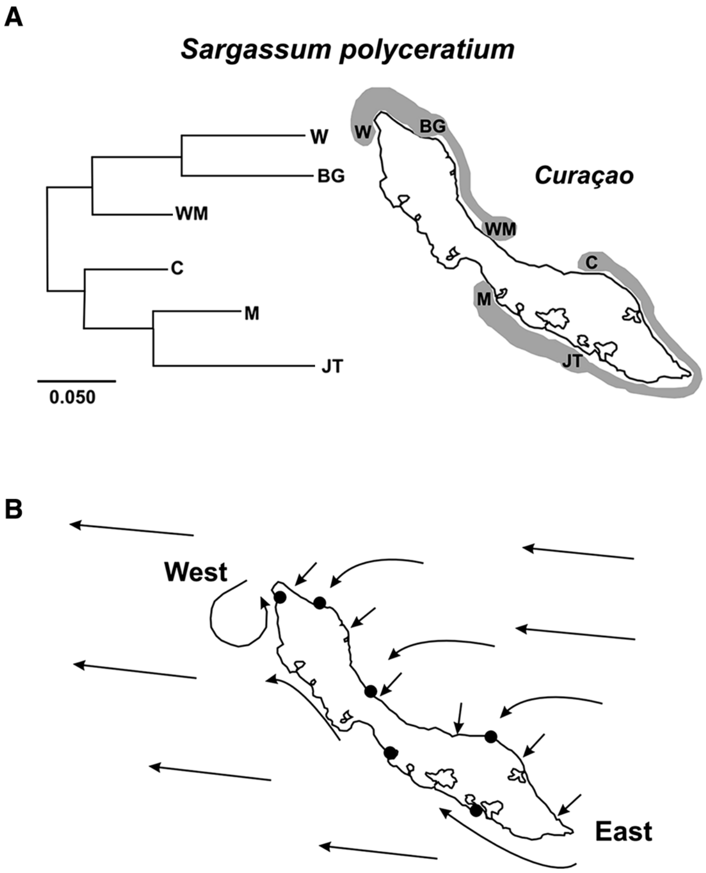

Figure 11 Genetic population structure of *Sargassum polyceratium* on the Caribbean island of Curaçao. (A) Neighbour-joining diagrams for pairwise genetic distances (using RAPD data) of populations from shallow water sites — two distinct clusters, one in the north and one in the south can be distinguished. (B) Typical current and wind patterns around Curaçao. Figures modified after Engelen et al. (2001).

Mangrove forests Mangroves produce a wide variety of detritus that is positively buoyant, including wood (Si et al. 2000) and leaves (e.g., Wehrtmann & Dittel 1990). While substantial research has been conducted on the fate of fallen leaves in mangrove forests (Lee 1999, Jennerjahn & Ittekkot 2002, Alongi et al. 2004), surprisingly little information is available on the amounts and characteristics of fallen wood: "Despite considerable research interest in the ecology of mangrove forests, there is a surprising paucity of information concerning the role of wood in these systems" (Romero et al. 2005). Leaves and small twigs become available every year with seasonal peaks at the end of the summer/fall (Mfilinge et al. 2005), while large pieces of wood only are supplied to the aquatic system following episodic events, such as hurricanes (Krauss et al. 2005). A large proportion of this detritus is exported to nearby coastal habitats (Odum & Heald 1975) as has been demonstrated by numerous studies on trophic links in mangrove systems (Marchand et al. 2003, Alongi et al. 2004), but little information is available about the transport mechanisms. Fallen leaves and twigs of many species are positively buoyant (see, e.g., photograph in Stieglitz & Ridd 2001) and they may locally be very abundant: "Remarkable concentrations of floating debris, especially of mangrove leaves, were at several tidal fronts" (Wehrtmann & Dittel 1990). In general, it appears safe to assume that leaves of most species have only a limited survival time (days) at the sea surface (see Kathiresan & Bingham 2001). Seeds of mangroves may have higher longevities, i.e., several weeks (Steinke & Ward 2003). No information is available about the buoyancy of mangrove wood and its longevity at the sea surface. This makes it difficult to estimate potential transport distances within estuaries and bays.

Since mangrove leaves, twigs and seeds are not in contact with sea water before entering the rafting circuit, they may serve as rafts for terrestrial organisms. It is considered likely that terrestrial arthropods or their developmental stages, which are inquilines in leaves, leaf-stems, twigs or seeds (Feller & Mathis 1997), are dispersed within and between neighbouring mangrove forests, similar to what has been shown by Hemminga et al. (1990) for insects in saltmarsh vegetation (see above). Feller & McKee (1999) mentioned for the wood-boring beetle *Elaphidion mimeticum*, that "dispersal of this species from the mainland to the offshore mangrove islands probably occurred via rafting in wood". Even though aerial parts of mangroves are only of limited value as dispersal vector to marine organisms, some highly mobile ephemeral rafters such as megalopae or juveniles of decapod crustaceans, and also peracarid crustaceans, are known to utilise them as transport vehicles (Wehrtmann & Dittel 1990).

Parts of mangroves that are exposed to sea water before going afloat may be more important as substratum for potential marine rafters. For example, submerged aerial roots of the red mangrove *Rhizophora mangle* are colonised by a diverse biota, mostly composed of sessile suspension feeders (Bingham & Young 1995). These organisms may be transported to new sites, when roots break off. This is facilitated by boring organisms, such as teredinid bivalves or sphaeromatid isopods. In particular, isopod borers have been held responsible for breakage of mangrove roots, and subsequent loss of mangrove trees (Rehm & Humm 1973, Svavarsson et al. 2002). Thus, with their boring activity, isopods may indirectly facilitate dispersal of the biota growing on/in aerial roots of mangroves. Indeed, Brooks (2004) suggested that *Sphaeroma terebrans* may be dispersed with the roots of *Rhizophora mangle*. Detached roots may float for up to 2 months (Estevez 1978, cited in Brooks 2004) and thus they may be efficiently dispersed by tidal currents within mangrove forests and lagoons. There is some indication that population connectivity of *Sphaeroma terebrans* within enclosed bays is high. Baratti et al. (2005) observed little genetic variation among individuals collected within each of four sites in Kenya (two sites), Tanzania and Florida, but they revealed substantial differences between sites (Figure 12). They also reported a limited degree of connectivity between the East African populations, and they suggested occasional rafting dispersal with floating mangrove wood. Reid (2002) also mentioned that littorinid gastropods that inhabit mangrove fringes may be dispersed via rafting (possibly on floating wood). Local populations of boring isopods and other root biota appear not to be dispersal-limited, and their distribution within bays and lagoons may rather be influenced by abiotic factors such as temperature, salinity, tidal level or seston load (Brooks 2004).

Dispersal dynamics on frequent rafting routes

Supply of floating substrata in seagrass beds, salt marshes, macroalgal belts and in mangroves is highly predictable. In some of these environments, substrata are supplied continuously, but with some seasonal variation in abundance and size of floating items. Most of these substrata have a limited survival time at the sea surface (days), but occasionally they may float for several weeks. Longevity of substrata appears sufficient to guarantee efficient dispersal within estuaries, lagoons and bays. In these systems, organisms that already grow on these substrata at the moment of detachment or that are capable of holding onto them may become efficiently dispersed. Since many of the habitats discussed above intercept the sea surface at some time during the tidal cycle or generate layers with reduced flow above them (Dame et al. 2000), they are also very efficient in retaining floating substrata. Thus, rafting dispersal may be an important component of the population dynamics of

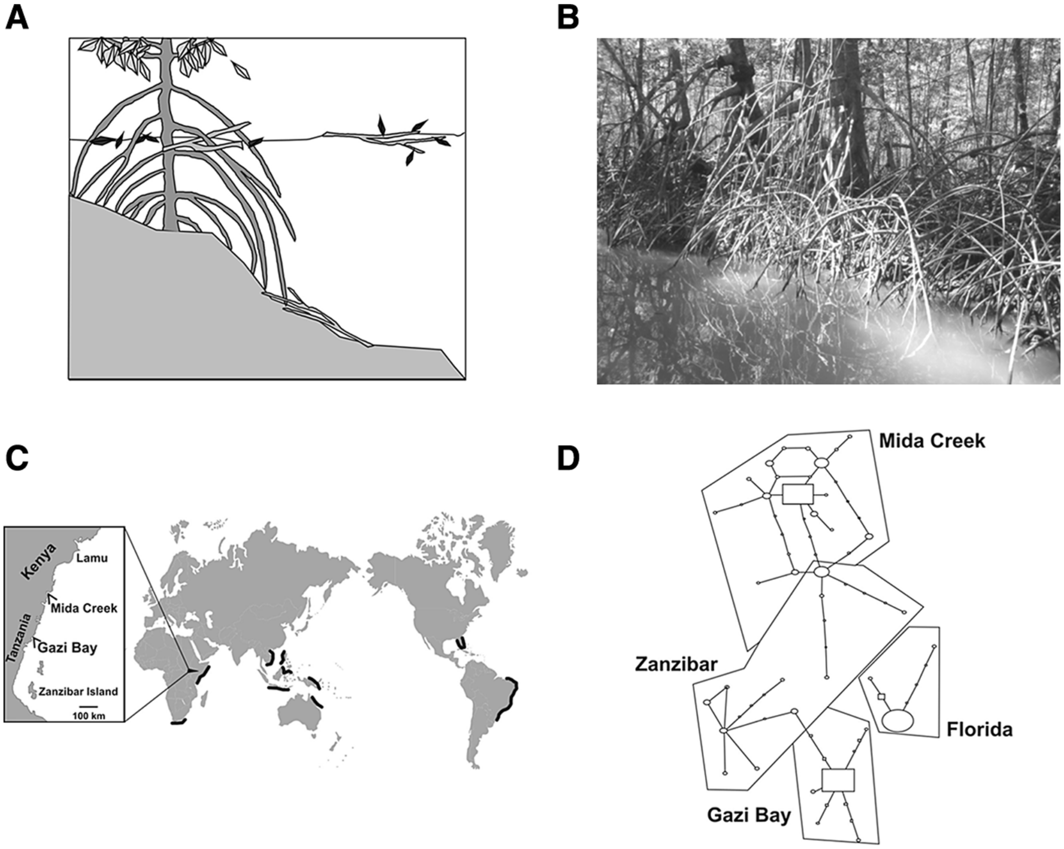

Figure 12 Dynamics on frequent rafting routes supported by mangroves. (A) Detached roots, branches or leaves float at the sea surface and are dispersed by currents. (B) Dense meshwork of aerial roots of the red mangrove *Rhizophora mangle* (photo courtesy of Ingo Wehrtmann, Universidad de Costa Rica, Costa Rica). (C) Global distribution of the isopod *Sphaeroma terebrans*, which excavates burrows in aerial roots of *R. mangle*, and map of study sites along the coast of E Africa. (D) Haplotype minimum spanning network of partial sequence of mitochondrial cytochrome oxidase I gene from different populations of *S. terebrans,* size of ovals (haplotypes) and squares (haplotype with highest outgroup probability) represent the frequency of haplotypes; after Baratti et al. (2005).

organisms living in these habitats. Colonisation of habitat patches may proceed rapidly and via multiple immigration events. In dense subpopulations, emigration events may commonly occur, resulting in rapid spreading of individuals from local populations within estuaries, lagoons and bays, permitting efficient exploitation of resources. The realised geographic distribution of these species within bays will thus depend on environmental factors (both biotic and abiotic), rather than on dispersal supply as long as source populations persist within bays or estuaries (see also Wildish 1970).

If subpopulations are effectively connected within a bay, but without input from local populations in adjacent bays, loss of genetic diversity could be expected (see Figure 6). Some indication for this comes from a study by Hoagland (1985) who observed absence of rare alleles in a small introduced population of the gastropod *Crepidula fornicata* in southern England. When input from neighbouring populations occurs, genetic diversity may increase. Dupont et al. (2003) suggested that jump-dispersal (in that case mediated by human transfer) between local populations in neighbouring bays may be responsible for the high genetic diversity observed in French populations.

This indirectly confirms the expectation of high genetic diversity in local populations of rafters on frequent rafting routes that occasionally receive inputs from external populations (see Figure 6).

Based on the high predictability of rafting opportunities, it can be hypothesised that some species may have evolved particular morphological and behavioural adaptations, allowing them to exploit the opportunities offered by these substrata. Mobile species able to cling efficiently to floating substrata and to swim rapidly in search of new rafts or benthic habitats appear to be preadapted to exploit opportunities for rafting dispersal. Seagrass- and algal-dwelling isopods from the genera *Cleantis*, *Erichsonella* and *Idotea*, amphipods and hippolytid shrimp seem to be the most likely candidates. They are frequently found on floating seagrass blades (M. Thiel, personal observation), but presently it is not known whether these are accidental rafters or whether, under certain conditions, some individuals actively seek out floating blades in order to be transported to other parts of a seagrass bed or even to neighbouring habitat patches.

Occasionally floating items may also be flushed out of estuaries or bays. Baratti et al. (2005) suggested that strong ebbing currents could eject floating mangrove parts into coastal waters, where they may then be transported over greater distances. Snyder & Gooch (1973) mentioned that (rafting) "snails [*Littorina saxatilis*] may occasionally be swept offshore during violent storms and be deposited at new sites". Hemminga et al. (1990) also remarked that saltmarsh vegetation may occasionally leave estuaries. Once carried out of estuaries, lagoons or bay systems into coastal offshore waters, the probability of successful transport to suitable habitats will decrease substantially, because in addition to estuarine shores (seagrasses, salt marshes, macroalgal belt, mangrove forests), many of these floating substrata may end up on inhospitable shores (sandy beaches, exposed rocky shores, etc.). Dispersal dynamics of floating substrata from frequent rafting routes that are carried into offshore waters are expected to be more similar to those on intermittent rafting routes. Local populations of organisms rafting on intermediate-sized algae and on floating mangrove debris may thus exhibit connectivity that is characteristic of the frequent rafting routes within bays, but the metapopulation connectivity of these species outside of bays may resemble that typical for organisms dispersed on intermittent rafting routes.

Intermittent natural rafting routes

Regular supply of floating substrata on intermittent rafting routes

As already outlined in the previous section there may exist substantial overlap between frequent and intermittent routes. The main difference between them is the spatial scale at which they occur. While frequent rafting routes occur within bays or adjacent or continuous patches of habitat, intermittent routes connect different bays or non-adjacent patches of habitat. Since intermittent routes encompass a longer voyage, they present a more selective filter for species, and thus, for many species the likelihood of successful rafting may be lower than on frequent rafting routes.

In coastal offshore waters, floating substrata may be available on a regular basis, but abundance and floating direction can vary substantially between years. Substrata are supplied from coastal sources (e.g., kelp forests or rivers). These floating substrata are dispersed within alongshore coastal currents or with major oceanic currents. Strong winds may also influence the floating direction and velocity of these substrata (Harrold & Lisin 1989, Johansen 1999). In the case of giant kelps, these are already inhabited by a wide variety of species before becoming detached, while wood may or may not be colonised when entering offshore waters, depending on its origin and residence time in nearshore coastal waters. Both substrata have intermediate longevities, and can thus travel over intermediate distances throughout biogeographic regions. In addition to the giant kelps, intermediate-sized macroalgae are available on a regular basis in coastal waters, and these can also transport organisms within offshore currents (see above). Many observations of these substrata in coastal currents and in the open ocean are available (for summary see Thiel & Gutow 2005a), but surprisingly little is known about the local populations connected via these substrata.

Given that floating substrata are common on intermittent rafting routes, it can be predicted that these routes may lead to high-to-intermediate levels of population connectivity. Since distances connected by intermittent routes are relatively large (100–5000 km), not all local populations will be continuously connected via this rafting route. Small local populations may be temporarily isolated, possibly resulting in founder effects. Also, as a consequence of comparatively large distances over which intermittent rafting routes are effective, IBD may increasingly gain in importance if hydrographic conditions regularly result in the same rafting trajectory. Under these conditions, the relatedness of neighbouring local populations will depend to a high degree on current velocity and directions. Stepping-stone dispersal is expected to be a predominant pattern on intermittent rafting routes that have a fixed route. This usually leads to colonisation of neighbouring local populations, and thus, distant local populations may only be connected via intermediate local populations (Figure 13). However, since floating substrata on intermittent rafting routes have a

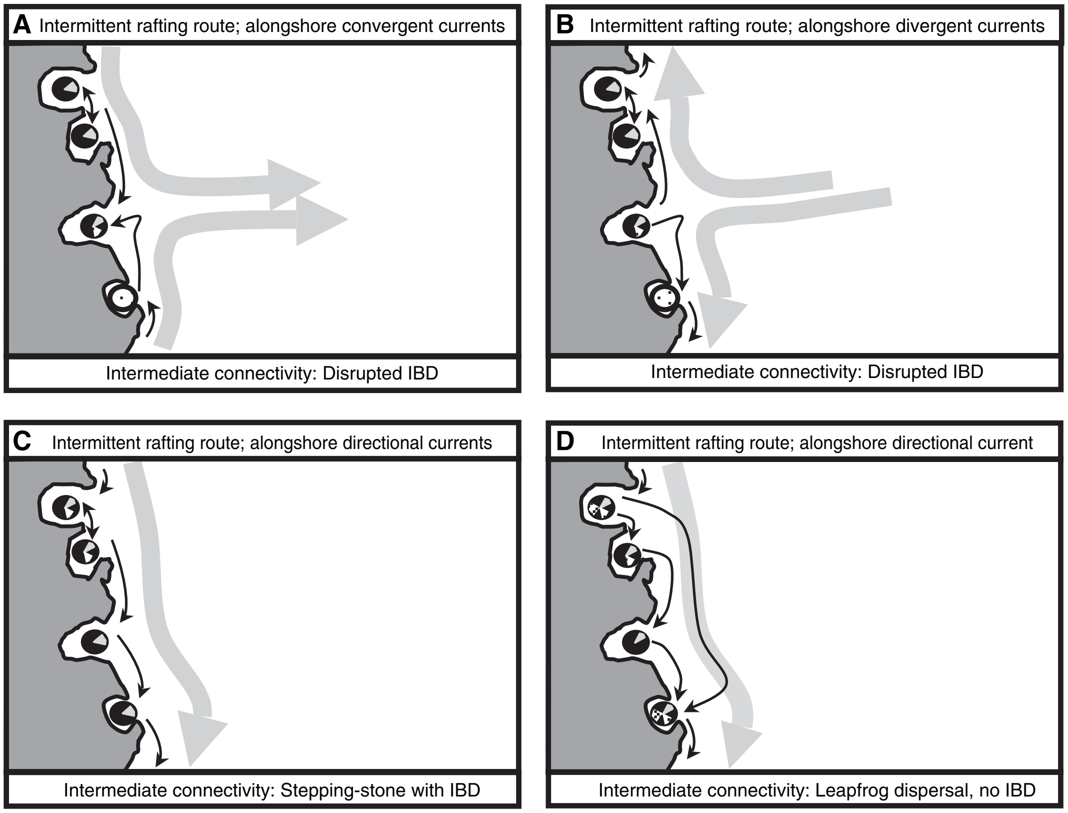

Figure 13 Scheme showing four possible scenarios on intermittent rafting routes and the expected genetic consequences. (A) shows an intermittent rafting route with convergent currents, while (B) shows a route with divergent currents; in both cases the alongshore populations are not expected to show an IBD pattern because not all local populations are connected by currents. (C) shows an intermittent rafting route with consistent alongshore currents resulting in local populations being connected in a stepping-stone manner and in an IBD pattern of genetic differentiation. (D) shows an intermittent rafting route with consistent alongshore currents where rafters may occasionally be transported over long distances jumping over adjacent local populations, which results in lack of IBD.

relatively high longevity, gene flow in an alongshore direction may not occur in a stepping-stone fashion (or other dispersal/colonisation mechanisms that may ultimately lead to IBD), but rather in a leapfrog fashion where propagules may leap over immediately neighbouring populations and immigrate into distant populations (Figure 13). In these situations, the pattern of genetic structure of the metapopulation should not be IBD. It is important to characterise this specific form of jump-dispersal, because a particular pattern in genetic population structure might result from leapfrog dispersal, namely that distant populations are more similar than adjacent local populations. Leapfrog dispersal may occur at all scales, because there exists a high variability in individual dispersal distances among rafters.

Genetic diversity of many species connected via intermittent rafting routes can be expected to be structured as a metapopulation with varying degrees of connectivity among local populations. Local populations will be more or less both temporarily isolated and connected, such that in some cases gene flow obscures the effects of genetic drift (either in the form of bottlenecks or founder effects), which would be reflected in a low genetic differentiation among local populations. At the other extreme, intermittent routes may sometimes act as a strong filter that results in a lower probability of successful colonisation by rafters, but that is still frequent enough to prevent speciation. In these cases, genetic differentiation among local populations will be higher.

Examples of intermittent rafting routes

Kelp forests In temperate regions of the Pacific and of the Southern Ocean, giant kelps grow between *ca* latitudes 30° and 60° in both hemispheres (Steneck et al. 2002). These kelp forests contain many species that are positively buoyant thanks to gas-filled structures. Detachment of these kelps may be caused by strong wave action (Dayton & Tegner 1984), by high grazer activity (e.g., Tegner et al. 1995), or a combination of both (Barrales & Lobban 1975). Following detachment, kelp with floating structures rise to the sea surface (Kingsford & Choat 1985, Kingsford 1992) where they are transported with major currents or pushed by prevailing winds (Harrold & Lisin 1989). Some authors reported that the abundances of floating kelp increased during late summer/early fall (e.g., Kingsford 1992), while other studies revealed no clear seasonal trend (Hobday 2000b).

Kelp forests grow in nearshore coastal habitats, and consequently detached individuals may be exported immediately onto nearby beaches where they constitute an important subsidy to the community of sandy beach detritivores (Orr et al. 2005). Kelp species with limited buoyancy or those that have lost buoyancy due to degradation processes may also sink to the sea floor, where they accumulate in submarine canyons constituting an important food source for benthic organisms (Vetter & Dayton 1999). However, abundant reports of floating kelps at far distances from the nearest source populations also indicate that they can potentially travel substantial distances while afloat (Helmuth et al. 1994, Kingsford 1995, Hobday 2000b, Smith 2002, Macaya et al. 2005). During offshore voyages, these kelps may carry a diverse community of associated organisms, which, upon landfall, may colonise benthic habitats.

Large kelp from the genera *Macrocystis*, *Nereocystis*, *Pelagophycus* and *Durvillaea* possess a large and structurally complex holdfast, which is inhabited by a wide diversity of organisms (e.g., Ojeda & Santelices 1984, Smith & Simpson 1995, Adami & Gordillo 1999, Thiel & Vásquez 2000). Depending on their biology and on the structure of the holdfast, these organisms may persist in the holdfast after detachment. For example, many inhabitants of holdfasts of *Macrocystis pyrifera* survived for several months in detached holdfasts (Edgar 1987, Vásquez 1993).

Connectivity between neighbouring kelp forests is hypothesised to be high. Some indication for this comes from genetic studies on positively buoyant kelp species. For the elk kelp *Pelagophycus porra*, Miller et al. (2000) revealed that individuals from several Channel Islands off southern California were too similar to represent different species, but they observed a trend of isolation.

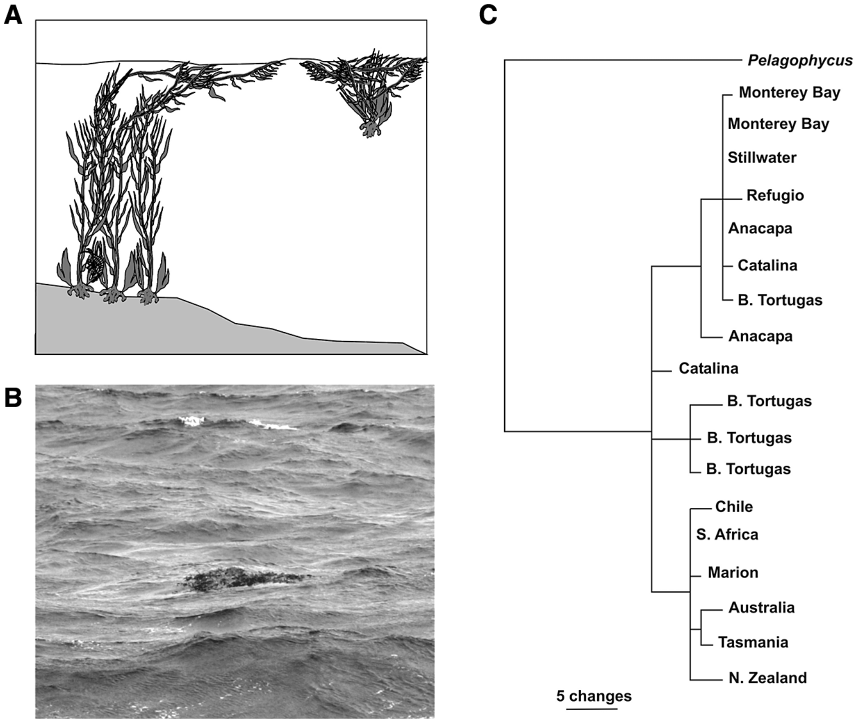

Figure 14 Dynamics on intermittent rafting routes supported by giant kelps. (A) Detached blades, branches or whole individuals float at the sea surface and are dispersed by currents. (B) Floating giant kelp *Macrocystis pyrifera* along the SE Pacific coast of Chile. (C) Phylogram based on nuclear ITS2 sequences of populations of *M. pyrifera*, indicating the close relationship of populations from the southern and northern hemisphere; after Coyer et al. (2001).

Interestingly, in a subsequent ‘distance network analysis’ some individuals from different islands clustered together, and even though they observed floating sporophytes, the authors did not mention rafting dispersal as a potential explanation. Using rDNA, Coyer et al. (2001) examined the genetic relatedness among four putative species of *Macrocystis* (Figure 14), and their results led them to suggest that “*Macrocystis* may be a monospecific genus (*M. pyrifera*)”. They furthermore noted high “intra-individual variability” in the samples from the northern hemisphere (in particular those from the Channel Islands). Inferring rafting dispersal of fertile sporophytes, they hypothesised that “southern genotypes ‘hybridize’ with northern genotypes in intermediate areas such as Santa Catalina Island” (Coyer et al. 2001). This scenario would fit the hypothesised gene flow on regular rafting routes with alongshore convergent currents (Figure 13).

Another indication of efficient dispersal via floating kelps comes from the wide geographic distribution of some common kelp inhabitants. Despite lacking a pelagic dispersal stage, the kelp-boring isopod *Limnoria chilensis* is found in kelp holdfasts extending over a wide geographic range of >4000 km between 20 and 55˚S (Thiel 2003a). Other kelp inhabitants with direct development also have wide geographic distributions (Knight-Jones & Knight-Jones 1984, Helmuth et al. 1994). This evidence for rafting dispersal admittedly is circumstantial, and it is emphasised that future studies on the population connectivity of organisms associated with giant kelp are highly desirable. Intermediate-sized algae (*Ascophyllum* spp., *Fucus* spp., *Sargassum* spp.) are also frequently found in coastal currents (Thiel & Gutow 2005a), which they may have reached after detachment from sheltered bays or from outer-coast rocky shores. These algae can also contribute to population connectivity within these systems via effective transport of organisms without planktonic larval stages (e.g., *Littorina sitkana*, Kyle & Boulding 2000; *Amphipholis squamata*, Sponer & Roy 2002; *Nucella lapillus*, Colson & Hughes 2004).

The relatively high abundance of floating giant kelp in temperate coastal currents, and their intermediate longevity of several months (Thiel & Gutow 2005a), suggest that these are efficient dispersal vectors within biogeographic regions. Recolonisation of disturbed patches may proceed relatively slowly over several years. In particular toward the limits of the distributional ranges, where extinctions can occur relatively frequently, impoverished genetic diversity can be expected.

Floating trees Rivers regularly transport large amounts of floating wood to the sea. In the northern hemisphere, north of *ca* 60°N, this occurs every year in the spring following snow melt (Maser & Sedell 1994, Johansen 1999). At low latitudes, around the equator, wood becomes available on a less regular basis, with relatively high interannual variation in abundances (Solana-Sansores 2001, Castro et al. 2002). If floating wood is immediately pushed into offshore waters, colonisation by marine organisms will occur during the journey (i.e., in the pelagic environment without direct contact with benthic communities). Wood may also be retained in or close to benthic nearshore communities (e.g., in salt marshes, kelp forests or in mangrove systems), and during this time become colonised by common coastal organisms. While wood may serve as the dispersal vehicle for many different marine organisms, its utility for terrestrial organisms is relatively limited. Only species which are not directly exposed to saltwater (e.g., in self-excavated burrows), or which resist immersion in saltwater (e.g., dormant stages), may survive extensive trips on floating wood. After reaching offshore waters, floating wood is presumed to follow a similar fate as kelp rafts. A large proportion of the total pool of floating wood may be thrown onto beaches during onshore storms, while the other fraction will sink to the sea floor where they sustain a diverse community of wood-boring organisms (Distel et al. 2000).

There are surprisingly few studies on population connectivity via floating wood, despite the fact that this substratum is relatively abundant in some regions. In the Arctic Ocean, the distribution of some coastal plant species is assumed to be the result of seed dispersal via rafting (Johansen & Hytteborn 2001) (Figure 15). Baratti et al. (2005) inferred limited exchange between local bay populations of the boring isopod *Sphaeroma terebrans* along the outer East African coast (see Figure 12). They suggested that isopod-bearing roots may occasionally be flushed out of bays into offshore waters. Lapègue et al. (2002) demonstrated close genetic relationships between mangrove oysters from West Africa and eastern South America and they suggested rafting (possibly on mangrove wood?) (Figure 15). In the Caribbean, there is an indication that population connectivity between island population of lizards may be achieved via rafting (Calsbeek & Smith 2003). Wood may be the primary rafting substratum for lizards as underlined by a direct observation of a group of iguanas that arrived on the Caribbean island Anguilla on a tree-raft (Censky et al. 1998). Insects were found on driftwood stranded on sandy beaches (Wheeler 1916) or floating in the sea (Heatwole & Levins 1972). Several other authors had suggested wood as dispersal substratum connecting insect populations of island groups in archipelagos and between islands off continental coasts (Abe 1984, Niedbala 1998, Coulson et al. 2002). Most of these observations are from subtropical and tropical areas, underlining the importance of floating wood as connecting vector in these regions.

Dispersal dynamics on intermittent rafting routes

While floating items (kelp and wood) can be underway in large quantities on intermittent rafting routes, the strength of the connectivity between local populations in general is lower than on frequent routes, primarily because transport distances are farther and local populations are more dispersed, diminishing the probability of landfall in suitable habitats. Nevertheless, fast recolonisation

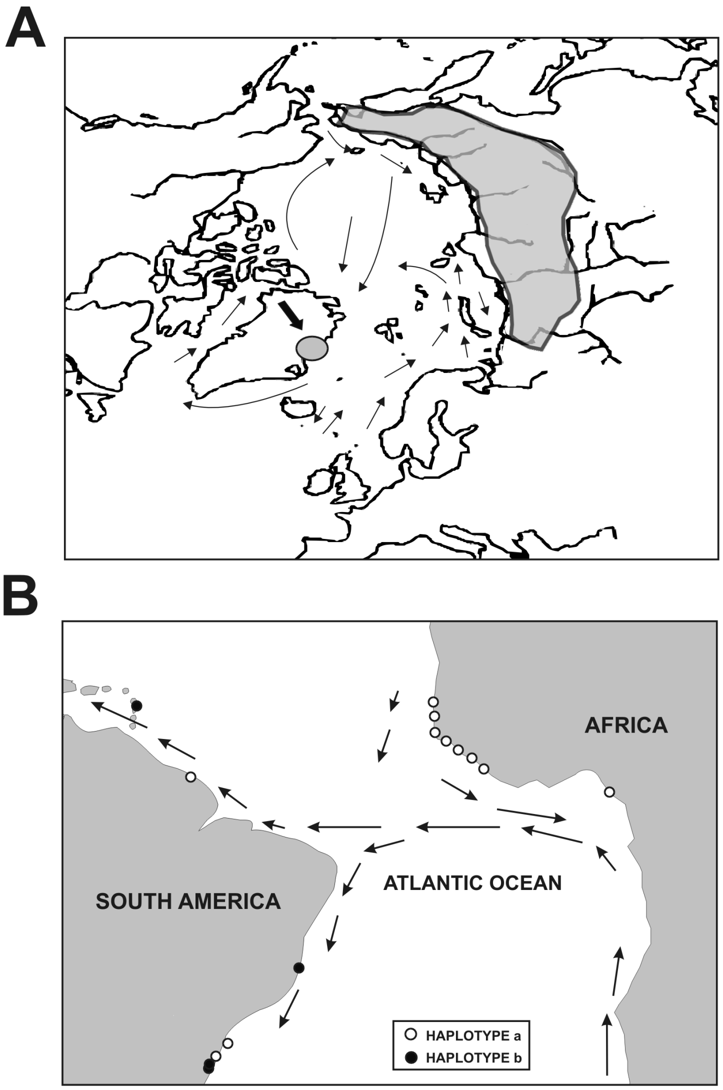

Figure 15 Intermittent rafting routes supported by floating trees. (A) Distribution pattern of *Potentilla stipularis* from Arctic coasts and predominant current patterns in the Arctic Ocean; modified after Johansen & Hytteborn (2001). (B) Distribution of 16S mtDNA haplotypes of mangrove oysters from W Africa and eastern S America and predominant current patterns in the S Atlantic; modified after Lapègue et al. (2002).

of unpopulated areas (Colson & Hughes 2004), and high genetic relatedness among distant local populations of some species, show that rafting dispersal on these intermittent rafting routes can be effective. Gene flow can be directional when alongshore currents are highly persistent, but there are also apparent examples of gene flow in variable directions. Dispersal via rafting often seems not to proceed in a stepping-stone fashion, commonly resulting in lack of IBD. A pattern of leapfrog migration, where travelling individuals are passing adjacent local populations and reach distant locations, appears to be a recurrent observation on intermittent rafting routes, irrespective of the floating substratum. The first example for this was found in one of the earliest studies on the genetic

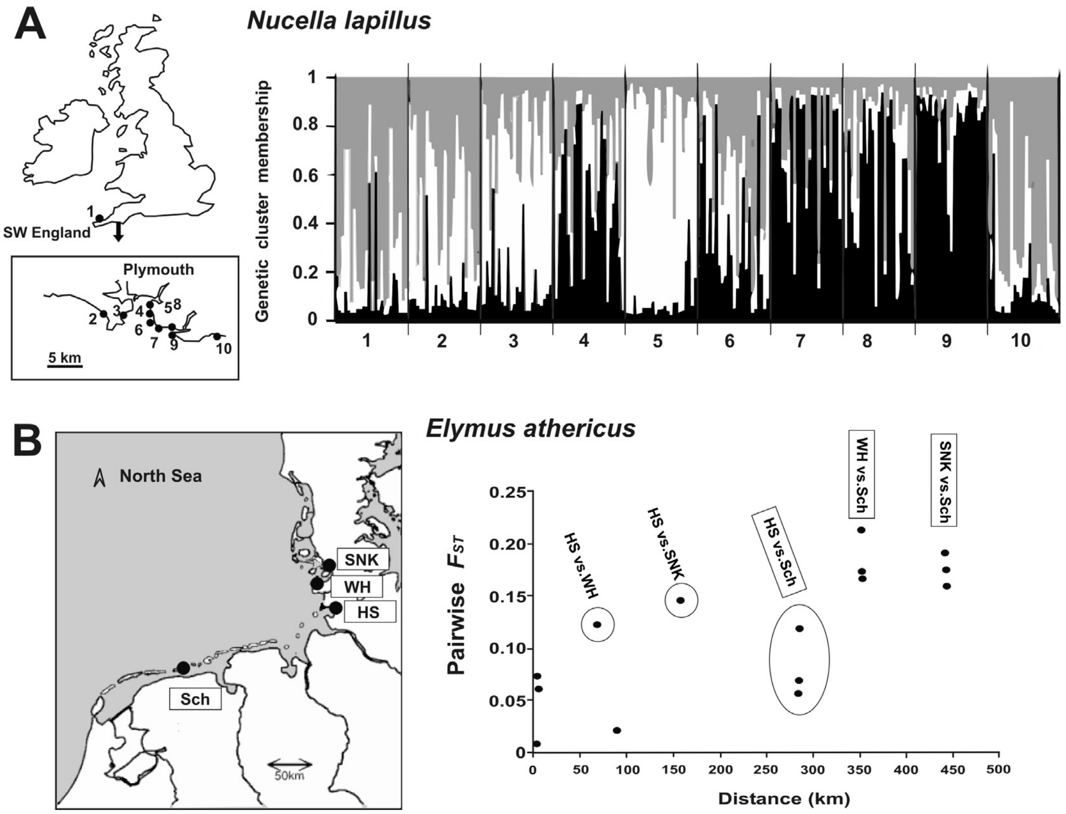

Figure 16 Relationships between local populations of an intertidal gastropod and a saltmarsh plant, assumed to being dispersed along intermittent rafting routes. (A) Sampling sites of local populations of the gastropod *Nucella lapillus* in SW England, and genetic cluster membership (based on microsatellites) of individuals collected at each site; the two most distant populations (1 and 10) show strongest similarities; modified after Colson & Hughes (2004). (B) Sampling sites of *Elymus athericus* from salt marshes on the SE coasts of the North Sea, and pairwise F_{ST} (based on microsatellites) plotted against geographic distance showing IBD pattern for the sampled populations; the local population from Helmsand (HS) is as closely related to a distant population (Sch) as to two adjacent populations (WH and SNK); modified after Bockelmann et al. (2003).

population structure of a marine invertebrate, the intertidal snail *Littorina saxatilis* (Snyder & Gooch 1973). These authors observed that "significant population differentiation may occur over distances of as little as 2 km, while widely separated populations may be nearly identical". Colson & Hughes (2004) reported a similar pattern for local populations of *Nucella lapillus*: "The similarity between SW1 (St Agnes in North Cornwall) and SW10 (Stoke Beach in South Devon) is remarkable, considering the geographical distance between the two populations", and they suggested "that the major dispersal routes involve relatively long-distance exchanges between open sea sites, bypassing Plymouth Sound" (Figure 16). In a study on the genetic population structure of the saltmarsh plant *Elymus athericus*, Bockelmann et al. (2003) also observed that distant populations were more similar than immediately adjacent populations: "Surprisingly, the Helmsand [HS] population was more similar to the populations on Schiermonikoog [Sch], although it is situated in a clayey mainland marsh in the northeastern Wadden Sea such as Sönke-Nissen-Koog Vorland [SNK] and Westerhever [WH]" (Figure 16). For the seagrass *Thalassia testudinum*, Waycott & Barnes (2001) revealed high levels of gene flow over distances of >2500 km (between Panama and Bermuda), and they suggested long-distance movements of vegetative fragments (possibly via rafting) as the principal explanation for the same clone being present in Panama and at Bermuda. Indication for the high floating potential of *T. testudinum* also comes from the finding of fragments of this seagrass in the deep sea off the Caribbean coasts (Wolff 1979), even though Flindt et al. (2004) assigned this species a low floating potential. It is suggested that many of these cases could be the result of leapfrog dispersal, where travellers jumped over long distances, leaving nearby populations out of the loop.

For several rafting species, though, there is an indication of decreasing genetic diversity toward the limits of their biogeographic distribution (Marko 2004, 2005), suggesting that dispersal may occur along a chain of stepping stones. The reasons for decreasing genetic diversity toward range limits are primarily four-fold, namely (i) lack of suitable dispersal opportunities, (ii) limited propagule production, (iii) rapid range extension via few founding individuals or (iv) differential natural selection, which permits survival of different genotypes in source and sink regions. These factors may act in combination or separately — if they act in unison, their impacts might be enhanced. Toward the down-current end of intermittent rafting routes, dispersal may taper out and the frequency of events may take on a sporadic character similar to that on episodic rafting routes (see below).

Based on global patterns of substratum supply, several intermittent rafting routes can be identified (Figure 17). Important intermittent rafting routes are known in the boundary currents of the Pacific, on the coasts of the North Atlantic, probably in the boundary currents of the South Atlantic (little is known from these regions), around southern New Zealand, also along the coasts around the equator, but at lower frequency than on the other intermittent rafting routes (Figure 17). In some of these regions (e.g., in the Humboldt and California Currents) during ENSO events, large-scale regional extinctions may occur. Rafting can contribute to a rapid recolonisation after such events, albeit possibly with few colonisers resulting in low genetic diversity (for algae see Martínez et al. 2003, for invertebrates Marko 2004).

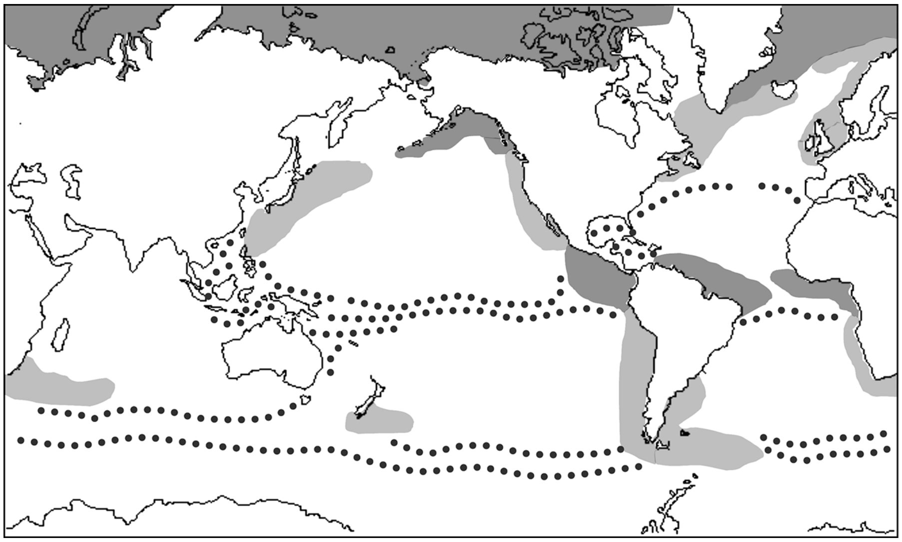

Figure 17 Global distribution of important intermittent (shaded areas) and episodic (dotted lines) rafting routes. Regions with high abundances of floating wood and floating macroalgae indicated by dark and light shading, respectively.

Episodic natural rafting routes

Sporadic supply of floating substrata on episodic rafting routes

In many regions of the world, for most of the time floating items may be virtually absent on the sea surface. However, after certain events, large numbers of these items suddenly become available as rafting substrata. This is, for example, the case with volcanic pumice, which may be supplied in large quantities after volcanic eruptions (Sutherland 1965; Jokiel 1989, 1990a; Bryan et al. 2004). Similarly, after cyclones, flood events or tsunamis enormous quantities of terrestrial debris may reach the oceans (Carey et al. 2001). Following these events, huge armadas of floating substrata may be transported with the predominant current systems, offering abundant rafting opportunities for potential travellers.

Many of the substrata that become available episodically have very high longevities since they are either of abiotic origin (volcanic pumice) or consist of inorganic materials (skeletons) that are resistant to decay processes. Also terrestrial debris (e.g., large trees or processed wood) may survive for a relatively long time at the sea surface. Consequently, many of the floating items that are supplied sporadically may be transported over relatively large distances. Due to their origin either in terrestrial environments or in the open ocean, most of these substrata will only be colonised after starting their journey at the sea surface. The frequencies and localities at which these substrata are supplied to the ocean are difficult to predict. In general, volcanic pumice is most common in regions with high volcanic activity (e.g., the Pacific Ocean and the Mediterranean). Important volcanic eruptions, during which large quantities of volcanic pumice are released, appear to occur on a timescale of the order of several decades or centuries. For example surface eruptions were recorded in 1883 in Krakatau (Thornton 1997, Jokiel & Cox 2003) and in 1952 on San Benedicto (Richards 1958). Underwater eruptions producing buoyant pumice appear to take place over similar timescales (Sutherland 1965, Frick & Kent 1984, Fushimi et al. 1991, Bryan et al. 2004), in particular in the Pacific Ocean.

Throughout a region with high tectonic activity, tsunamis may also wash terrestrial debris into the sea along wide stretches of impacted coastlines. Along the Pacific Rim, tsunami events are recorded to occur at a frequency of tens to hundreds of years (Witter et al. 2001, Pinegina et al. 2003, Kulikov et al. 2005). Similar frequencies are reported from other active margins (e.g., in parts of the Mediterranean (Altinok & Ersoy 2000)). In the tropics, large quantities of terrestrial debris may also be flushed out to sea after passage of hurricanes and typhoons. These tropical cyclones recur each year (e.g., Chan & Liu 2004), but their pathways and the input sites of terrestrial debris are highly unpredictable (Landsea et al. 1996, Weber 2005). Their frequency of occurrence in a given locality may be on the order of decades or centuries. Buoyant skeletal materials of marine organisms (floating corals, cephalopod shells, egg cases) only become available episodically, but then may be very abundant (Kornicker & Squires 1962, DeVantier 1992, Cadée 2002). In addition to these sporadically supplied substrata, some of the regularly available items such as floating macroalgae or wood may occasionally also travel on episodic rafting routes (e.g., during particular climatic or oceanographic events such as ENSO).

In general, the temporal pattern of travel opportunities on these episodic rafting routes depends on the frequency of events that supply floating substrata. The unpredictability of most of these events makes it difficult (in many cases impossible) to provide estimates of the time intervals between subsequent rafting episodes. However, despite these uncertainties some simple statements can be made. In most cases, episodic events occur at intervals of many years, often decades or even centuries. It can thus be safely stated that the generation times of most small, coastal or terrestrial organisms are substantially shorter than the time intervals between supply events. Consequently, individuals supplying propagules to a given rafting episode will be descendents of several generations of residents that arrived after previous rafting events. In contrast, in clonal organisms, generation times may be of a similar magnitude as the intervals between rafting episodes. Individuals that established after one episode may be the same ones providing propagules for a subsequent rafting episode.

As a consequence of the relationships between generation time and dispersal events, small sexually reproducing species with short lifetimes may reproduce over many generations without any (or with very little) exchange via rafting. During these time periods, dispersal will depend primarily on autonomous dispersal capabilities of organisms. This may lead to small effective population sizes of these organisms (i.e., on islands or in relatively isolated bays), with a high likelihood of founder effects to occur. In general, the degree of isolation of local populations will be negatively correlated with the potential for autonomous dispersal of a species (unless the episodic event has transported colonists into an area with frequent or intermittent rafting routes). Species with direct development can be expected to be most affected by periods of isolation of local populations. Interestingly, once rafting opportunities arise, some of these species are particularly well adapted for LDD and successful colonisation of new habitats (Thiel & Gutow 2005b). As a result of relatively long periods of isolation, local populations may diverge or even go extinct. Consequently, organisms that are transported during episodic rafting events may arrive in areas where conspecifics have experienced substantial genetic changes or are completely absent. Even when some degree of divergence has occurred or the new colonisers come into secondary contact with incipient species that derived from a common ancestral lineage, hybridisation may take place. If genetic changes have not yet led to reproductive barriers, genetic diversity of the metapopulation may reach high levels. In contrast, if allopatric evolution has led to reproductive isolation or if conspecifics are absent, founding populations may become established as a new species to the area. The genetic diversity of these local populations will depend on their history of isolation and the number and gene pool of arriving individuals. Since founding populations of direct developers on episodic rafting routes usually are small, genetic diversity of these may be relatively low. Thus, the dispersal dynamics on episodic rafting routes may lead to contrasting scenarios in the population biology of sexually reproducing organisms with short generation times. Genetic diversity in local populations may either show high or low levels, depending on whether arriving individuals can interbreed with local residents or not (Figure 18).

In general, it can be predicted that the evolutionary consequences of episodic rafting routes depend on the relationship between generation times of rafting organisms and the time interval between subsequent rafting episodes.

Examples of episodic rafting routes

Volcanic pumice During volcanic eruptions enormous quantities of positively buoyant pumice can be released (e.g., Sutherland 1965, Jokiel 1990a, Bryan et al. 2004). Pieces of pumice usually are relatively small (several millimetres in diameter), but may occasionally be larger, reaching fist size — even pieces of >0.5 m diameter have been reported (Jokiel & Cox 2003). Pumice that is supplied to the sea may originate from island volcanoes (Richards 1958, Thornton 1997), or also from eruptions of underwater volcanoes (e.g., Coombs & Landis 1966, Fushimi et al. 1991, Bryan et al. 2004). Pumice pieces can float for many months and even years before disintegrating or washing ashore. During this time, the pumice and rafting organisms may be distributed throughout all major ocean basins (Frick & Kent 1984, Jokiel & Cox 2003, Bryan et al. 2004) (Figure 19).

Diverse marine organisms are known to be transported with volcanic pumice. Algae, sponges, corals, polychaetes and bivalves have been found growing on volcanic pumice (Jokiel 1984, 1989; Bryan et al. 2004). How these organisms colonise the floating pumice in the first place is not well known. Pumice, as most other floating substrata on episodic rafting routes, enters the sea in a clean

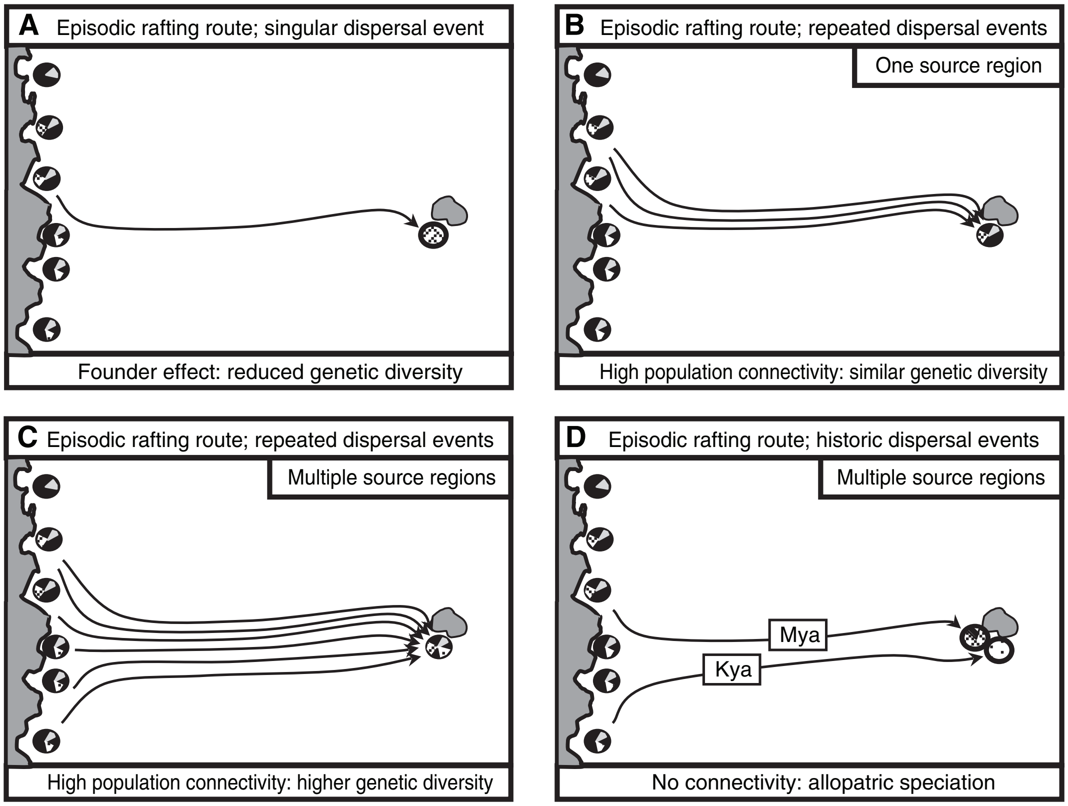

Figure 18 Scheme showing four possible scenarios on episodic rafting routes and the expected genetic and biogeographic consequences. (A) showing a local island population arising from a singular dispersal event, where founder effects lead to a strong reduction in genetic diversity in the sink population. (B) showing a local island population supported by repeated dispersal events from a particular source region, resulting in close similarity between source and sink populations. (C) showing a local population supported by repeated dispersal events from several source regions, resulting in a high genetic diversity in the sink population. (D) showing a situation with several historic dispersal events, where local populations in the sink region have diverged significantly after the first dispersal event and could not anymore interbreed with subsequent colonists, leading to the establishment of two different species in the sink region.

state. Thus, it is most likely that pumice is colonised while floating, probably via planktonic (larval) stages. Many corals found on pumice have planktonic larval stages (Jokiel 1989), which is also true for other organisms reported from pumice, such as, for example, bivalves or stalked barnacles. In a laboratory experiment, Jokiel & Cox (2003) showed that similar numbers of planula larvae of *Pocillopora damicornis* settled and developed into juvenile colonies on volcanic pumice as on calcareous rock. They emphasised that *P. damicornis* produces larvae throughout the year, potentially permitting continuous colonisation of floating pumice. Bryan et al. (2004) remarked on the temporal coincidence between a pumice supply event and a spawning event: “It is noteworthy that the eruption and generation of the pumice rafts in this instance just preceded late spring coral spawning events in the southwest Pacific”. The necessity for close temporal overlap between pumice availability and propagule supply in a given locality enhances the sporadic character of dispersal on these episodic rafting routes.

Several studies provide indication that volcanic pumice may serve as a dispersal vector with the potential of connecting distant populations. Strongest evidence comes from the studies by Jokiel

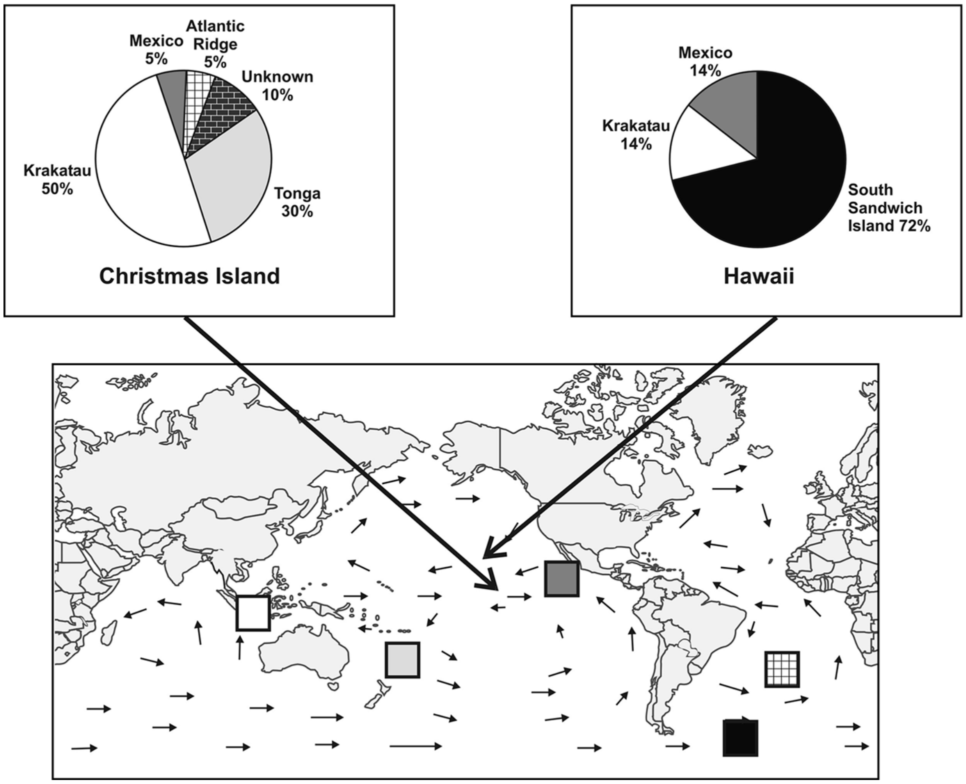

Figure 19 Origins of volcanic pumice found on beaches on Hawaii and Christmas islands, and major oceanographic currents assumed to transport floating pumice from the different source regions; modified after Jokiel & Cox 2003. Shadings in map indicate sources of origin shown in the pie diagrams.

(1984, 1989, 1990a,b), who sampled volcanic pumice throughout the equatorial Pacific. His studies revealed that some species (e.g., *P. damicornis*) are frequently dispersed via pumice (Jokiel 1984, 1990b), though he remarked that organic substrata such as wood and seeds might be "far more important than pumice rafts in establishment of new populations of corals", because rafting colonies are easily shed from these organic substrata when scratching over the reef (Jokiel 1989). Regardless of the floating substratum, rafting appears to be an important dispersal mechanism for some coral species. Observations of rafted colonies can be compared with studies on the geographic distribution or genetic diversity of these corals. *Pocillopora damicornis* is distributed throughout the tropical Pacific and Indic oceans and there is relatively good indication that distant populations may be episodically connected (e.g., during El Niño events) (Glynn & Ault 2000). However, populations from the East Pacific are spawners whereas those from the West Pacific are brooders (Glynn & Ault 2000), suggesting that connectivity between distant populations could be limited and might already have led to cryptic allopatric speciation. Ayre & Hughes (2004) revealed gene flow over large distances for *P. damicornis* and other corals along the Great Barrier Reef, but they did not specify whether dispersal might be achieved via larvae or via rafting. They did, however, emphasise that genetic exchange between distant populations is a highly episodic event: "Long-distance dispersal by corals to geographically isolated reefs cannot be achieved incrementally and is likely to be very rare" (Ayre & Hughes 2004). Interestingly, for this region, several reports of pumice-rafted

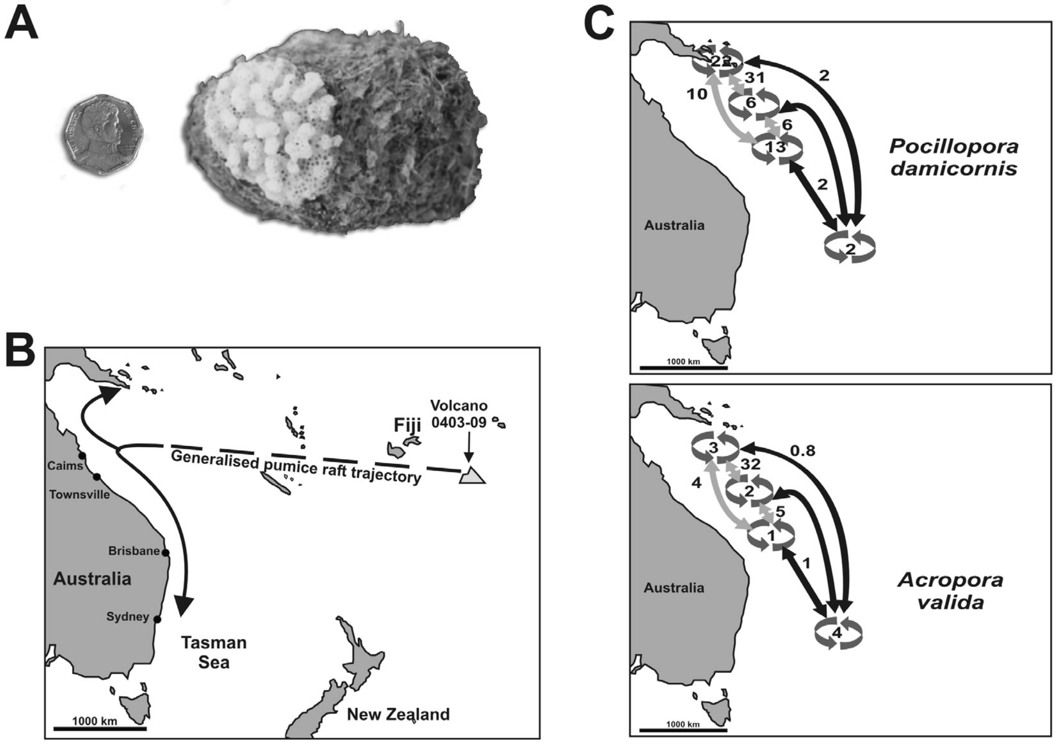

Figure 20 (A) A small colony of the coral *Pocillopora damicornis*, growing on an algae-covered piece of volcanic pumice (photo courtesy of Scott Bryan, Yale University, U.S.) (diameter of coin is 16 mm), and (B) map of the SW Pacific indicating the inferred rafting routes of floating pumice originating from an eruption in the Tonga-Kermadec arc; modified after Bryan et al. (2004). (C) Estimates of gene flow (Nm) for two coral species from the Great Barrier Reef, one of which (*P. damicornis*) is very commonly reported as a rafter on volcanic pumice; modified after Ayre & Hughes (2004).

corals (including *P. damicornis*, *Seriatopora* sp. and *Styllophora* sp.) have been published (Jokiel 1990b, Bryan et al. 2004), suggesting that gene flow could indeed be achieved via rafting of adult colonies (Figure 20). Even though Ayre & Hughes (2004) do not discuss rafting, their results of gene flow on different spatial scales closely matches the predictions for processes on episodic rafting routes made above: “While long-distance gene flow over multiple generations is sufficient to limit genetic differentiation along the length of the Great Barrier Reef, most recruitment by corals on ecological time frames is decidedly local”. Results from a study by Wörheide et al. 2002 reported similar scales of connectivity for the tropical sponge *Leucetta ‘chagosensis’* (Figure 21). They suggested that “small-distance dispersal was involved in the range expansion of clade 3–1, whereas some long-distance movements may be inferred for clade 3–4”, but they did not mention how LDD was achieved (possibly via pumice?).

Little is known about dispersal and population connectivity via floating pumice for other organisms. This probably is due to the fact, that dispersal events are rare and that many other organisms (e.g., algae or bivalves) may quickly fall off pumice pieces after stranding (Jokiel 1990a). Ó Foighil et al. (1999) reported the presence of *Ostrea chilensis* in New Zealand and in Chile separated by >5000 km of open ocean (Figure 21). Since this species features direct development,

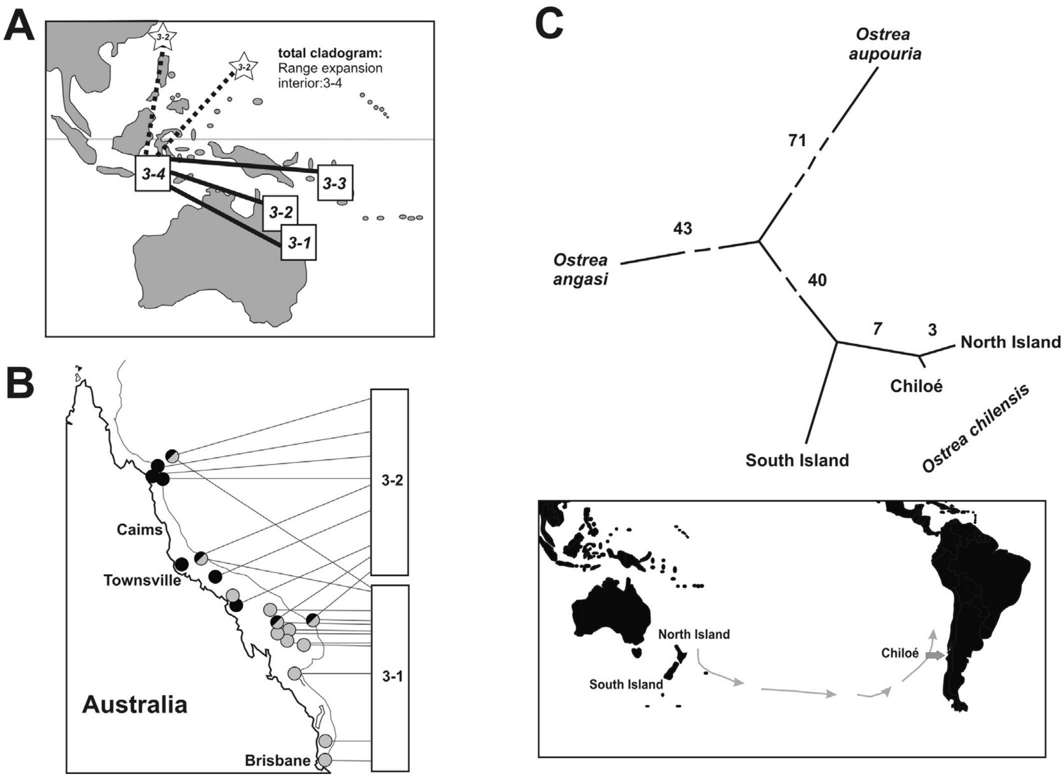

Figure 21 (A) Distribution of the principal clades revealed for the tropical sponge *Leucetta 'chagosensis'* throughout its distribution range in the Indo-Pacific, and (B) distribution of the two clades found on the Great Barrier Reef; modified after Wörheide et al. (2002). (C) Unrooted phylogram based on mtDNA Cytochrome Oxidase I sequences depicting relationships between three populations of *Ostrea chilensis* (two from New Zealand and one from Chile) and two other species of the genus, and map of the Southern Ocean indicating the current direction of the West Wind Drift; modified after Ó Foighil et al. (1999).

these authors suggested that the trans-Pacific distribution pattern of *O. chilensis* may be the result of pumice-rafting. Empirical evidence for this transport mechanism and for continuing gene flow between New Zealand and Chilean populations, however, is not available at present.

Terrestrial debris (after flood events, cyclones or tsunamis) Supply frequencies of terrestrial debris are similar to that of volcanic pumice. However, terrestrial debris supplied during episodic events comprises a heterogeneous assemblage of different substrata, from fragments of annual plants to entire trees. While it is well known that large amounts of floating substrata are travelling in adjacent seas after these events, little is known about the quantities and temporal dynamics. Tropical cyclones occur every year in the western parts of the central Pacific and the central Atlantic, but storm tracks vary substantially among years. A synthesis of the data provided by Landsea et al. (1996) shows that the hitpoints of hurricanes (where hurricane tracks and shorelines cross) vary substantially between years (Figure 22). Consequently, dispersal export from particular localities (e.g., islands) via terrestrial debris will occur only episodically. Storm and rain events were identified as main causes for interannual variation in abundance of floating terrestrial debris (Heatwole & Levins 1972, Zarate-Villafranco & Ortega-García 2000).

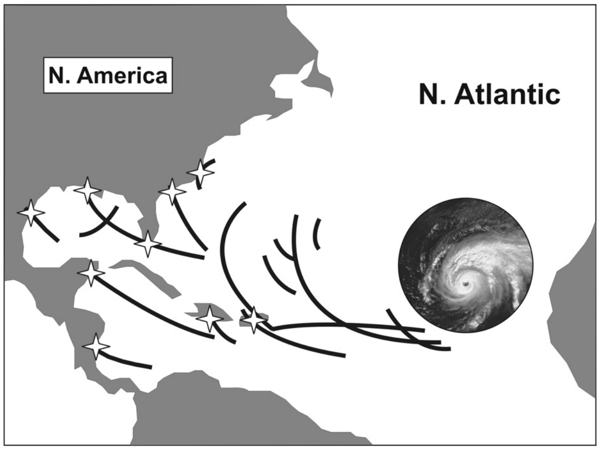

Figure 22 Tracks of intense hurricanes in the W Atlantic over the eight-year period 1987–1995, showing that annual sites of hurricane landfall (star symbols) (and subsequent production of sporadic rafting opportunities) are spread throughout the region; modified after Landsea et al. (1996).

The importance of hurricane and storm events for episodic appearance of rafting opportunities is well known. For example, Simberloff & Wilson (1969), who studied the colonisation patterns on small mangrove islands in Florida Bay, noted that rafting dispersal may usually be of minor importance, because "except during hurricanes, there is very little floating debris". In general, these events appear to have particular importance in the tropics where flood events, cyclones and tsunamis are most effective in transporting terrestrial debris to the sea. In the case of cyclone-related supply this is explainable by the fact that these phenomena occur mainly in the tropics. In the case of flood events and tsunamis these may achieve particular significance in the tropics due to the concentration of (a) many large and unregulated rivers in these areas, and (b) low-lying coral islands with little protection against tsunami or cyclone waves.

Organisms found on this debris include terrestrial species such as insects and reptiles (Wheeler 1916, Heatwole & Levins 1972, Censky et al. 1998), but also marine organisms. Due to the singularity of events, little is known about connectivity between local populations via rafting on terrestrial debris. The strongest indication that terrestrial debris (in particular trees) may aid in transport of organisms comes from terrestrial vertebrates (reptiles). Supporting evidence comes from observations of individuals on rafts and from phylogeographic studies. Disembarkation of reptiles from rafts of terrestrial debris has been observed by Barbour (1916) and Censky et al. (1998). Several phylogeographic studies suggest over-water dispersal of terrestrial vertebrates, and in many of these cases, authors suggested rafting on terrestrial debris (Raxworthy et al. 2002, Calsbeek & Smith 2003, Carranza & Arnold 2003, Glor et al. 2005) (Figure 23). Yoder et al. (2003) suggested that Carnivora on Madagascar originated from one single dispersal event (Figure 23). They also emphasised that those groups that colonised feature ecophysiological specialisations that may have allowed relatively long trips in an unhospitable environment (e.g., a raft in the open ocean).

Clearly, evidence for rafting dispersal via terrestrial debris supplied by episodic events is circumstantial. However, independent molecular studies provide increasing indication that this process may occasionally have led to successful colonisation and that it may be of major importance for the biodiversity of remote locations.

Giant kelp and other substrata Due to the sporadic character of dispersal events and the fact that they may have happened far back in the past, often it is difficult or impossible to know the floating

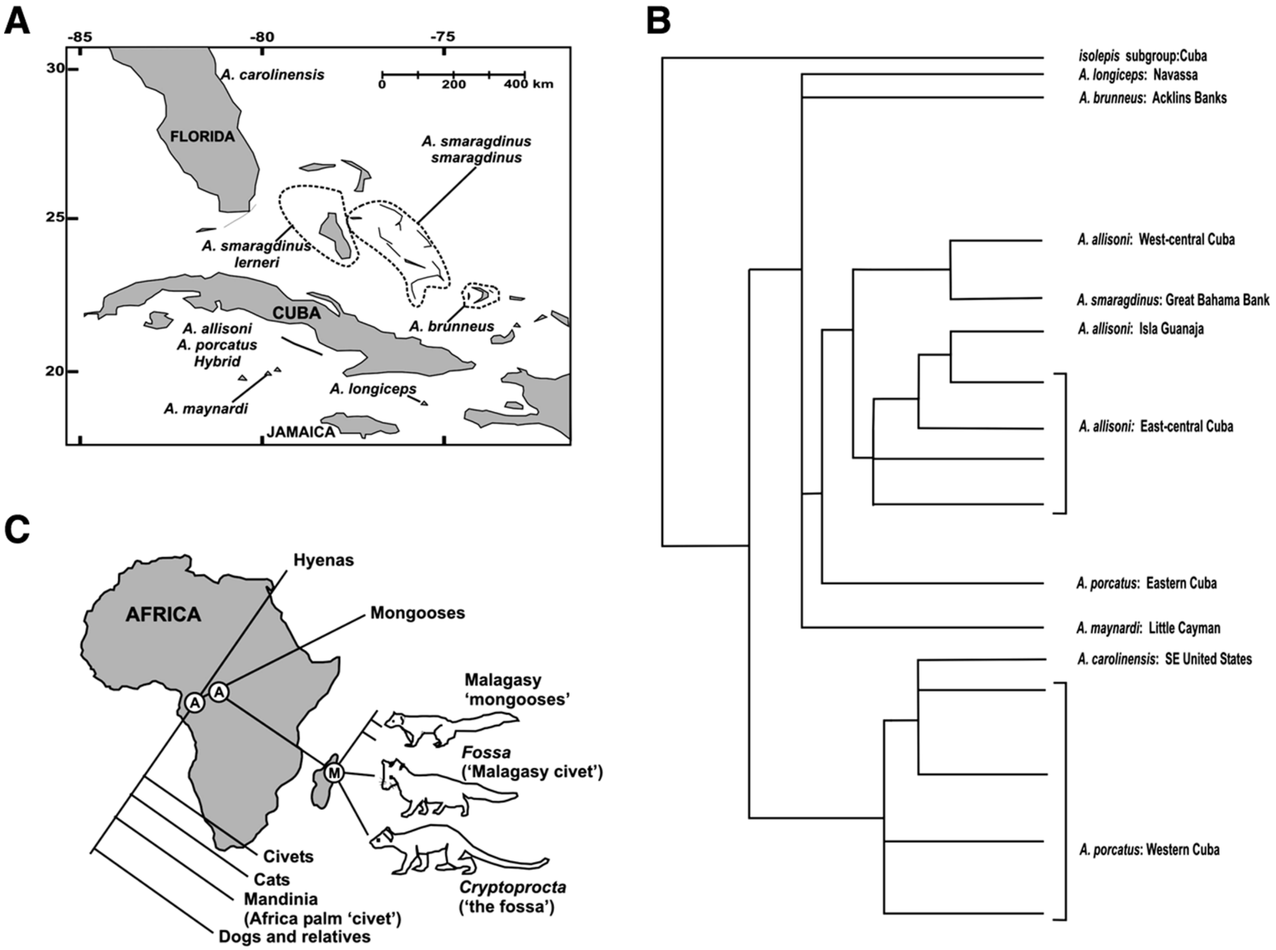

Figure 23 (A) Sampling sites of *Anolis* lizards from Caribbean islands, and (B) cladogram showing the phylogenetic relationships inferred from mtDNA data of the different *Anolis* species from the Caribbean islands; modified after Glor et al. (2005). (C) Proposed biogeography of carnivores from Africa and Madagascar; genetic data suggest that taxa found on Madagascar have originated from a single dispersal event from an African predecessor; modified after Yoder et al. (2003).

substratum on which organisms have been dispersed. Some authors have used life history of present day organisms to infer potential substrata, while others have simply suggested rafting without venturing into the characteristics of rafts.

Some substrata that usually travel on intermittent rafting routes (giant kelp and wood) may also sporadically be transported over distances more characteristic of episodic rafting routes. This may occur when storms or other climatic events push these substrata out of their common routes or accelerate transport velocities. During these occasions, substrata may become transported to localities that they would not normally reach. For example, giant kelp, thought to survive for several months at the sea surface, may not be capable of bridging the enormous distances of open ocean between South Africa and Australia or between New Zealand and South America. There is, however, both distributional and genetic evidence for occasional connections via floating substrata. Many coastal species are found on distant subantarctic islands and rafting on floating kelp is commonly inferred (Davenport & Stevenson 1998, Edgar & Burton 2000).

A study by Waters & Roy (2004a) indicated that colonisation of Australia by the seastar *Patiriella exigua* resulted from a singular dispersal event from African source populations (Figure 24). This seastar also is found in the holdfasts of giant kelp, and Mortensen (1933) had suggested that dispersal of this species may occur via floating kelp. Based on phylogeographic relationships of topshell gastropods with short-lived larvae, Donald et al. (2005) suggested that repeated LDD events via rafting had occurred during the evolutionary history of these species. In the case of the species *Diloma nigerrima* a dispersal event between New Zealand and Chile was dated to have happened approximately 0.6 Mya, apparently too short for significant genetic divergence to take place (Figure 25).

Episodic dispersal on large floating macroalgae may also play a role in the northern North Atlantic. Based on historical analyses and on the present-day distribution of important rocky-shore

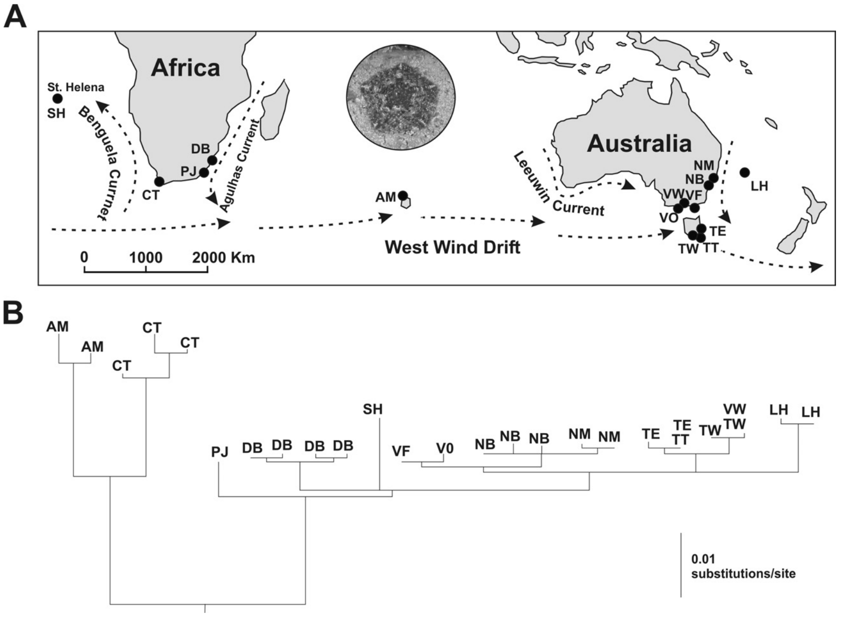

Figure 24 Episodic rafting route in the West Wind Drift between Africa and Australia, possibly supported via floating giant kelp. (A) Sampling sites of different populations of *Patiriella exigua*; insert shows the seastar *Patiriella exigua* (which reproduces via benthic crawl-away larvae) from S Africa (photo courtesy of Eliecer Diaz, Rhodes University, S Africa). (B) Phylogram based on mtDNA Cytochrome Oxidase I (CO I) sequences; modified after Waters & Roy (2004a).

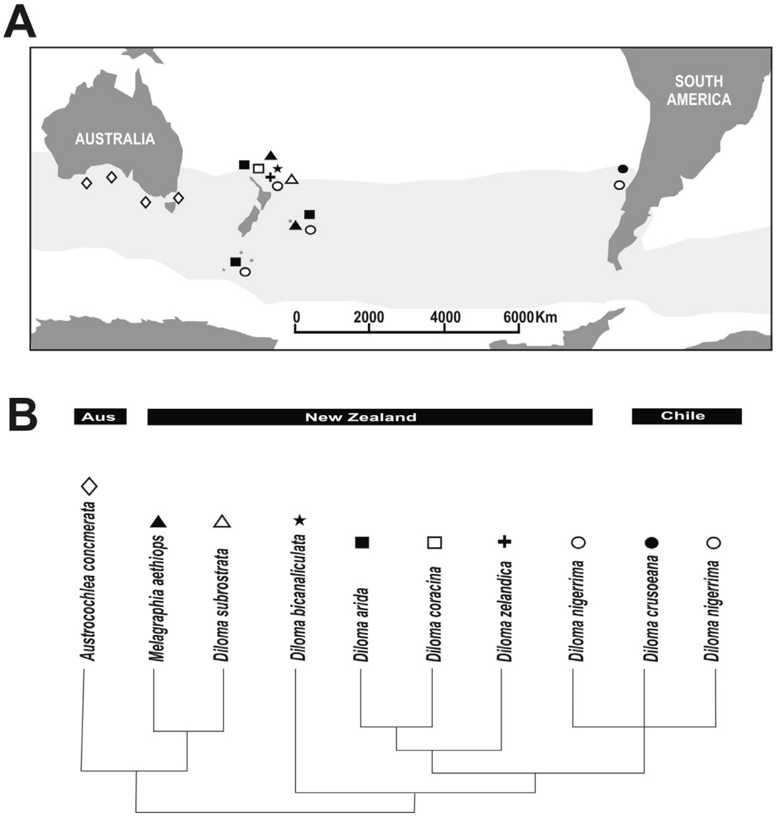

Figure 25 Episodic rafting route in the West Wind Drift between New Zealand and S America, possibly supported via floating bullkelp *Durvillaea antarctica*. (A) Sampling sites of different gastropod species from the family Trochidae; geographic distribution of bullkelp *D. antarctica* indicated by light shading. (B) Phylogenetic tree based on mtDNA 16S, COI and nuclear DNA actin sequences for selected species from the S Pacific; modified after Donald et al. (2005).

organisms, Ingólfsson (1992) inferred a rafting route between northern Norway and Newfoundland and Nova Scotia on the western side of the North Atlantic, with Iceland and southern Greenland serving as intermediate stepping stones. Wares & Cunningham (2001) supported this suggestion via genetic studies. For example, they found genetic connectivity between North American and European populations of *Idotea baltica* (Figure 26), a species commonly found on floating algae (Ingólfsson 1995, Gutow & Franke 2003). They also revealed that the North American populations of *Nucella lapillus* and *Littorina obtusata*, with benthic crawling progeny, had originated from European populations (Wares & Cunningham 2001). In all cases rafting transport on floating algae appears to be the most likely dispersal mechanism. Ó Foighil & Jozefowicz (1999) reported phylogenetic relationships between clades of *Lasaea* from Florida and Bermuda on the western side of the North Atlantic and between clades from the Azores and the Iberian peninsula on the eastern side of the North Atlantic, which was confirmed in a later more extensive study (Ó Foighil et al. 2001) (Figure 27). They suggested rafting but did not mention the substrata on which these bivalves may have been transported. Regardless of whether dispersal has occurred on floating kelp, wood or other substrata, most of these studies underline the importance of episodic rafting events and subsequent periods of isolation.

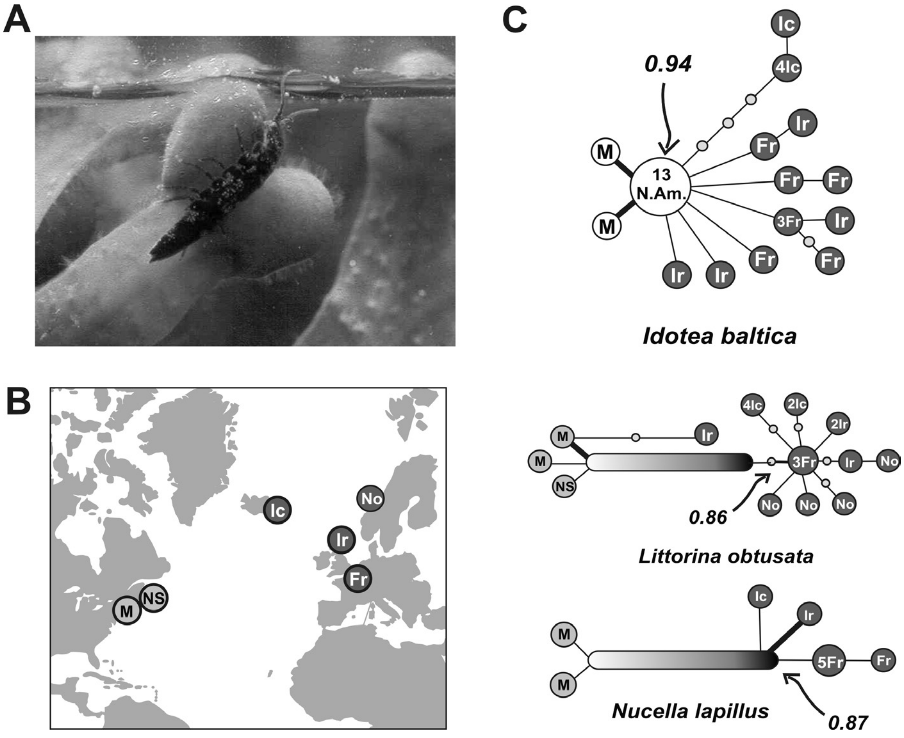

Figure 26 (A) The isopod *Idotea baltica*, which releases fully developed juveniles, on fucoid algae (photo courtesy of Veijo Jormalainen, University of Turku, Finland). (B) Map of the N Atlantic with sampling sites: M – Maine, NS – Nova Scotia, Ic – Iceland, No – Norway, Ir – Ireland, Fr – France. (C) Haplotype networks (based on mtDNA COI sequences) for populations of *Idotea baltica* (direct development), *Nucella lapillus* and *Littorina obtusata* (crawl-away progeny) from the N Atlantic; modified after Wares & Cunningham (2001).

Dispersal dynamics on episodic rafting routes

Based on the examples presented, it appears that episodic rafting routes are most important in the tropics and in subpolar regions (Figure 17). While in the tropics these rafting routes are constituted by episodic supply of floating substrata (pumice and terrestrial debris), in subpolar regions they may represent episodic extensions of intermittent rafting routes (supported by giant kelps and wood).

Interestingly, the three main substrata mentioned herein (pumice, terrestrial debris, giant kelps) appear to transport different groups or organisms. Volcanic pumice and calcareous animal skeletons are usually only colonised after starting their pelagic voyage (i.e., by marine organisms that have (short-lived) planktonic larvae). Also terrestrial debris is colonised by marine organisms while afloat, but trees or other terrestrial vegetation may additionally carry many initial terrestrial colonists such as insects, spiders or vertebrates with them to sea. In contrast, large kelps, which are colonised while growing in benthic habitats, appear to have been mainly responsible for dispersal of various marine organisms with direct development. These observations underline the importance of substratum origin and characteristics, in particular for rafting over long distances.

Many authors discussed the relationship between connectivity and the possibility of population divergence. For example, Ayre & Hughes (2004) remarked on low levels of gene flow between distant local populations of corals, just sufficient to counteract genetic divergence (see above). In this context, Bryan et al. (2004) suggested pumice rafting as an important connecting process: "Speciation events and volcanicity may be linked such that the periodic development of globalism

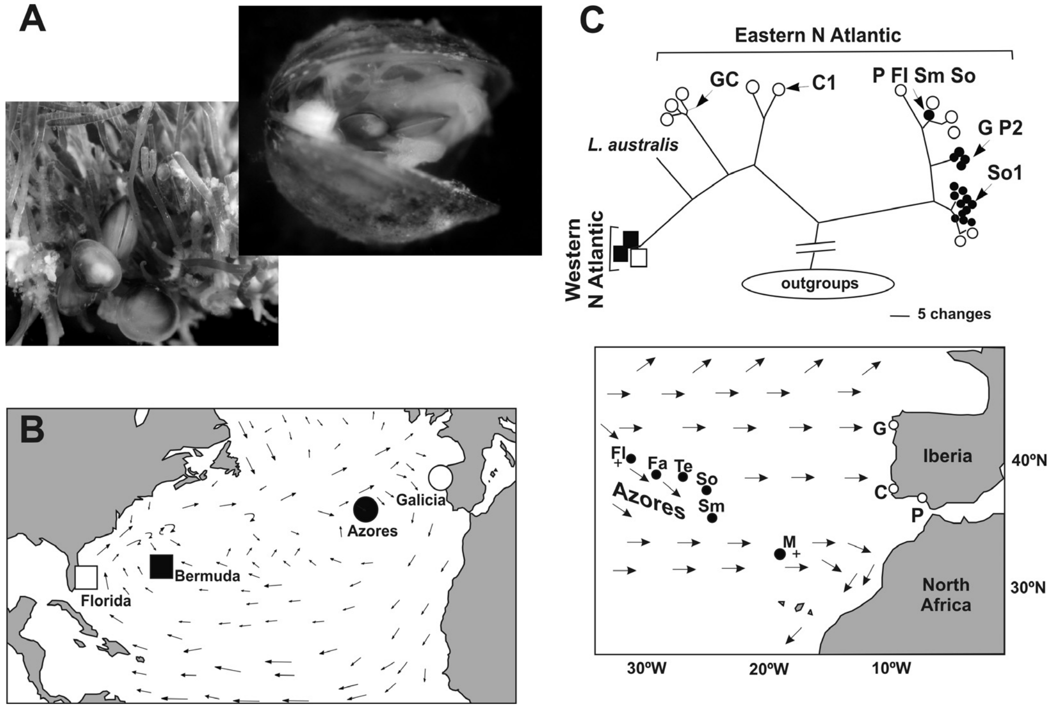

Figure 27 (A) Nest of an unidentified *Lasaea* species from Chile, and adult brooding juveniles. (B) Study regions of populations of *Lasaea* spp. in the western and eastern N Atlantic; map modified after Ó Foighil & Jozefowicz (1999). (C) The unrooted phylogram (based on mtDNA 16S sequences) showing the genetic relationships of the N Atlantic clades of *Lasaea*, which suggests a western and an eastern clade in the N Atlantic. Six different dispersal events were inferred between the Azores and the Iberian Peninsula (for sampling sites of eastern N Atlantic populations see detailed map); modified after Ó Foighil et al. (2001).

for some taxa (e.g., corals, gastropods, bryozoans) may correlate in time and/or space with particular igneous events". If gene flow is insufficient, speciation processes may occur: "Species that have a capacity for sporadic dispersal may undergo dramatic range expansions followed by isolation, genetic divergence, and possible speciation" (Waters & Roy 2004a). Other authors reached similar conclusions: "…The foregoing leads to the expectation that endemism through founder speciation is most likely for organisms that rarely enter the transport medium but survive well in it" (Paulay & Meyer 2002). These authors went on to say: "Organisms that rarely enter the dispersal medium but survive well there are the most likely to undergo founder speciation. The high levels of endemicity observed in rafted, direct developing marine mollusks, and bird- and raft-dispersed terrestrial organisms support this hypothesis". Additionally, many rafting species that survive LDD via rafting are also pre-adapted to become successful colonisers after making landfall (see Thiel & Gutow 2005b). Occasionally, rafting organisms on episodic rafting routes may even cross biogeographic borders or barriers: "The several months of transportation time provides the opportunity for biogeographic exchange, and it may be a mechanism by which biogeographic mixing in the marine realm occurs naturally" (Bryan et al. 2004). If this is followed by successful colonisation, it will lead to an enrichment of the local biota, thereby increasing local biodiversity.

In general, connectivity between populations is very low on episodic rafting routes. This may, in extreme cases, lead to singular colonisation by few individuals, resulting in a founder effect. This may facilitate allopatric speciation, in particular in sexually reproducing organisms with short generation times. Furthermore, since episodic rafting routes often are supported by floating substrata of high longevity (volcanic pumice, calcareous skeletons, large trees), they may often result in LDD, transporting rafters to new habitats. Here these organisms may be confronted with established communities and conditions, exposing colonists to a selective environment different from their source regions. Thus, for several reasons dispersal via episodic rafting routes may result in rapid evolutionary changes in rafting organisms. Interrupting the sporadic pattern of these episodic rafting events may have important consequences for biodiversity.

Artificial rafting routes

In this review artificial rafting routes are considered to be those sustained by floating substrata of anthropogenic origin, in particular plastics. These have gained increasing attention in recent years (Winston 1982, Barnes 2002), because supply has increased during the past century, and plastics are now present throughout the world oceans. For two main reasons, plastics do not fit the natural rafting routes discussed above: (a) they are delivered to the oceans almost anywhere, in estuaries, bays and in the open ocean, albeit with regional differences in intensity and (b) some of them are extremely long-lived and can therefore be transported over very long distances. They share some features with substrata found on frequent rafting routes (abundant supply), but they differ in other features (plastics offer no food value and are highly persistent). Similarly, some of their characteristics resemble those of substrata on episodic rafting routes (low food value and high longevity), but other characteristics are very different (plastics are supplied relatively consistently).

Plastics are present on all previously described natural rafting routes, but they may gain particular importance on the intermittent and in particular on the episodic rafting routes. As outlined above, organisms on frequent rafting routes have abundant dispersal opportunities on natural floating substrata, because these are usually available in large quantities. Some of these organisms may also hitch a ride on floating plastics, but given the high connectivity between local populations already achieved via natural substrata, this may be relatively unimportant. In contrast, on intermittent and episodic rafting routes, plastics (and other anthropogenic debris) may lead to a dramatic increase in dispersal opportunities and due to their continuous supply may disrupt the sporadic character of natural dispersal events. Previous authors have suggested that episodic rafting routes, for example those sustained by volcanic pumice, may permit "periodic globalism" of some organisms (sensu Bryan et al. 2004). Chronic supply of plastics may enhance the risk of globalisation of these species and homogenisation of the species biodiversity, in particular in regions where episodic rafting events have predominated in the past, for example in the Southern Ocean (Barnes & Fraser 2003).

Rafting organisms found on plastics are diverse and they include, among others, sponges, hydrozoans, bryozoans, ascidians, polychaetes, bivalves and crustaceans (Thiel & Gutow 2005b). Interestingly, corals have also been found on floating plastics or glass, including species from the genus *Pocillopora*, commonly reported from floating pumice (Jokiel 1984, 1989; Winston et al. 1997). This indeed indicates that plastics may serve as alternative rafting substratum for the same organisms usually transported by pumice or other sporadically supplied substrata.

Floating plastics are occasionally suggested as dispersal agents connecting localities. For example, Aliani & Molcard (2003) discussed that many organisms found on floating plastics in the western Mediterranean can become widely dispersed along shorelines of this region. Winston et al. (1997) expressed similar concerns for the western South Pacific. Stevens et al. (1996) found many bryozoan species, which are usually growing on natural buoyant substrata, also on floating plastics — some rafting colonies were even sexually mature, leading the authors to infer that these species "could adapt to a pseudoplanktonic lifestyle". Such an adaptation would then facilitate LDD. Due to their relatively recent appearance in the world oceans, no molecular study has yet identified floating plastics as potential dispersal vectors. However, given the ubiquity of plastics and other anthropogenic floating substrata and their diverse assemblage of rafters, it is considered highly likely that these may serve as connecting agents.

Rafting dispersal

Marine connectivity

Marine benthic invertebrates inhabit patchy environments. As described above, patches harbour local populations that may be connected by dispersal, either through larvae, rafting or other mechanisms. Connectivity among local populations of rafters will largely depend on the environmental conditions of the place they inhabit. The genetic structure of local populations is determined in part by the direction, magnitude, and frequency of dispersal among local populations. Just as it has been widely demonstrated for species with planktonic developmental stages (Palumbi 1995, Bohonak 1999), oceanographic, ecological, behavioural and historic factors may limit rafting dispersal as well. All of these factors determine the relationships between local populations and the magnitude of the effects of deterministic and random evolutionary forces (i.e., natural selection and genetic drift, respectively). Since there are several factors that, in combination, affect the dispersal potential of a species and it cannot be inferred from a single element (i.e., mode of development, Colson & Hughes 2004), estimates of gene flow have been used to understand the factors that shape connectivity among local populations. Gene flow can be indirectly estimated from population differentiation data, and represents a measure of realised dispersal potential. Gene flow estimates for a number of benthic marine invertebrates have indicated that both organisms with planktonic and direct development can achieve LDD. Larval dispersal is assumed to be the major means of dispersal for organisms with planktonic development, while rafting is considered to promote the dispersal of organisms with direct development (e.g., Johannesson 1988, Ó Foighil 1989, Davenport & Stevenson 1998). Organisms with planktonic development, too, may be dispersed through rafting, which is, however, hard to demonstrate since rafting is an explanation that often is supported indirectly by the rejection of alternative hypotheses, such as vicariance, anthropogenic and larval dispersal (e.g., Castilla & Guiñez 2000, Waters & Roy 2004a, Donald et al. 2005). Several studies stress the importance of considering the biology of a species beyond its developmental mode in order to predict its dispersal potential (e.g., Colson & Hughes 2004). While species with planktonic larvae may disperse over much shorter distances than expected from their larval lifetime, those with direct development may be transported distances far exceeding what would be expected based on their autonomous dispersal potential. Evidence is mounting that rafting can have a strong impact on the genetic structure and geographic range of distribution of some species, particularly of those with direct development. It thus may be timely not only to abolish the Rockall Paradox but also to go a step further and consider rafting as an important mechanism for the connectivity of marine communities.

Use of genetic data to estimate gene flow

Molecular genetic tools allow for studying the allele frequencies of populations and inferring their demographic history. There is a diversity of molecular markers, among which proteins, mitochondrial DNA (mtDNA), microsatellites and fingerprinting methods (e.g., RFLP, RAPDS) are preferred for studies on the population level (Parker et al. 1998, Sunnucks 2000, Hellberg et al. 2002, Féral et al. 2003). MtDNA has been extensively used to reveal phylogeographic patterns and population structure of a wide diversity of marine taxa (e.g., Palumbi et al. 1997, Avise 2000, Wilke & Davis 2000, Collin 2001, Breton et al. 2003, Waters & Roy 2004b). Microsatellites, proteins, and fingerprinting methods have been widely used to infer population structure often at more than one geographic scale (e.g., Edmands & Potts 1997; Ayre & Hughes 2000, 2004; Goldson et al. 2001; Colson & Hughes 2004). Many of these studies include estimates of population differentiation that also allow for estimating gene flow as the number of migrants per generation among local populations (e.g., Ayre et al. 1997, Ayre & Hughes 2000, De Matthaeis et al. 2000, Vianna et al. 2003).

The genetic structure of a metapopulation depends on local dispersal dynamics influenced by both the migration rate (m) and the effective population size (N) of the metapopulation (Hellberg et al. 2002). A commonly reported measure of population differentiation is the fixation index, F_{ST}, developed by Wright (1931, 1965) that refers specifically to the differentiation among subpopulations (S) of the total population (T) and allows for the estimation of Nm (the product of effective population size and migration rate). Nm is interpreted as the number of migrants per generation, and can be calculated from F_{ST}-values by the following relationship: $F_{ST} = 1/(1 + 4\text{Nm})$ (Wright 1969). Generally, F_{ST}-values smaller than 0.2 (Nm = 1) represent less than one individual migrant per generation, which is considered insufficient to prevent population differentiation. Values of Nm greater than 1, corresponding to slightly higher levels of gene flow, are high enough to prevent differential fixation of alleles in different subpopulations (Wright 1969). Since many studies have reported F_{ST} values at a wide variety of spatial scales, it is used in the present analysis as a measure for comparison of genetic differentiation data from the literature. F_{ST} is a powerful tool to estimate genetic differentiation among populations. Populations at or close to equilibrium conditions will behave somewhat like the model underlying the F_{ST} coefficient and thus its value will be biologically meaningful. Caution needs to be used, though, because F_{ST} values could be misleading and in particular for populations, which commonly deviate from equilibrium assumptions underlying the mathematical model that F_{ST} is based on (see Grosberg & Cunningham 2001). Whitlock & McCauley (1999) address the general limitations of the model and its unrealistic biological assumptions that may affect the meaningfulness of the numerical value. Based on their analysis, they suggest that "comparisons of large groups of species are likely to be more informative, as many of the differences may average out" (see also Neigel 1997, 2002). In the present review, such an analysis is undertaken, and genetic structure data are compiled and analysed for a large group of marine invertebrates. F_{ST} approaches have revealed patterns of genetic structure over a wide range of biological scenarios and have indicated that the genetic structure of populations is shaped by several factors, including gene flow barriers that are thought to be due to environmental factors (see below). Data should be carefully interpreted; in some cases genetic differentiation of populations may be reflecting historic rather than ongoing events. For example, gastropod species of the genus *Nucella* with similar dispersal potentials (they lay egg capsules from which juveniles emerge) display extremely different patterns of population structure across the same geographic range (Marko 2004). Usually these differences have been attributed to dispersal potential, but in this case, the species have similar dispersal potentials based on their developmental mode. The results of that study address the importance of ecological and historical differences for the genetic structure of populations. F_{ST} cannot detect gene flow asymmetry as it only shows a measure of total differentiation among populations without considering independently the contribution of each of the compared populations to the differentiation among them. Measures of asymmetric gene flow are particularly desirable in the context of rafting, and can be predicted by some alternative means, although these are scarce in the literature. An example is given by Wares et al. (2001) who used a cladistic analysis to detect asymmetrical migrations. They studied genetic differentiation of two barnacle species and a sea urchin across Point Conception in California, which had been suggested as a strong barrier to gene flow. The cladistic approach allowed them to determine that there was an excess of southward migration events across Point Conception. In the context of rafting it is desirable to have estimates of magnitude and direction of dispersal among local populations of potential rafters to better understand the dynamics of rafting routes. In cases of unique rafting events that lead to allopatric speciation (on episodic routes), the direction of the dispersal route can be detected with phylogenetic analyses. Intermittent and frequent rafting routes, however, prevent speciation by maintaining sufficient connectivity among local populations. In these cases, the genetic structure of populations will depend on the magnitude and direction of migration, even though asymmetrical gene flow is not often detected, total gene flow estimates (Nm) can be inferred (from F_{ST} values) and are likely to reflect the summed contributions of populations or groups of populations to the total exchange among them. There exists a variety of other measures of population differentiation that alleviate many of the problems associated with F_{ST}, but most are scarcely reported in marine population genetic studies and thus are not useful for comparison of a large number of studies. The numerous reports of F_{ST}-like values allow estimation of realised dispersal of many marine taxa (Neigel 1997, Bohonak 1999) and will be used herein to make broad comparisons of the dispersal potential of benthic marine invertebrate taxa.

Genetic homogeneity vs. genetic structure of populations

Even though marine environments seem to lack apparent barriers to gene flow, populations only sometimes show panmixia and genetic differentiation exists even when wide dispersal is predicted based on larval developmental mode. Marine populations usually show reduced heterozygosity (e.g., Ayre & Hughes 2000), explained largely by the restricted dispersal of marine organisms and consequent effects of inbreeding and local population differentiation, which can generate a Wahlund effect (i.e., decreased heterozygosities resulting from the sampling of subdivided populations) (e.g., Johnson & Black 1984a). Planktonically developing taxa intrinsically provide good models to study the potentially restricting effects of the environment on gene flow. Several factors such as oceanographic conditions, physical barriers, life-history features, historic demography and ecological or behavioural barriers can hinder the realised dispersal of marine taxa (Hedgecock 1986, Palumbi 1994). The same barriers that have been described for species with planktonic dispersal should apply to dispersal through rafting, too.

Many studies have detected limited gene flow in species that presumably have a high potential for dispersal. There are many factors that can act as gene flow barriers and that promote geographic differentiation. Gene flow barriers can be inferred from genetic structure and population differentiation data. For example, Sköld et al. (2003) found that genetic differentiation of populations of the widely dispersing seastar *Coscinasterias muricata* in the New Zealand fjords is not correlated with geographic distance. They suggested that recent colonisation and isolation from open coasts explain the apparent island model of the population. Perrin et al. (2004) also studied population differentiation of this species along the New Zealand fjords and found that at a macrogeographical scale (>1000 km) there was restricted gene flow between the North and South Island. At a mesogeographical scale (tens to hundreds of km) there was significant population differentiation among fjords and the open coast. The pattern among fjords suggests that populations from the north and the south meet in what appears to be a secondary contact zone. For this species, distance alone does not explain population differentiation and it is likely that hydrography prevents mixing of propagules and contributes to isolation of local populations. Local populations seem to have expanded recently and subsequently differentiated as a consequence of isolation. Perrin et al. (2004) suggest that once the larvae of *C. muricata* "are transported out of the fjord, the likelihood of entering another fjord is less than being transported further along the open coast. For this species, the fjords might act as barriers to dispersal of differing strength, facilitating genetic drift within fjord populations." Along the New Zealand coast, Waters & Roy (2004b) found that upwelling in the central regions blocks gene flow and leads to genetic differentiation between the populations of the seastar *Patiriella regularis* from the north and south that are subject to different oceanographic conditions. Just as upwelling can transport propagules away from coastal systems, it may bring propagules toward the coast when it reverses its direction (Palumbi 2003). It is likely that if an upwelling zone poses a barrier to gene flow in species with planktonic development, it will also affect the connectivity of populations of rafters.

Habitat structure may highly influence population structure, sometimes because different habitats may differ in the rafting opportunities they offer (see above). Johannesson & Tatarenkov (1997) found that the population structure of the brooding gastropod *Littorina saxatilis* on islands of the Swedish coast was highly related to habitat structure. Similarly, Johannesson et al. (2004) reported that genetic structure among *L. saxatilis* on high rocky shores was different from the ones on low rocky shores. Populations on high rocky shores appear to be more isolated which, as stated by the authors, "might be true if the main mechanism of dispersal among islands is by rafting".

Some studies show the prevailing pattern, namely that populations of organisms with extensive planktonic larval stages are not genetically subdivided. For example, the marine bryozoan *Membranipora membranacea* does not show genetic differentiation among populations across the Atlantic Ocean, even though there is morphological variation caused by phenotypic plasticity (Schwaninger 1999). Surprisingly, this species seems to maintain gene flow over long geographic stretches, which could be due to rafting (it has been reported on floating substrata, see Aliani & Molcard 2003) or other mechanisms (e.g., human transport). Conversely, other studies have shown that species with direct development tend to be highly structured due to restricted gene flow (e.g., Hellberg 1994, Ayre et al. 1997, McFadden 1997). This seems to be the case in the gorgonian coral *Pseudopterogorgia elisabethae,* which has restricted dispersal potential (larvae live less than two days) and shows high genetic differentiation among populations following an IBD pattern (Gutiérrez-Rodríguez & Lasker 2004). Contrary to expectations based on developmental mode alone, there are examples of directly developing species that show that LDD has taken place or that there is little differentiation among populations. For example, the direct developers *Littorina sitkana* and *Nucella lapillus* display high levels of gene flow over relatively wide geographic scales (>1500 km) (Kyle & Boulding 2000, Colson & Hughes 2004) (Figure 16). Based on the above, it becomes evident that connectivity cannot be predicted solely on the basis of mode of development (see also Ó Foighil et al. 1999, Colson & Hughes 2004).

Rafting-mediated gene flow

In the past, dispersal rates have been frequently inferred based on presence/absence and duration of a planktonic dispersal stage. However, there are many examples of organisms with planktonic development that, based on population differentiation, have restricted dispersal among local populations (e.g., Barber et al. 2000, McCartney et al. 2000). On the other end of the scale, species that lack a planktonic dispersal stage may disperse long distances by alternative means such as rafting. Comparisons of gene flow estimates from a wide variety of benthic marine taxa clearly show that populations of organisms with contrasting modes of dispersal can achieve comparable levels of gene flow and that rafting is a significant means of dispersal at more than one spatial scale, particularly for species with direct development (see below).

Rafting has been inferred for 33 out of 124 marine invertebrate species for which genetic differentiation data are available (Table 1). In many of the studies, rafting was inferred because realised gene flow strongly exceeded the expectations based on life history characteristics (i.e., absence of a planktonic larval stage), or because of the absence of IBD in brooders suggested the existence of LDD. For 113 of the 124 reviewed species data were reported that allowed an examination of realised gene flow over variable spatial scales (from metres to global distribution) (Table 1). Only reports that include F_{ST}-like values have been incorporated in this analysis. From the F_{ST}-like values given, gene flow (Nm; number of migrants per generation) was estimated according to the equation of Wright (1969) (Table 1). Whenever possible, genetic differentiation data for more than one geographic scale were recorded for each species (see Table 1). Values of

Table 1 Genetic structure of populations of several marine invertebrate taxa reported in the literature

Species	Dev.	Genetic system	Geographic location	Spatial scale (km)	Genetic structure	Nm	IBD	Rafting inferred	Reference
Porifera									
Crambe crambe	L	Microsatellites	Mediterranean, Madeira and Canary Islands	3000	θ = 0.18	1.14	Yes	No	Duran et al. 2004a
		ncDNA		3000	% var = 9.78		Yes		Duran et al. 2004b
		mtDNA		3000	F_{ST} = 0.565	0.19	No		Duran et al. 2004c
Haliclona sp.	D	Allozymes	SW Australia	400	θ = 0.121	1.82	No data	No	Whalan et al. 2005
Hydrozoa									
Obelia geniculata	P	mtDNA	N Atlantic	5000	F_{ST} = 0.26	0.71	No data	Yes, on seaweeds	Govindarajan et al. 2005
Anthozoa									
Acropora cuneata	D	Allozymes	E Australia, GBR and Lord Howe Island	2400	θ = 0.29	0.61	Yes	No	Ayre & Hughes 2004
				1700	θ = 0.08	2.87	No		Ayre & Hughes 2004
				1200	θ = 0.05	4.75	No		Ayre & Hughes 2000
				8	θ = 0.15	1.42	No		Ayre & Hughes 2000
A. cytherea	P	Allozymes	E Australia, GBR	1200	θ = 0.03	8.08	No	No	Ayre & Hughes 2000
				8	θ = 0.08	2.89	No		Ayre & Hughes 2000
A. hyacinthus	P	Allozymes	E Australia, GBR	1200	θ = 0.05	4.75	No	No	Ayre & Hughes 2000
				8	θ = 0.07	3.32	No		Ayre & Hughes 2000
A. millepora	P	Allozymes	E Australia, GBR	1200	θ = 0.01	24.75	No	No	Ayre & Hughes 2000
				8	θ = 0.1	2.25	No		Ayre & Hughes 2000
A. nasuta	P	Microsatellites and ncDNA	NE Australia, GBR	500	F_{ST} = 0.034	7.1	No data	No	Mackenzie et al. 2004
				35	F_{ST} = 0.025	9.75			
A. palifera	D	Allozymes	E Australia, GBR	1200	θ = 0.02	12.25	No	No	Ayre & Hughes 2000
				8	θ = 0.09	2.53	No		Ayre & Hughes 2000
A. palmata	P	Microsatellites	Caribbean and Bahamas	>3000	θ = 0.036 R_{ST} = 0.153	6.69	No data	No	Baums et al. 2005
				1800	θ = 0.04 R_{ST} = 0.221	6			
				840	θ = 0.032 R_{ST} = 0.150	7.56			

A. valida	P	Allozymes	E Australia, GBR and Lord Howe Island	2500	θ = 0.21	0.94	Yes	No	Ayre & Hughes 2004
				1700	θ = 0.038	6.33	No		Ayre & Hughes 2004
				1200	θ = 0.02	12.25	No		Ayre & Hughes 2000
				8	θ = 0.28	0.64	No		Ayre & Hughes 2000
Actinia bermudensis	D	Allozymes	Bermuda and Brazil	4000	F_{ST} = 0.434	0.33	Yes	No	Vianna et al. 2003
				2000	F_{ST} = 0.21	0.94			Vianna et al. 2003
			Brazil	1150	F_{ST} = 0.262	2.33	Yes	No	Russo et al. 1994
A. tenebrosa	P	Allozymes	SE Australia	1050	F_{ST} = 0.375	0.42	No	No	Ayre et al. 1991
Alcyonium rudyi	D	Allozymes	NE Pacific	1100	θ = 0.3	0.58	No	No	McFadden 1997
				600	θ = 0.34	0.49			
				50	θ = 0.29	0.61			
Anthopleura elegantissima	P	Allozymes	NE Pacific	1800	θ = 0.14	1.54	No data	Yes, on eelgrass or algae	Edmands & Potts 1997
Anthothoe albocincta	P	Allozymes	SE Australia	930	θ = 0.29	0.61	No	No	Billingham & Ayre 1996
Balanophyllia elegans	D	Allozymes	California	3000	θ = 0.28	0.64	Yes	Yes, on macroalgae (Bushing 1994)	Hellberg 1994
				1000	θ = 0.22	0.87			Hellberg 1996
				100	θ = 0.195	1.03			
Bunodosoma caissarum	P	Allozymes	Brazil	1150	F_{ST} = 0.042	5.7	Yes	No	Russo et al. 1994
Clavularia koellikeri	D	Allozymes	NE Australia, GBR	1000	θ = 0.09	2.53	No	No	Bastidas et al. 2002
				30	θ = 0.134	1.62			
				4	θ = 0.189	1.07			
Epiactis lisbethae	D	Allozymes	NE Pacific	1800	θ = 0.36	0.44	No Info	Yes, on eelgrass or algae	Edmands & Potts 1997
E. prolifera	D	Allozymes	NE Pacific	1800	θ = 0.32	0.53	No Info	Yes, on eelgrass or algae	Edmands & Potts 1997
E. ritteri	D	Allozymes	NE Pacific	1800	θ = 0.16	1.31	No Info	Yes, on eelgrass or algae	Edmands & Potts 1997
Oulactis muscosa	P	Allozymes	SE Australia	735	F_{ST} = 0.0295	8.23	No data	No	Hunt & Ayre 1989
				0.024	F_{ST} = 0.0045	55.31	No data		
Paracyathus stearnsii	P	Allozymes	California	1000	θ = 0	very large	No	No	Hellberg 1996
				100	θ = 0.004	63.25			

Table 1 (continued) Genetic structure of populations of several marine invertebrate taxa reported in the literature

Species	Dev.	Genetic system	Geographic location	Spatial scale (km)	Genetic structure	Nm	IBD	Rafting inferred	Reference
Pocillopora damicornis	D	Allozymes	E Australia, GBR	2400	$\theta = 0.15$	1.42	Yes	Yes, on pumice (Jokiel & Cox 2003)	Ayre & Hughes 2004
				1200	$\theta = 0.01$	24.75 (31)	No		Ayre & Hughes 2000
				8	$\theta = 0.04$	6	No		Ayre & Hughes 2000
			SW Australia	400	$F_{ST} = 0.165$	1.27	No		Stoddart 1984
P. meandrina	P	Microsatellites	Indo-W Pacific	2000	$\theta = 0.056$	4.21	Yes	No	Magalon et al. 2005
				7.5	$\theta = 0.019$	12.91			
Pseudopterogorgia elisabethae	P s.l.	Microsatellites	Bahamas	450	$\theta = 0.48$	0.27	Yes	No	Gutiérrez-Rodríguez & Lasker 2004
Seriatopora hystrix	D	Allozymes	E Australia, GBR and Lord Howe Island	2400	$\theta = 0.19$	1.067	Yes	No	Ayre & Hughes 2004
				1700	$\theta = 0.23$	0.84	No		Ayre & Hughes 2004
				1200	$\theta = 0.15$	1.42	No		Ayre & Hughes 2000
				8	$\theta = 0.28$	0.64	No		Ayre & Hughes 2000
			GBR	90	$F_{ST} = 0.43$	0.33	No data		Ayre & Dufty 1994
Sinularia flexibilis	P	Allozymes	NE Australia, GBR	1300	$\theta = 0.0065$	38.21	No	No	Bastidas et al. 2001
				30	$\theta = 0.026$	9.37			
				4	$\theta = 0.041$	5.85			
Styllophora pistillata	D	Allozymes	E Australia, GBR and Lord Howe Island	2400	$\theta = 0.15$	1.42	Yes	No	Ayre & Hughes 2004
				1700	$\theta = 0.026$	9.37	No		Ayre & Hughes 2004
				1200	$\theta = 0.09$	2.53	No		Ayre & Hughes 2000
				8	$\theta = 0.18$	1.14	No		Ayre & Hughes 2000
Polychaeta									
Hediste diversicolor	D	mtDNA	N Atlantic and Mediterranean	5500	% var = 45.3		No data	No	Breton et al. 2003
		Allozymes		2500	$\theta = 0.347$	0.47	Yes		Virgilio & Abbiati 2004
				175	$\theta = 0.097$	2.33	No		
Neanthes virens	P	mtDNA	W Pacific, NE and NW Atlantic, N Sea	>30,000	% var = 0		No data	No	Breton et al. 2003
Pectinaria koreni	P	Microsatellites	British coasts and English Channel	200	$F_{ST} = 0.04$	6	No	No	Jolly et al. 2003a

Cirripedia									
Balanus glandula	P	mtDNA	California	1600	$\theta = 0.045$	5.31 (*7.35)	No data	No	Wares et al. 2001
		mtDNA and ncDNA		1500	$\Phi_{ST} = 0.38$	0.41			Sotka et al. 2004
Chthamalus fissus	P	mtDNA	California	800	$\theta = 0.045$	5.31 (*1.9)	No data	No	Wares et al. 2001
Hoplocarida									
Haptosquilla pulchella	P	mtDNA	Indo-W Pacific	5000	$\Phi_{ST} = 0.87$	0.037	No	No	Barber et al. 2002
Eucarida									
Callinectes bellicosus	P	mtDNA	E Pacific	600	$\Phi_{ST} = 0$	very large	No	No	Pfeiler et al. 2005
Euphausia superba	P	mtDNA	Circumantarctic	>7000	$\Phi_{ST} = 0.021$	11.65	No data	No	Zane et al. 1998
Lithopenaeus setiferus	P	Microsatellites	W Atlantic and Gulf of Mexico	4700	$F_{ST} = 0.02$	12.25	Yes, weak	No	Ball & Chapman 2003
Penaeus monodon	P	ncDNA	W Indian Ocean and W Pacific	2000	$F_{ST} = 0.075$	3.08	No data	No	Duda & Palumbi 1999
				>7500	$F_{ST} = 0.505$	0.25			
				>7500	$F_{ST} = 0.398$	0.38			
Scylla serrata	P	mtDNA	E Indian Ocean and Red Sea	8000	$F_{ST} = 0.04$	6	No	No	Fratini & Vannini 2002
Synalpheus brooksi	D	Allozymes	Caribbean	4800	$\theta = 0.54$	0.21	No data	No	Duffy 1993
S. pectiniger	P	Allozymes	Caribbean	4800	$\theta = 0.14$	1.54	No data	No	Duffy 1993
Peracarida									
Corophium volutator	D	RAPD	Gulf of Maine	160	$\Phi_{ST} = 0.205$	0.97	No	No	Wilson et al. 1997
Gammarus locusta	D	RAPD	Portugal	500	$F_{ST} = 0.074$	1.27	No data	Yes, on macroalgae	Costa et al. 2004
		Allozymes			$F_{ST} = 0.057$	4.14	No data		Coelho et al. 2002
Idotea chelipes	D	Allozymes	SE British coastal lagoons	100	$F_{ST} = 0.164$	1.27	No data	Yes, on macroalage	Jolly et al. 2003b

Table 1 (continued) Genetic structure of populations of several marine invertebrate taxa reported in the literature

Species	Dev.	Genetic system	Geographic location	Spatial scale (km)	Genetic structure	Nm	IBD	Rafting inferred	Reference
Jaera albifrons	D	Allozymes	Anglesey, UK	200	$G_{PT} = 0.121$	1.82	No data	No	Carvalho & Piertney 1997
			South Wales	100	$F_{ST} = 0.083$	2.76	No data	No	Piertney & Carvalho 1994
			Anglesey, UK	100	$G_{PT} = 0.032$	7.56			Carvalho & Piertney 1997
				0.06	$G_{PT} = 0.09$	2.53			Carvalho & Piertney 1997
J. forsmani	D	Allozymes	Anglesey, UK	200	$G_{PT} = 0.056$	4.21	No data	No	Carvalho & Piertney 1997
				100	$G_{PT} = 0.047$	5.07			
				0.06	$G_{PT} = 0.009$	27.53			
J. ischiosetosa	D	Allozymes	Anglesey, UK	200	$G_{PT} = 0.059$	3.99	No data	No	Carvalho & Piertney 1997
				100	$G_{PT} = 0.049$	4.85			
				0.06	$G_{PT} = 0.011$	22.48			
J. nordmanni	D	Allozymes	Anglesey, UK	200	$G_{PT} = 0.077$	3	No data	No	Carvalho & Piertney 1997
				100	$G_{PT} = 0.050$	4.75			
				0.06	$G_{PT} = 0.028$	8.67			
J. praehirsuta	D	Allozymes	Anglesey, UK	200	$G_{PT} = 0.207$	0.96	No data	No	Carvalho & Piertney 1997
				100	$G_{PT} = 0.174$	1.19			
				0.06	$G_{PT} = 0.033$	7.33			
Orchestia montagui	D	Allozymes	Mediterranean	>3000	$\theta = 0.198$	1.01	Yes	Yes, on macroalgae	De Matthaeis et al. 2000
O. stephenseni	D	Allozymes	Mediterranean	>3000	$\theta = 0.452$	0.30	No	Yes, on macroalgae	De Matthaeis et al. 2000
Paracorophium excavatum	D	Allozymes	New Zealand	1600	$F_{ST} = 0.7$	0.11	Yes	No	Stevens & Hogg 2004
P. lucasi	D	Allozymes	New Zealand	1600	$F_{ST} = 0.66$	0.13	Yes, but weak	No	Stevens & Hogg 2004
Platorchestia platensis	D	Allozymes	Mediterranean	>3000	$\theta = 0.071$	3.27	No	Yes, on macroalgae	De Matthaeis et al. 2000

Sphaeroma terebrans	D	mtDNA	E Africa and Florida USA	30,000 500	$F_{ST} = 0.85$ $F_{ST} = 0.58$	0.04 0.18	No	Yes, on mangrove woods	Baratti et al. 2005
Talitrus saltator	D	Allozymes	Mediterranean	>3000	$\theta = 0.843$	0.05	Yes	Yes, on macroalgae	De Matthaeis et al. 2000
Prosobranchia									
Bedeva hanleyi	CJ	Allozymes	SE Australian coast	180	$F_{ST} = 0.14$	1.54	May be	Yes	Hoskin 1997
Cerithium lividulum	D	Allozymes	Mediterranean	1750	$F_{ST} = 0.582$	0.18	No data	No	Boisselier-Dubayle & Gofas 1999
C. vulgatum	P	Allozymes	Mediterranean	1750	$F_{ST} = 0.158$	1.33	No data	No	Boisselier-Dubayle & Gofas 1999
Cominella lineolata	CJ	Allozymes	SE Australian coast	162	$F_{ST} = 0.52$	0.23	May be	Yes	Hoskin 1997
Crepidula atrasolea	D	mtDNA	NW Atlantic	1300	APV= 54.3		Yes	No	Collin 2001
C. convexa Northern species	D	mtDNA	NW Atlantic	1300	APV= 76.1		Yes	Yes, on seagrass	Collin 2001
C. convexa Southern species	L	mtDNA	NW Atlantic	4500	APV= 87.2		Yes		Collin 2001
C. depressa	P	mtDNA	NW Atlantic	1300	APV= -7,4		No	No	Collin 2001
C. fornicata	P	mtDNA	NW Atlantic	2600	APV= 22.1		No	No	Collin 2001
*Echinolittorina lineolata***	P	Allozymes	Brazil	4000	$F_{ST} = 0.054$	4.38	Yes	No	Andrade et al. 2003
Hydrobia ulvae	P	mtDNA	NW European coasts	6000	$F_{ST} = 0.25$	0.75	No	Yes	Wilke & Davis 2000
H. ventrosa	D	mtDNA	NW European coasts and Mediterranean	6000	$F_{ST} = 0.41$	0.36	Yes	Yes	Wilke & Davis 2000
Littoraria angulifera	D	Allozymes	Brazil	4000	$F_{ST} = 0.185$	1.1	No	Yes, on mangrove trees (David Reid, pers. comm.)	Andrade et al. 2003

Table 1 (continued) Genetic structure of populations of several marine invertebrate taxa reported in the literature

Species	Dev.	Genetic system	Geographic location	Spatial scale (km)	Genetic structure	Nm	IBD	Rafting inferred	Reference
L. flava	P	Allozymes	Brazil	4000	$F_{ST} = 0.028$	8.68	Yes	Yes, on mangrove trunks (David Reid, pers. comm.)	Andrade et al. 2003
Littorina cingulata	P	Allozymes	NW Australia	1500	$F_{ST} = 0.031$	7.81	No	No	Johnson & Black 1998
				1120	$F_{ST} = 0.021$	11.66	No		
				160	$F_{ST} = 0.013$	18.98	Yes		
L. littorea	P	Allozymes	Swedish coast	300	$G_{PT} = 0.021$	11.66	No	No	Janson 1987a
L. plena	P	mtDNA	NE Pacific	245	$\Phi_{ST} = 0.065$	3.6	No	No	Kyle & Boulding 2000
L. saxatilis	D	Allozymes	W Swedish coast	300	$G_{PT} = 0.078$	2.96	Yes	Yes (Johannesson et al. 2004)	Janson 1987a
			Koster archipelago	300	$G_{PT} = 0.095$	2.38	No data		Janson 1987b
			W Swedish coast	75	$G_{ST} = 0.008$	2.88	Yes		Johannesson & Tatarenkov 1997
		RAPD	W Swedish coast	150	% var = 8.6		Yes		Johannesson et al. 2004
L. scutulata	P	mtDNA	NE Pacific	745	$\Phi_{ST} = 0$	Very large	No	No	Kyle & Boulding 2000
L. sitkana	D	mtDNA	NE Pacific	3600	$\Phi_{ST} = 0$	Very large	No	Yes, on intertidal rockweeds (*Fucus distichus*)	Kyle & Boulding 2000
L. subrotundata	D	mtDNA	NE Pacific	3600	$\Phi_{ST} = 0.12$	1.83	Yes	No	Kyle & Boulding 2000
Morula marginalba	P	Allozymes	SE Australian coast	162	$F_{ST} = 0.017$	14.46	May be	Yes	Hoskin 1997
Nerita atramentosa	P	mtDNA	S Australia, Tasmania and New Zealand	2000	% var = 0.84		No	No	Waters et al. 2005
Nucella lamellosa	D	mtDNA haplot. mtDNA seq.	NW Pacific	5000	% var = 0.06 % var = 0.11		Yes	No	Marko 2004

N. lapillus	D	Microsatellites	British coasts	1600	θ = 0.11 % var = 7.31	2.02	No	Yes	Colson & Hughes 2004
				0.15	θ = 0.06 % var = 5.44	3.92			
N. ostrina	D	mtDNA haplot.	NW Pacific	5000	% var = 0.05		No	No	Marko 2004
		mtDNA seq.			% var = 0.08				
Siphonaria jeanae	P	Allozymes	W Australia	2500	F_{ST} = 0.0011	227.02	Only one of the 4 loci	No	Johnson & Black 1984a,b
				500	F_{ST} = 0.0018	138.64			
				50	F_{ST} = 0.0019	131.33			
				10	F_{ST} = 0.0032	77.87			
				0.05	F_{ST} = 0.0043	57.89			
Opisthobranchia									
Adalaria proxima	L	Allozymes	British Isles	1600	θ = 0.3	0.58	No	Yes, on fucoids (Todd et al. 1998)	Todd et al. 1998, Lambert et al. 2003
				26	θ = 0.2	1			
Goniodoris nodosa	P	Allozymes	British Isles	1600	θ = 0	very large	No	No	Todd et al. 1998, Lambert et al. 2003
Bivalvia									
Donax deltoides	P	Allozymes	SE Australia	1200	F_{ST} = 0.009	27.53	No	No	Murray-Jones & Ayre 1997
Macoma balthica	P	mtDNA	N Europe and Alaska	18,000	F_{ST} = 0.669	0.12	No data	No	Luttikhuizen et al. 2003
Spisula s. solidissima	P	mtDNA	NW Atlantic	4500	Φ_{ST} = 0.338	0.49	No	No	Hare & Weinberg 2005
Tridacna maxima	P	Allozymes	Indo-W Pacific	>5000	θ = 0.156	1.35	No data	No	Benzie & Williams 1997
				2600	θ = 0.084	2.73			
				<700	θ < 0.003	83.08			
Cephalopoda									
Pareledone turqueti	D	Allozymes	South Georgia	0.15	θ = 0.54	0.22	No data	No	Allcock et al. 1997
Asteroidea									
Acanthaster planci	P	Allozymes	E Pacific and Indian Oceans, GBR	700	θ = 0.035	6.89	Yes	No	Benzie 1999
				10,000	θ = 0.273	0.67			

Table 1 (continued) Genetic structure of populations of several marine invertebrate taxa reported in the literature

Species	Dev.	Genetic system	Geographic location	Spatial scale (km)	Genetic structure	Nm	IBD	Rafting inferred	Reference
Asterina gibbosa	CJ	AFLP	NW European coasts and Mediterranean	1000	$F_{ST} = 0.395$	0.38	Yes	(Yes), personal comments by R. Emson	Baus et al. 2005
Coscinasterias muricata	P	mtDNA	New Zealand fiords	>1000	$\Phi_{ST} = 0.152$	1.4	Yes	Yes (Waters & Roy 2003)	Perrin et al. 2004
		Allozymes		2000	$F_{ST} = 0.061$	3.85			Sköld et al. 2003
				270	$F_{ST} = 0.025$	9.75			
Linckia laevigata	P	RFLP	Indian Ocean	12,500	$\theta = 0.206$	0.96 (1.9)	Yes	No	Williams & Benzie 1998
				10,500	$\Phi_{ST} = 0.224$	0.87 (1.7)			
		Allozymes	Indo-W Pacific	12,500	$\theta = 0.002$	124.75	No		Williams & Benzie 1996
Patiriella calcar	P	Allozymes	SE Australia	230	$\theta = 0.0008$	312.25	No	No	Hunt 1993
P. exigua	D	mtDNA	S Africa, S Australia and Tasmania	600	% div = 0.9		No data	Yes, on macroalgae or wood	Waters & Roy 2004a
				1900	% div = 1.8				
				3800	% div = 3.2				
		Allozymes		230	$\theta = 0.462$	0.29	No		Hunt 1993
P. regularis	P	mtDNA	New Zealand coasts	1400	$F_{ST} = 0.072$	3.22	Yes	No	Waters & Roy 2004b
Echinoidea									
Diadema antillarum	P	mtDNA	W and E Atlantic	14,000	$\theta = 0.62$	0.15	No data	No	Lessios et al. 2001
				10,000	$\theta = 0.46$	0.29			
				5000	$\theta = 0.02$	12.25			
D. mexicanum	P	mtDNA	E Pacific, Galápagos	7000	$\theta = 0$	very large	No	No	Lessios et al. 2001
D. paucispinum	P	mtDNA	Pacific and Indian Oceans	12,000	$\theta = 0.04$	6	No	No	Lessios et al. 2001
				2500	$\theta = 0.1$	2.25	Yes		
D. savignyi	P	mtDNA	Indian Ocean, W and C Pacific	35,000	$\theta = 0.06$	3.92	No	No	Lessios et al. 2001

Echinothrix diadema	P	Allozymes and mtDNA	N Pacific Ocean Islands	>5000 >5000 2000	F_{ST} = 0.064 F_{ST} = 0.01 F_{ST} = 0.022	3.66 24.75 11	No data	No	Lessios et al. 1998
Echinometra lucunter	P	mtDNA	Caribbean and Brazil	10,000	F_{ST} = 0.261	0.71	No data	No	McCartney et al. 2000
E. mathaei	P	mtDNA	Indo-W Pacific	>10,000	F_{ST} = 0.389	0.39	Yes	No	Palumbi et al. 1997
E. oblonga	P	mtDNA	Indo-W Pacific	>10,000	F_{ST} = 0.306	0.57	Yes	No	Palumbi et al. 1997
E. vanbrunti	P	mtDNA	E Pacific	4700	F_{ST} = 0.057	4.14	No data	No	McCartney et al. 2000
E. viridis	P	mtDNA	Caribbean	2600	F_{ST} = 0.361	0.44	No data	No	McCartney et al. 2000
Heliocidaris erythrogramma	P s.l.	RFLP	Australia and Tasmania	3400 1500	G_{ST} = 0.62 G_{ST} = 0.34	0.15 0.49	No data	No	McMillan et al. 1992
H. tuberculata	P	RFLP	E Australia	3400	G_{ST} = 0.12	1.83	No data	No	McMillan et al. 1992
Paracentrotus lividus	P	mtDNA	SW Europe	5000	F_{ST} = 0.01	24.75	No	No	Duran et al. 2004d
Strongylocentrotus purpuratus	P	Allozymes and mtDNA	California	870	F_{ST} = 0.03	8.08	No data	Yes, on algae (Hobday 2000a)	Edmands et al. 1996
Holothuroidea									
Cucumaria miniata	P	mtDNA	NE Pacific	2350	Φ_{ST} = 0.05	4.75 (10)	No data	No	Arndt & Smith 1998
C. pseudocurata	D	mtDNA	NE Pacific	2300	Φ_{ST} = 0.97	0.01 (0.017)	No data	Yes, on surf grass *Phyllospadix scouleri*	Arndt & Smith 1998
Ophiuroidea									
Amphipholis squamata	D	RFLP and mtDNA	New Zealand	1600	Φ = 0.45	0.31	Yes, but low	Yes, on macroalgae or debris (Sponer & Roy 2002)	Sponer & Roy 2002
		RAPD	W Mediterranean	0.003	F_{ST} = 0.15	1.42	No		Féral et al. 2001
Ectoprocta (Bryozoa)									
Alcyonidium gelatinosum	L	RAPD	British Isles	800	F_{ST} = 0.077	3	No data	Yes, on algae	Porter et al. 2002

Table 1 (continued) Genetic structure of populations of several marine invertebrate taxa reported in the literature

Species	Dev.	Genetic system	Geographic location	Spatial scale (km)	Genetic structure	Nm	IBD	Rafting inferred	Reference
A. mytili	P	RAPD	British Isles	1500	$F_{ST} = 0.105$	2.13	No data	No	Porter et al. 2002
Celleporella hyalina	L	RAPD	North Wales	10	% var = 5.29		Yes	No	Goldson et al. 2001
Electra pilosa	P	RAPD	North Wales	10	% var = 0		No	Yes, on algae (Vallentin 1895, Todd et al. 1998)	Goldson et al. 2001
Membranipora membranacea	P	Allozymes	NE Pacific, NE and NW Atlantic	14,000 4600 2200	$\theta = 0.726$ $\theta = 0.019$ $\theta = 0.014$	0.09 12.91 17.61	No data	Yes, on plastic (Aliani & Molcard 2003)	Schwaninger 1999
Tunicata									
Botrylloides magnicoecum	D	Allozymes	SE Australia	190	$F_{ST} = 0.202$	0.99	Yes	No	Ayre et al. 1997
Pyura gibbosa gibbosa	P	Allozymes	SE Australia	215	$F_{ST} = 0.002$	124.75	No	No	Ayre et al. 1997
Stolonica australis	D	Allozymes	SE Australia	140	$F_{ST} = 0.210$	0.94	Yes	No	Ayre et al. 1997

Notes: Most studies provided an F_{ST}-like measure of population genetic differentiation. For each species information is included about its mode of development, molecular marker (genetic system) used to infer population structure, geographic location of the studies, spatial scales for which population genetic differentiation data are available (most were calculated from maps or coordinates provided in the literature), estimates of genetic differentiation (genetic structure) among populations (original parameter given by authors is presented), presence or absence of an isolation by distance pattern (IBD), whether rafting has been inferred for the taxon and references of the genetic studies from which population differentiation data was obtained. Nm was calculated using the equation of Wright (1969) (see text). Values of Nm provided by the authors that differ from those calculated by us are given in parentheses.

Dev. = mode of development; P = planktonic development; D = direct development; L = short-lived lecitotrophic larvae; CL = crawling larvae; CJ = crawling juveniles; s.l. = short lived; mtDNA = mitochondrial DNA; ncDNA = nuclear DNA; % var = percentage of molecular variance; % div = percentage sequence divergence; APV = among population variance; approximately equal to F_{ST} (Excoffier et al. 1992); AGD= average genetic diversity; G_{PT} = coefficient of gene differentiation between populations; * = CME or cladistic migration events; **species reported by author under a different name.

Nm and geographic scale for which differentiation values where available were classified by mode of development of the studied species. The direct development categories included all organisms that brood their progeny up to a juvenile or crawl-away stage or that have very short-lived larvae (<2 days). All others were classified as organisms with planktonic larval development. Both broad developmental mode categories were further subdivided into organisms for which rafting is not known (No Rafting) and those organisms for which rafting has been reported in the literature or inferred based on available knowledge (Rafting). Log-scatter plots of Nm vs. geographic scale of the studies show that all categories of organisms (combinations of Direct/Planktonic development and Rafting/No Rafting) are highly variable in the degree of connectivity between distant populations and that they can achieve extensive gene flow (Figure 28). As expected, most of the species with high realised gene flow over the greatest distances have planktonic larval stages (both rafters and non-rafters). However, contrary to classical expectations, several direct-developing species were also found to show high connectivity at intermediate-to-long distances. Thus, rafting is an important

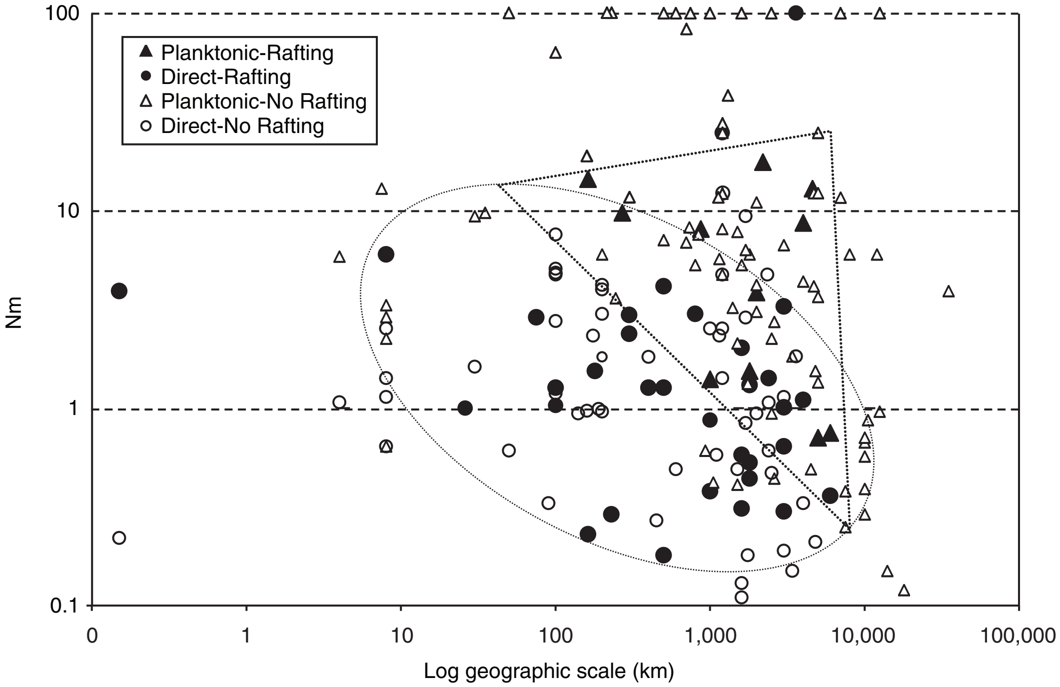

Figure 28 Relationship between the geographical scale and migration rate calculated as Nm according to Wright (1969) for the species shown in Table 1 for which F_{ST}-like genetic measures were available. F_{ST}-like values that resulted in Nm values greater than 100 were all left at 100 migrants per generation. Horizontal dashed lines mark the limit between arbitrarily defined low (<1), medium (1–10) and high (>10 migrants per generation) levels of genetic connectivity. It is important to note that the geographical scale does not necessarily relate to the geographic range of distribution of species and that it corresponds to the scale at which population genetic differentiation values were available. The scatter plot shows that rafting leads to low-to-moderate and sometimes high levels of genetic connectivity at a broad range of geographic scales. The oval groups Nm values of most rafters with direct development (33 of 37 reports; 89.2%) and shows that rafting has a strong impact on connectivity of direct-developing species between 10 and up to almost 10,000 km, leading to medium Nm values. The triangle groups all 12 reports (100%) of rafters with planktonic development. There is an area of overlap between the oval and the triangle and then the triangle also encompasses an area of medium to high connectivity from 100 to almost 10,000 km.

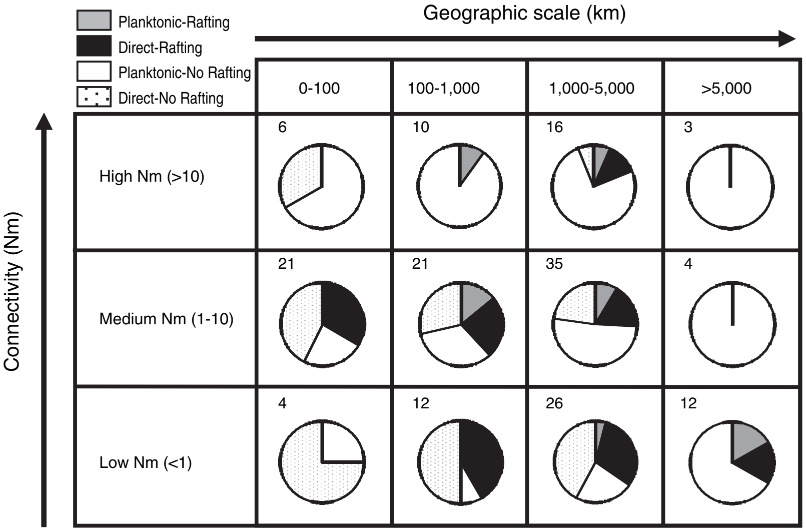

Figure 29 Contribution of rafting to genetic connectivity at different geographical scales. Values of Nm for different species shown in scatter plot (Figure 28) were classified according to level of connectivity and geographic scale. Levels of connectivity estimated as number of migrants per generations were low (<1), medium (1–10) and high (>10). The pie charts within each cell represent the proportion of organisms in each of the four categories of organisms (Rafting/No rafting and Direct/Planktonic development) that are characterised by low, intermediate and high migration rates (Nm). Numbers in the upper left corners indicate the total number of species for which population differentiation data were available at each geographical scale; note that for some species data were available for more than one geographical scale, so the total adds up to more than 113. When more than one Nm value was available for the same geographical scale and species, the Nm was recalculated from the average genetic differentiation.

means of dispersal for many brooders at different geographic scales (Figure 28). The impact of rafting on migration rates of marine invertebrates at different spatial scales (0–100, 100–1000, 1000–5000, and >5000 km) can be further explored in Figure 29 where data are presented as the number of species of each of the four broad categories that achieve high (>10), intermediate (1–10) and low (<1) levels of gene flow measured as Nm at the different spatial scales. While most direct developers were reported to have low levels of gene flow (35 of all 81 species that have direct development), there are several reports of moderate to high levels of gene flow among direct developers at intermediate distances (1000–5000 km) (17 out of 51 species), and many of these are species for which rafting has been inferred (8 out of 17 species). It is important to acknowledge that rafting may be unrecognised as a dispersal means for many species and its contribution is likely to be underestimated.

A detailed overview of the studies that have reported population genetic differentiation for species for which rafting has been inferred (Table 1) will now be given. The examples presented are partitioned according to the four geographic scales previously defined (Figure 29). It is worth noting that the scale at which a species is described herein reflects the spatial scale used in the respective study and it does not necessarily correspond with its entire geographic range of distribution. The geographical scale at which rafting has important effects on population connectivity will depend on local conditions and the species considered. As shown in Figure 1 and Figure 2, rafting may be an important factor to consider at varying levels of a continuum of biological processes from local population dynamics to cladogenesis.

Rafting-mediated connectivity at the geographic scale of 0–100 km

Rafting has been invoked as a means of dispersal at this geographic scale only for direct developers, including the anthozoans *Balanophyllia elegans* from California (Bushing 1994, Hellberg 1996) and *Pocillopora damicornis* from the Great Barrier Reef (GBR) in eastern Australia (Ayre & Hughes 2000, Jokiel & Cox 2003), the mesogastropod *Littorina saxatilis* from the western Swedish coasts (Johannesson & Tatarenkov 1997), the neogastropod *Nucella lapillus* from the British coasts (Colson & Hughes 2004), the nudibranch *Adalaria proxima* from the northeastern Atlantic (Todd et al. 1998), the isopod *Idotea chelipes* from southeastern British coastal lagoons (Jolly et al. 2003b), and the brittle star *Amphipholis squamata* from the western Mediterranean (Féral et al. 2003).

Balanophyllia elegans, commonly known as the orange cup coral, has direct development and has been reported rafting on macroalgae on the coast of California (Bushing 1994). Gene flow between populations of *B. elegans* separated by approximately 100 km is sufficient to prevent local genetic differentiation (Nm = 1.03) (Hellberg 1996), while at greater distances (1000–5000 km) gene flow is slightly lower (see below). According to Ayre & Hughes (2000) both restricted dispersal among populations and inbreeding contribute to the fine-scale genetic structure in *Pocillopora damicornis* from the GBR (Ayre & Hughes 2000), a brooding coral that is presumed to have high dispersal potential through rafting on pumice (e.g., Jokiel & Cox 2003) (Figure 20). Over a local scale of 8 km along the GBR, the genetic differentiation data of *P. damicornis* do not demonstrate an IBD pattern and translate to high gene flow (Nm ~ 6; Ayre & Hughes 2000). In both these anthozoans, frequent rafting routes may be contributing to population connectivity at a local spatial scale, counteracting the effects of genetic drift, and thus becoming an important evolutionary agent at this spatial scale.

For the direct-developing rough periwinkle, *Littorina saxatilis*, Johannesson & Tatarenkov (1997) reported genetic differentiation values at the scale of 75 km for western Sweden, consistent with two to five migrants per generation. Johannesson et al. (2004) suggested that rafting may be a means of dispersal for this species. Colson and Hughes (2004) found that the egg-laying dog whelk *Nucella lapillus* of the British coasts lacks a pattern of IBD and that medium distance movements (10–150 km) are relatively common (Figure 20). Rafting is considered to be contributing to the high levels of gene flow among populations of this direct developer.

The nudibranch *Adalaria proxima* may occasionally be dispersing by rafting on fucoids, either as adults or as egg-masses (Todd et al. 1998). Populations of *A. proxima* separated by 26 km display sufficient gene flow to prevent population differentiation (Nm = 1; Todd et al. 1998, Lambert et al. 2003). However, the authors observed a significant IBD pattern, possibly because at this scale dispersal is mostly via the larval stage and "the larvae are behaviourally constrained from becoming pelagic, or remain epibenthic, and thereby are subject to only restricted dispersal" (Todd et al. 1998).

At this geographic scale, populations of the isopod *Idotea chelipes* from British coastal lagoons show gene flow levels of 1.27 migrants per generation (Jolly et al. 2003b). The authors suggested that the outer coast may act as a barrier to gene flow between bays leading to the observed genetic differentiation. They recognised rafting as a possible means for LDD, but since lagoons are the typical habitat of *I. chelipes* along the British coast and are discontinuously distributed, the likelihood to reach suitable habitats through rafting once leaving the lagoon is low (Jolly et al. 2003b).

All the examples given above fit well with connectivity levels resulting from dispersal through frequent rafting routes (or possibly strong intermittent routes), that as defined were predominant at distances of 0–100 km. Contrary to this, the brooding brittle-star *Amphipholis squamata* has very low gene flow at this geographic scale. Rafting has been inferred for this species (on macroalgae or debris, see Sponer & Roy 2002), even though for a very small scale of 3 m local gene flow is very low (Nm = 1.42). Thus, rafting does not seem to be considerably affecting population structure of *A. squamata* at a microgeographic scale, possibly due to the fact that the rafting routes of the species may be episodic, and thus be contributing to the worldwide distribution of the species and speciation (see below).

It is possible that many more direct developers than reported are also dispersing via rafting at this geographic scale. In the previous section, it was argued that at a small geographic scale, frequent rafting routes could lead to high connectivity among local populations for example within a bay or a system of bays. It is likely that many more brooders than presently reported use frequent rafting routes to disperse at distances under 100 km (e.g., within bays or estuaries) and that rafting accounts for most of the connectivity among populations of benthic marine brooders at this geographic scale.

Rafting-mediated connectivity at the geographic scale of 100–1000 km

The levels of gene flow of the orange cup coral, *Balanophyllia elegans*, at a scale of 1000 km are sufficiently low to allow population differentiation (Nm = 0.87). *Pocillopora damicornis*, the brooding coral from the GBR also mentioned in the previous section as having high gene flow at a microgeographic scale, maintains connectivity presumably through rafting on pumice with at least one migrant per generation at a scale of 400 km (Stoddart 1984) (Figure 20), which is sufficient to prevent significant genetic differentiation. Intermittent rafting routes are probably ensuring genetic connectedness among populations located 400 km apart, and thus, it is up to this scale or further that rafting is affecting the metapopulation structure of *P. damicornis*. Additionally, Stoddart (1984) did not find a significant association between genetic and geographic distance for this species (i.e., no IBD). This pattern might be the consequence of LDD of individuals via an intermittent rafting route in a leapfrog fashion (Figure 13).

Colonies of the bryozoan *Alcyonidium gelatinosum* from the British Isles have been found on *Fucus serratus* and presumably have the potential for rafting on this or other macroalgae (Porter et al. 2002). This species has a short-lived lecitotrophic larva that probably only allows for home range dispersal. At the spatial scale of 800 km this bryozoan displays levels of genetic differentiation consistent with an average gene flow of three migrants per generation. This value is comparable to the migration rate of a sympatric congener with planktonic development (Porter et al. 2002).

Rafting has also been invoked at this geographic scale for several gastropods. The gastropods *Bedeva hanleyi* and *Cominella lineolata* from the coast of southeastern Australia have crawling larvae with very restricted dispersal and are thought to disperse via plankton or by rafting on substrata such as logs and algae (Hoskin 1997). The Nm of *Bedeva hanleyi* is 1.54 at 180 km, while *Cominella lineolata* only has an Nm of 0.23 at a similar spatial scale. It may be that *Bedeva hanleyi* is a better rafter and can make better use of intermittent rafting routes for dispersal than *Cominella lineolata*, achieving sufficient gene flow at a scale of 180 km, to prevent genetic differentiation. Estimated gene flow for the direct developing *Littorina saxatilis* over 300 km of the Swedish west coast and in the Koster Archipelago is approximately 2.67 migrants per generation (Janson 1987a,b).

The isopod *Sphaeroma terebrans* shows relatively low levels of gene flow over 500 km along the East African coast (Nm = 0.18; Baratti et al. 2005). These isopods spend most of their lives in mangrove roots and they are presumed to raft when roots break off and float away. In spite of this, populations of *S. terebrans* appear to comprise ancient lineages with restricted dispersal, as evidenced by their strong genetic differentiation (Baratti et al. 2005) (Figure 12). Successful rafting dispersal on this geographic scale may be limited in this species by the low probability of reaching suitable environments via rafting along the outer coast on detached mangrove roots (Figure 5).

Along a stretch of 500 km of the Portuguese coast, populations of the amphipod *Gammarus locusta* show low population differentiation, attributable to relatively high levels of gene flow in the area (Coelho et al. 2002, Costa et al. 2004). This is a direct-developing species associated with macroalgae and “loose-lying bunches of drift-macroalgae” (Costa et al. 2004), and the low genetic differentiation could indicate that *G. locusta* achieves gene flow (between 3.13 and 4.14 migrants per generation) through rafting. According to the authors “drifting attached to macroalgae is probably an important means of dispersal for this species” (Costa et al. 2004).

The seastar *Asterina gibbosa* releases crawling juveniles with low dispersal potential, although it has been inferred to raft occasionally (Baus et al. 2005, R. Emson personal communication). At a scale of 1000 km it exhibits low levels of connectivity (Nm = 0.38) (Baus et al. 2005).

All the examples given above fit the predictions of intermittent rafting routes, allowing more or less connectivity at this mesogeographic scale depending on the strength and frequency of the rafting connection. Weak intermittent or episodic rafting routes seem to be the cause of low levels of connectivity (0.29 migrants per generation) (Hunt 1993) of populations of the brooding starfish *Patiriella exigua* along 230 km of the southeastern Australian coasts. Even though it is thought to disperse via rafting on macroalgae or wood (Waters & Roy 2004a), the levels of connectivity are low but sufficient to maintain the geographic range of distribution, yet possibly contribute to speciation in the long term (see section on episodic rafting routes). The high genetic structure found for *P. exigua* that is not clearly associated to geographic distance (Hunt 1993) is consistent with rafting dispersal, although not very frequent, as has been suggested by Waters & Roy (2004a).

As can be observed in Figure 28 and Figure 29, around 100–1000 km there are many brooders that achieve intermediate-to-high levels of gene flow, some of which have not been inferred as rafters. It is likely that many more direct-developing species than those that have so far been reported disperse via intermittent rafting routes at this spatial scale.

Species with planktonic development that are thought to raft (based on non-genetic data) may also be achieving high gene flow via rafting at this scale. For example, the rafting gastropod *Morula marginalba* from southeastern Australia has high gene flow (Nm = 14.46) at a scale of 160 km (Hoskin 1997). The urchin *Strongylocentrotus purpuratus*, which also has been found on floating algae on the coasts of California (Hobday 2000c), exchanges at least 8 migrants per generation at a scale of 870 km (Edmands et al. 1996). Finally the seastar *Coscinasterias muricata* achieves a connectivity of 9.75 migrants per generation along the New Zealand fjords (Sköld et al. 2003). For all these species, rafting through intermittent routes probably represents an additional means of dispersal that may ensure connectivity even when environmental conditions do not allow for successful larval-mediated dispersal and in these cases the rafters are most likely the juveniles or adults.

Rafting-mediated connectivity at the geographic scale of 1000–5000 km

There are many examples of direct-developing species, which presumably are dispersed by rafting at this geographic scale, including bryozoans (Hellberg 1994), anthozoans (Hellberg 1994, 1996; Ayre & Hughes 2004; Govindarajan et al. 2005), actiniarians (Edmands & Potts 1997), gastropods (Kyle & Boulding 2000, Andrade et al. 2003, Colson & Hughes 2004), peracarids (De Matthaeis et al. 2000, Stevens & Hogg 2004), holothurians (Arndt & Smith 1998), asteroids (Baus et al. 2005) and ophiurids (Sponer & Roy 2002).

At a scale of 3000 km the orange cup coral *Balanophyllia elegans* has lower values of Nm (= 0.64) than those reported for shorter distances (Hellberg 1994). Rafting may have similar effects at this spatial scale to what was described at the scale of 1000 km for this species (i.e., intermittent rafting routes may allow for gene flow, albeit low, among distant populations). The brooding coral *Pocillopora damicornis* from the GBR has an Nm of 1.42 (only slight levels of genetic differentiation) at a scale of 2400 km (Ayre & Hughes 2004), which possibly is a consequence of pumice rafting given the geographic distance (see also above) (Figure 20). This species has high levels of gene flow at the scale of 0–100 km, which decreases at the scale of 1200–3000 km, but were still slightly sufficient to prevent significant genetic differentiation. The directly developing anemones of the genus *Epiactis* from the coasts of British Columbia to Southern California show a lower connectivity among populations at this geographic scale. With only 0.44–1.31 migrants per generation on average, at the scale of 1800 km these species show overall low levels of migration (Edmands & Potts 1997). However, some LDD dispersal is expected, especially for *E. ritteri* that has the highest Nm value (sufficient to prevent genetic differentiation), which may be achieved through rafting on algae.

Littorina sitkana, which also has been inferred to raft at this spatial scale (3600 km), has a very high Nm ($F_{ST} = 0$) (Kyle & Boulding 2000). The authors suggested that in the northeast Pacific "rafting of egg masses or adults on floating rockweed may account for long-range gene flow between populations after winter storms, which dislodge the rockweed". They also discuss that there may have been severe bottlenecks or local extinctions and recolonisations, which could account for the low intra- and high interpopulation variation (Kyle & Boulding 2000). Indeed rafting may lead to repeated colonisations that could be followed by founder effects, reducing within-population differentiation (see Harrison & Hastings 1996).

Andrade et al. (2003) found that the ovoviviparous gastropod *Littoraria angulifera* from mangroves and rocky shores of the Brazilian coast does not show a significant correlation between geographic and genetic distances within a 4000 km stretch of coast. The levels of gene flow are sufficient to prevent differentiation, accounting for 1.1 migrants per generation on average (Andrade et al. 2003). The authors conclude that there is random geographic dispersal of individuals but that the lack of IBD could also be due to a strong effect of genetic drift in addition to the effects of gene flow (Andrade et al. 2003). Dispersal of *L. angulifera* could be achieved through rafting: "*Littoraria angulifera* is an ovoviviparous species that inhabits trunks, branches and leaves of mangrove trees, and it therefore is likely to raft on driftwood or even floating foliage" (David Reid, personal communication). Given the reported connectivity among populations of *L. angulifera* from Brazilian mangroves (preventing significant genetic differentiation), it could be inferred that rafting routes, which may not be very strong or permanent, connect these populations. Possibly, climatic oscillations could favour temporary formation of strong intermittent rafting routes, leading to the low but detectable differentiation levels.

The previously mentioned study of *Nucella lapillus* from the British coasts also revealed a lack of IBD at the scale of 1600 km, suggesting considerable gene flow (Nm = 2; Colson & Hughes 2004) (Figure 16). The authors state that "populations of *N. lapillus* seem to fit a migrant model (with high numbers of colonists from several source populations) of dispersal rather than a stepping-stone". Rafting was suggested as a mechanism of dispersal for this brooding gastropod, and based on genetic diversity it could be predicted that there is not a single but rather many source populations. This is likely to be the case with intermittent rafting routes that could allow connectivity among populations, maybe seasonally or permanently.

The nudibranch *Adalaria proxima*, which exhibits IBD at a scale of 26 km, shows a lower connectivity at a scale of 1600 km around the British Isles (Nm = 0.58), but nevertheless sufficient to prevent very high levels of differentiation among distant populations (Todd et al. 1998). Possibly, over these distances, rafting dispersal gains in importance over larval dispersal, which seems to dominate the population dynamics at smaller spatial scales (see above).

De Matthaeis et al. (2000) reported differentiation data for four species of amphipod peracarids at a geographic scale of 3000 km along the Mediterranean coast and suggested that for these species rafting may occur via floating wracks. Of the four, *Orchestia montagui* and *Talitrus saltator* have a genetic differentiation following an IBD pattern, while the other two, *Orchestia stephenseni* and *Platorchestia platensis* do not display a significant association between genetic differentiation and geographic distance at the studied spatial scale. The last species shows the greatest Nm value (3.27). Consequently, dispersal of *P. platensis* may be through strong intermittent and frequent rafting routes.

The brooding holothuroid *Cucumaria pseudocurata* has been found on clumps of surf grass of *Phyllospadix scouleri* (Arndt & Smith 1998) and might sporadically disperse by rafting. However, over approximately 2300 km of the Pacific coast of North America, Arndt & Smith (1998) found a genetic differentiation consistent with very low dispersal (Nm = 0.17). If this species is dispersing by rafting, the rate of dispersal is very low compared to the generational time. Thus, populations feature high genetic differentiation but maintain widespread populations over time, even though some of the local populations may eventually speciate. The rafting routes connecting distant populations may be highly unstable and only establish when a series of favourable conditions are met. Similarly, Sponer & Roy (2002) proposed that the cosmopolitan brooding brittle-star *Amphipholis squamata* effectively disperses by rafting on macroalgae. They reported low gene flow (Nm = 0.31) at a scale of 1600 km along the coast of New Zealand, and conclude that epiplanktonic transport is an important dispersal mechanism for *A. squamata* in New Zealand, which may account for the widespread distribution of lineages. Results from Le Gac et al. (2004) challenge the rafting hypothesis proposed by Sponer & Roy (2002) and conclude that the "worldwide distribution of some clades only reflects the antiquity of clades, which are composed of several species". However, paleo-rafting and current rafting may still be the means of dispersal for this species that could have promoted its widespread distribution. Episodic rafting routes could allow sporadic or singular connectivity events that maintain the geographic range of distribution of lineages or lead to the divergence of lineages in isolation. A similar scenario could be inferred for *Patiriella exigua*. Waters & Roy (2004a) suggested that *P. exigua* could have dispersed from South Africa eastward across the Indian Ocean rafting on macroalgae or wood with assistance of the West Wind Drift (Figure 24). They found that the DNA sequences of individuals in South Africa are paraphyletic (suggested as the source population) while the Australian are monophyletic. Additional evidence of LDD comes from the Amsterdam Island population that is isolated (>3000 km) and whose haplotypes are more divergent than the ones from closer islands. Even though episodic rafting-mediated gene flow is inferred for this species, local levels of connectivity are low enough to allow genetic differentiation (Colgan et al. 2005). Indeed, "the population structure of *P. exigua* indicates that effective recent migration between New South Wales, Tasmania and South Australia has been so low that complete lineage sorting of haplotypes to regions has occurred" (Colgan et al. 2005).

There are also a few species with planktonic development that are inferred to raft, and where rafting may contribute to connectivity at this scale. For example, the actiniarian *Anthopleura elegantissima*, distributed from British Columbia to Southern California, is suggested to raft on eelgrass or algae and 1.54 migrants per generation are inferred from genetic differentiation data (Edmands & Potts 1997). The bryozoan *Membranipora membranacea*, frequently found growing on positively buoyant kelp and plastics, exchanges more than 15 individuals per generation at a scale >3000 km. The snail *Littoraria flava* may disperse by rafting at this geographic scale as it lives on mangrove trunks (as well as rocks) (David Reid, personal communication) and high connectivity among populations located 4000 km apart corresponds to 8.68 migrants per generation (Andrade et al. 2003). Rafting may also contribute to the connectivity of the populations of the seastar *Coscinasterias muricata* at this geographic scale (Waters & Roy 2003). Distances involved (1000–5000 km) may be extensive requiring long voyages (possibly exceeding the lifetime of planktonic larvae of many species), and rafting may permit some connectivity among their populations at these geographic distances.

Particularly interesting is the case of the widely distributed hydrozoan *Obelia geniculata*. This species has a relatively short-lived lecitotrophic planula larvae and the asexually produced medusa lives for approximately 1 month (Stepanjants et al. 1993, cited in Slobodov & Marfenin 2004). At least for the White Sea, these medusae are expected to disperse only for about 3–4 km, but the dispersal distance will depend on the speed and direction of the currents (Sergei Slobodov, personal communication). The hydroids grow on various substrata, including macroalgae, offering the possibility for rafting. In fact, *O. geniculata* has been inferred as a rafter in many regions of the world (see references in Thiel & Gutow 2005b). Within the North Atlantic and based on genetic data, Govindarajan et al. (2005) proposed as the most likely scenario that populations from Canada and Iceland had been sheltered in northern glacial refugia, and subsequently expanded southward. In general they found high genetic differentiation among the four North Atlantic populations studied (Massachusetts, New Brunswick, Iceland and France), with the exception of the New Brunswick and Iceland populations, which also share many unique haplotypes (Figure 30). This further supports the suggestion of a rafting route connecting the North American and Icelandic populations (see also Ingólfsson 1992, Wares & Cunningham 2001). The Massachusetts population, on the other hand, only has haplotypes shared with New Brunswick, suggesting recent southern expansion of the New Brunswick population (Govindarajan et al. 2005), possibly also achieved through rafting.

In summary, rafting has been invoked as an important means of dispersal for many species at the geographic scale of 1000–5000 km, showing an impact on the realised dispersal among populations of directly developing species (Figure 28 and Figure 29). Most of the examples given above correspond well with the predictions of intermittent rafting routes, bearing in mind that some of these routes may be stronger or more permanent in time than others and that this leads to varying levels of connectivity among populations at this geographic scale. These rafting routes are crucial for direct-developing species whose metapopulation structure is controlled by migration at this macrogeographic scale.

Rafting-mediated connectivity at the geographic scale >5000 km

At a wider geographic range (>5000 km), rafting does not seem to be a prevalent mechanism of dispersal, and when inferred it only contributes with low levels of gene flow, presumably through episodic rafting routes that may sometimes connect distant populations while others found new populations, thus expanding the geographic range of distribution or contributing to allopatric speciation.

The small but existent migration among populations of the isopod *Sphaeroma terebrans* across oceans might be achieved through rafting, and as stated by the authors, “In spite of the low vagility of *S. terebrans*, mechanisms of passive dispersal, probably through floating mangrove woods, could be responsible for the worldwide distribution of the taxon, which is until now considered cosmopolitan” (Baratti et al. 2005). They conclude that current patterns also affect “mangrove fragments with animals on board” resulting in genetic differentiation patterns, and that their reproductive strategy “is not sufficient to produce a high level of reproductive isolation between *S. terebrans* populations since passive dispersal through floating mangrove wood transported by currents could maintain a certain degree of gene flow between populations” (Baratti et al. 2005) (Figure 12). However, it cannot be excluded that this wood-boring isopod may not also be transported via anthropogenic vectors (e.g., on wooden ships).

Rafting has been suggested as a means of dispersal at a scale over 6000 km for two gastropod species of the genus *Hydrobia* from the European coasts with contrasting modes of development. *Hydrobia ventrosa* is a direct developer that exchanges approximately 0.36 migrants per generation at this spatial scale. Considering the continuum between intermittent and episodic rafting routes, these populations may be sufficiently connected via rafting to prevent allopatric speciation but not local population differentiation. The species with planktonic development, *H. ulvae*, does not show a pattern of IBD and gene flow corresponds to 0.75 migrants every generation as inferred from genetic differentiation data, which led the authors to conclude that rafting is a possible means of LDD dispersal for the species (Wilke & Davis 2000).

Finally, the bryozoan *Membranipora membranacea* with planktonic development shows low but detectable levels of gene flow (Nm = 0.09) at distances >10,000 km (Schwaninger 1999). Since

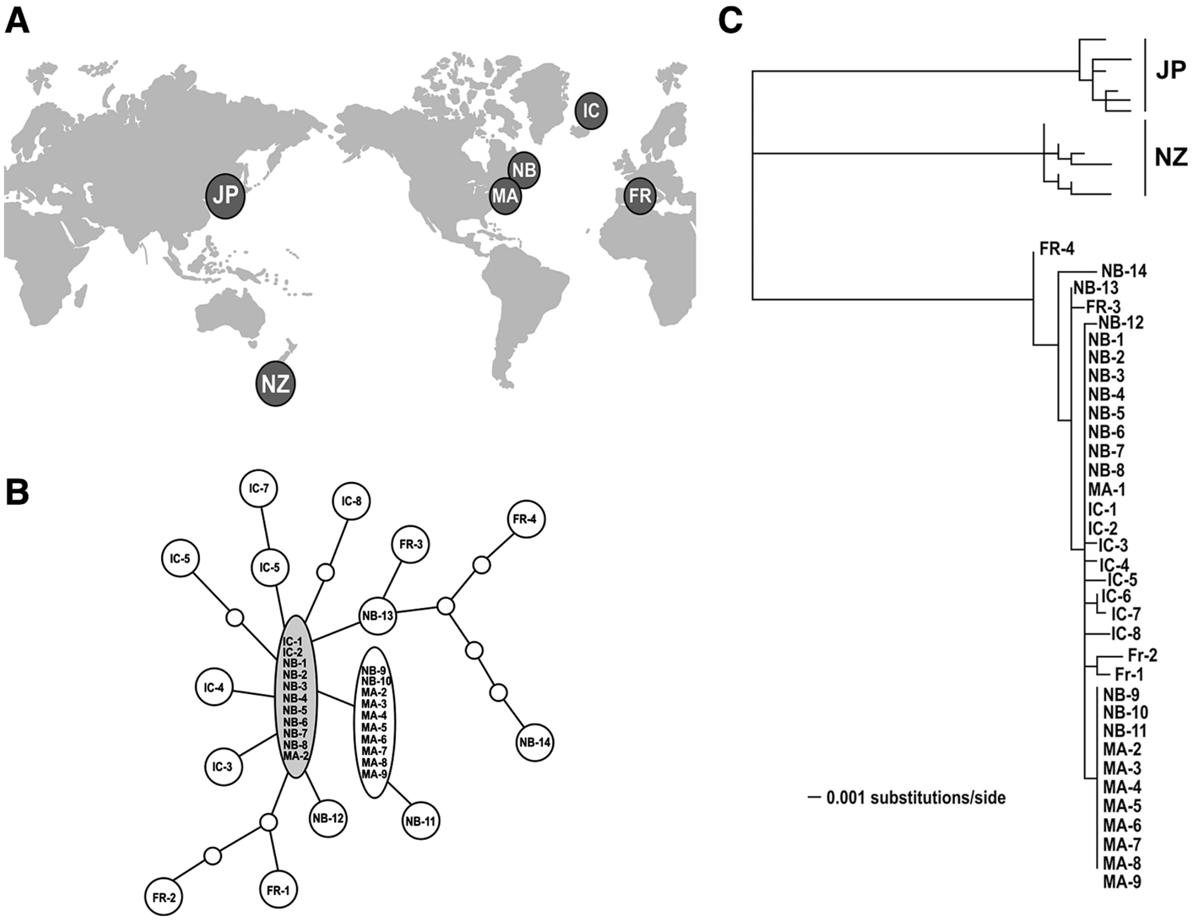

Figure 30 (A) Global distribution and sampling sites of the hydrozoan genus *Obelia geniculata*: JP – Japan, NZ – New Zealand, MA – Massachusetts, NB – New Brunswick, IC – Iceland, FR – France. (B) Haplotype network of mtDNA sequence data for populations of *O. geniculata* from the N Atlantic that shows that the Massachusetts population (MA) shares all haplotypes with New Brunswick (NB). (C) Phylogram based on same data for the populations of *O. geniculata* from Japan, New Zealand and the N Atlantic. This tree shows that within the N Atlantic many populations are paraphyletic (e.g., NB). Figures modified after Govindarajan et al. (2005).

distances considered here are extremely large for larval dispersal, episodic rafting routes mediated on plastic substrata (Aliani & Molcard 2003) could account for the cosmopolitan distribution of the species and the low but persistent gene flow that prevents allopatric speciation.

At this geographic scale and mostly toward 10,000 km, actual dispersal may be mostly human-mediated, but it cannot be excluded that rafting has occurred on isolated occasions in the evolutionary past. Rafting events may be so rare at this scale (e.g., one event every million years, episodic rafting routes) that populations have diverged significantly leading to allopatric speciation, and the observed genetic signals could be indicative of different species. Exemplifying this are the three deeply divergent clades (possibly cryptic species) of *Obelia geniculata* from Japan, New Zealand and the North Atlantic (Figure 30), which are thought to have originated >3 Mya. Rafting may have played a role in dispersing the ancestors of the populations from the different oceans (Govindarajan et al. 2005). Phylogeographic analysis of closely related species may be most suitable to reveal historic rafting events at this scale.

Gene flow patterns and contrasting developmental modes

In general, brooders show higher levels of genetic differentiation among local populations than species with planktonic larval development (McMillan et al. 1992, Duffy 1993, Hunt 1993, Edmands & Potts 1997, Arndt & Smith 1998, Chambers et al. 1998, Todd et al. 1998, Boisselier-Dubayle & Gofas 1999, Kyle & Boulding 2000, Wilke & Davis 2000, Collin 2001, Andrade et al. 2003) (Figure 29). In situations where gene flow is indeed low for direct-developing species, they usually show increasing genetic isolation with increasing geographic distance (IBD) (e.g., Hellberg 1994, Ayre et al. 1997, Wilke & Davis 2000, Collin 2001, Goldson et al. 2001, Vianna et al. 2003).

Several studies have compared genetic structure in taxa with different modes of development and have shown that sympatric sessile or semi-sessile species with contrasting modes of development often have similar genetic structure. Gene flow of sympatric species that are closely related (not necessarily congeners) may be constrained by similar dispersal barriers. The genetic differentiation values that have been reported among congeneric sympatric species with contrasting modes of development indicate that taxa with direct development generally display higher levels of genetic structure and IBD. Ayre et al. (1997) studied the genetic population structure of ascidians and corals from southeastern Australia, distinguishing solitary and colonial forms with high and limited dispersal potential, respectively. They found that solitary corals display little variation among local populations while local populations of colonial corals are highly differentiated. Comparison with data from other species inhabiting the same region confirmed their results (Hunt & Ayre 1989, Ayre et al. 1991, Hunt 1993, Billingham & Ayre 1996, Ayre et al. 1997, Hoskin 1997, Murray-Jones & Ayre 1997). The authors conclude that "even in a region where current flow is expected to be erratic, there is a clear contrast between the level of differentiation of broadcast-spawning and brooding species, and that for broadcast-spawning species the East Australian current is able to maintain high levels of gene flow and produce effectively panmictic breeding populations within the central and southern coasts of New South Wales" (Ayre et al. 1997).

Particularly interesting are studies of congeners that differ in their dispersal potential based on developmental mode alone. Many of these studies conclude that direct-developing species have highly structured populations and a more robust pattern of IBD than species with planktonic larval development (see Table 2).

Rafting can be invoked in cases where the phylogenetic and habitat characteristics of populations of species with contrasting modes of development are similar and the directly developing species lacks sufficient differentiation with respect to expectations (or does not fit an IBD pattern). For example, Ayre & Hughes (2000, 2004) have presented interesting results on the genetic divergence of populations of corals of the genus *Acropora* from the GBR in eastern Australia. In

Table 2 Comparison of population genetic differentiation values among congeners with different modes of development

Taxon	Genus	Direct development	Planktonic development	Reference
Anthozoa	*Acropora*	θ = *0.035 Nm = 6.89 1200 km	θ = *0.03 Nm = 8.08 1200 km	Ayre & Hughes 2000
	Acropora	F_{ST} = 0.29 Nm = 0.61 2400 km	F_{ST} = 0.21 Nm = 0.94 2500 km	Ayre & Hughes 2004
	Actinia	F_{ST} = 0.262 Nm = 2.33 1150 km	F_{ST} = 0.375 Nm = 0.42 1050 km	Ayre et al. 1991, Vianna et al. 2003
	Pocillopora	θ = 0.15 Nm = 1.42 2400 km	θ = 0.056 Nm = 4.21 2000 km	Ayre & Hughes 2004, Magalon et al. 2005
Eucarida	*Synalpheus*	θ = 0.54 Nm = 0.21 4800 km	θ = 0.14 Nm = 1.54 4800 km	Duffy 1993
Prosobranchia	*Cerithium*	F_{ST} = 0.58 Nm = 0.18 1750 km	F_{ST} = 0.158 Nm = 1.33 1750 km	Boisselier-Dubayle & Gofas 1999
	Crepidula	APV = *65.2 1300 km	APV = –7.4 1300 km	Collin 2001
	Hydrobia	F_{ST} = 0.41 Nm = 0.36 6000 km	F_{ST} = 0.25 Nm = 0.75 6000 km	Wilke & Davis 2000
	Littoraria	F_{ST} = 0.185 Nm = 1.1 4000 km	F_{ST} = 0.028 Nm = 8.68 4000 km	Andrade et al. 2003
	Littorina	Φ_{ST} = *0.06 Nm = 3.9 3600 km	Φ_{ST} = *0.03 Nm = 8 250–750 km	Kyle & Boulding 2000
Asteroidea	***Patiriella***	F_{ST} = 0.462 Nm = 0.29 230 km	F_{ST} = 0.0008 Nm = 312.25 230 km	Hunt 1993
Echinoidea	*Heliocidaris*	G_{ST} = 0.62 Nm = 0.15 3400 km	G_{ST} = 0.12 Nm = 1.83 3400 km	McMillan et al. 1992
Holothuroidea	***Cucumaria***	Φ_{ST} = 0.97 Nm = 0.01 2300 km	Φ_{ST} = 0.05 Nm = 4.75 2350 km	Arndt & Smith 1998
Ectoprocta (Bryozoa)	***Alcyonidium***	F_{ST} = 0.077 Nm = 3 800 km	F_{ST} = 0.105 Nm = 2.13 1500 km	Porter et al. 2002

Notes: For each genus we present estimates of genetic differentiation among populations (or their averages) for species with differing modes of development at similar spatial scales. Nm values were calculated according to Wright (1969). Genera in bold indicate that the species with direct development has been inferred to raft.

* Average value, details in Table 1.

their first study conducted at a scale of 1200 km they found that species with both direct and planktonic larval development were effectively panmictic (Ayre & Hughes 2000). Indeed all studied species display low genetic differentiation and relatively high number of migrants per generation. Subsequently they expanded the geographic scale of their study and found that at a scale of 2400 km, species with direct and planktonic larval development show similar genetic differentiation (Ayre & Hughes 2004). The above results suggest that corals with different developmental modes in the GBR have similar realised dispersal distances and frequencies. Some coral species of the genus *Acropora* are known to raft on pumice (Jokiel 1990a), and even though it is not direct evidence that the species included in the genetic studies (Ayre & Hughes 2000, 2004) is a rafter, it is possible that rafting mediated connectivity prevents genetic differentiation among populations of the direct-developing *Acropora cuneata*. Another example is provided by the comparison of the genetic differentiation in sea anemones provided by the studies of Vianna et al. (2003) and Ayre et al. (1991). They studied genetic differentiation in species of the genus *Actinia* with direct development from the coast of Bermuda and Brazil and with planktonic development from southeastern Australia, respectively. Interestingly, the direct-developing species displays lower genetic differentiation at a scale of 1150 km (Nm = 2.33) than the species with planktonic development at a similar scale (1050 km) (Nm = 0.42). Rafting has not been inferred for any of the two studied species of *Actinia*, but according to these data, the direct-developing *Actinia bermudensis* is achieving LDD by some means.

Another example that involves greater gene flow for direct-developing species than for species with planktonic development is seen in bryozoans of the genus *Alcyonidium,* but opposed to the examples given above, the species with short-lived lecitotrophic larvae (restricted potential for autonomous dispersal), *Alcyonidium gelatinosum*, has the potential for rafting on algae (Porter et al. 2002). These authors found that bryozoan species from the British Isles with direct development have less genetic differentiation at a scale of 800 km ($F_{ST} = 0.077$) than bryozoans with planktonic larval dispersal at a scale of 1500 km ($F_{ST} = 0.105$), which is likely due to rafting-mediated connectivity for the species with short-lived larvae.

Gastropods from the genus *Littorina* have been widely studied and compared with respect to their genetic structure and modes of development (Janson 1987a,b; Johannesson & Tatarenkov 1997; Johnson & Black 1998; Kyle & Boulding 2000; Andrade et al. 2003; Johannesson et al. 2004). Kyle & Boulding (2000) found that the direct-developing *L. sitkana* shows no genetic differentiation at the scale of >3000 km ($F_{ST} = 0$), and suggested that rafting has played an important role (see above). In general, species of *Littorina* that have planktonic larval development show similar or slightly less genetic differentiation at comparable scales than species with direct development.

All the above leads to the conclusion that rafting is an important means of dispersal at different spatial scales and as previously emphasised, dispersal potential cannot be inferred from developmental mode alone. From small to large spatial scales, connectivity achieved through rafting (as reported above), matches closely the described rafting routes, from frequent, to intermittent and episodic.

Rafting dispersal and evolution

Arrival in new habitats often leads to evolutionary change (Holt et al. 2005). This may be particularly true for species that have arrived on rafts as will be argued in the following subsections. One of the main differences between dispersal via rafting and planktonic larvae is that rafting, as opposed to larval dispersal, is usually not restricted to a particular ontogenetic stage. This may allow rafters to establish local populations during the rafting voyage (Thiel & Gutow 2005b). There are specific characteristics of the life history of many brooders that give additional evidence that they are particularly well adapted to colonise and persist after arriving in new habitats. Herein, genetic evidence will be reviewed that characterises the population structure of direct developers, and there will be discussion of the impact of rafting dispersal on (i) local recruitment and deme formation, (ii) colonisation across environmental gradients and (iii) the interplay between isolation and secondary admixture.

Local recruitment and deme formation

Rafting provides an effective means of dispersal for many brooders, particularly those that are likely to be found on floating substrata. Even though brooders may successfully achieve LDD through rafting, within a limited geographic area it has been observed that they show high levels of genetic differentiation (i.e., that they are highly microspatially structured) (Lessios et al. 1994, Johnson & Black 1995, Hoskin 1997). Organisms with direct development show distributions with greater patchiness than species with planktonic larval stages and within a patch they may contribute significantly to species diversity: "The fine scale spatial structure of direct-developing species was reflected in higher average species diversity within quadrats" (Johnson et al. 2001).

Peracarids are common rafters and display life-history characteristics that may enhance their probabilities of successful dispersal through rafting. They brood their eggs up to a crawl-away stage and in many species offspring recruit in close proximity to their parents (Flach 1992, Thiel et al. 1997, Thiel 1999). In the marine environment, some peracarids may live in algae and have a relatively high potential for passive dispersal by rafting. Thiel & Vásquez (2000) found that algal holdfast communities are characterised by dense aggregations of single peracarid species that do not correlate with holdfast size, suggesting that local recruitment of these species occurred within the holdfast. Juveniles often excavate their galleries as offshoots of the maternal gallery (Menzies 1957, Jones 1971, Conlan & Chess 1992, Thiel 2003a), as a consequence of extended parental care (for review see Thiel 2003b). Consequently, populations of brooders often show differentiation at a microgeographic spatial scale. For example, the isopod *Jaera albifrons* shows differentiation over a scale of a few metres, consistent with deme formation (Piertney & Carvalho 1994, 1995; Carvalho & Piertney 1997). Similarly, Lessios et al. (1994) identified differentiation at the scale of hundreds of metres in the isopod *Excirolana braziliensis*, and populations of the amphipod *Corophium volutator* show significant differentiation within the Bay of Fundy (Wilson et al. 1997). Thus, peracarids often exhibit microscale genetic structure consistent with local recruitment resulting in deme formation.

Johnson & Black (1995) studied the gene flow patterns in the brooding intertidal snail *Bembicium vittatum* in the Albrolhos Islands using direct and indirect methods. They found that along a continuous habitat there was a pattern of IBD that was absent in discontinuous habitats. Their results emphasise the importance of gene flow barriers on the genetic structure of species, particularly those with direct development. The recruitment pattern of these species, leading to deme formation within a microhabitat, could lead to high localised inbreeding (and potentially reduction in individual fitness) and divergence through genetic drift and localised selection (Piertney & Carvalho 1994, 1995). Deme formation appears to be common among species with direct development that inhabit patchy microhabitats (Piertney & Carvalho 1994, Sponer & Roy 2002, Colgan et al. 2005). However, Piertney & Carvalho 1995, found that the levels of genetic differentiation in *Jaera albifrons* resemble those found in other species with similar developmental modes that do not display deme formation, and thus, they concluded that "the ephemeral nature of some microhabitats may result in inbreeding being restricted to within one generation, reducing the overall effects of inbreeding depression and loss of heterozygosity in the localized population".

For brooders, local recruitment may represent an extreme advantage that enables them for LDD through rafting, as they may establish viable populations during the journey as well as during colonisation. In addition to local recruitment leading to deme formation, there are several other advantages that predispose direct developers for LDD; among the most important is their ability to disperse at any life stage (i.e., they are not restricted to the temporal duration of a particular ontogenetic stage in order to disperse).

Transport and colonisation across environmental gradients

On the microscale, rafting may occasionally transport organisms into habitats that are quite different from their native habitats. For example, this can happen across an intertidal gradient, where organisms from lower-shore habitats may be deposited on the higher shore. Due to their high colonisation potential, these rafting colonists may establish local populations, even in habitats with a new selective regime. Possibly this is occurring in species of *Littorina* from the North Pacific and North Atlantic, which are found both in the low and high intertidal zone. For the eastern North Atlantic, Panova & Johannesson (2004) reported divergent genetic adaptations between local populations of *L. saxatilis* from the lower and upper shore, which are in accordance with the respective selective pressures in either zone. Snyder & Gooch (1973) who studied this species in the western North Atlantic have discussed that "population isolation, with subsequent reduction in population size, promotes random drift and ultimate fixation of alleles. Shifting modes of natural selection over an ecologically heterogeneous area lead to genetic differences". Based on ecological responses of *L. saxatilis* from the low and high intertidal zone, Pardo & Johnson (2005) also suggested that "selection may favour genotypes with low growth potential in lower zones and those with high growth potential in higher zones". Cruz et al. (2004) suggested that divergence of ecotypes of *L. saxatilis*, which differ in size due to different selective environments, is enhanced by size-assortative mating patterns.

Sokolova & Boulding (2004) studied 'ecotypes' from the open shore and from salt marshes in two species of *Littorina* from the eastern North Pacific with consistent physiological differences. They suggested "that phenotypic differentiation in direct-developing species with limited dispersal is strongly affected by local adaptation and natural selection in heterogeneous habitats, and that strong local adaptation in the same type of habitat may result in convergent evolution producing superficially similar phenotypes". At least one of the species they studied (*L. sitkana*) is also thought to disperse frequently via rafting (Behrens Yamada 1989, Kyle & Boulding 2000).

Estevez (1994) reported isopods *Sphaeroma terebrans*, which usually bore into mangrove roots and wood, from rhizomes of saltmarsh plants. They suggested that isopods had arrived in the salt marsh on floating driftwood. Possibly, original founders colonised rhizomes due to lack of other suitable habitats. Nothing is known at present about the genetic relationship of rhizome populations and wood populations of *S. terebrans*.

For the saltmarsh plant *Elymus athericus*, Bockelmann et al. (2003) also reported that within-site populations from high and low shore differ more than between-site populations. They suggested "that markedly different selection regimes between these habitats, in particular intraspecific competition and herbivory, result in habitat adaptation and restricted gene flow over distances as small as 80 m".

Billard et al. (2005) revealed that Brittany populations of *Fucus vesiculosus* from the outer coast differed from those in bays. The authors suggested that this differentiation could be due to dispersal restrictions between bay and coastal populations. This is surprising since *F. vesiculosus* is probably the species from the genus *Fucus*, which is best adapted to float over considerable distances, and is commonly reported as floating in coastal waters of northwestern Europe (Tully & Ó Céidigh 1986, Davenport & Rees 1993, Franke et al. 1999, Vandendriessche et al., 2006). The possibility of differential selective pressures was not excluded by Billard et al. (2005): "Local population acclimation or adaptation to specific habitats causing lower establishment success between habitats cannot be ruled out as an additional explanation for this population differentiation".

The selective environments in the low and high intertidal zone or on the open shore and in sheltered bays are substantially different and this could result in genetic divergence of local populations across these gradients. For all of the species discussed above, rafting dispersal has been inferred or appears likely. However, why should these species be more prone to selective divergence across these gradients than other species? As mentioned above, rafting organisms have very little influence on selecting particular sites during the arrival process, and consequently they may be deposited over a wide range of ecological gradients. In contrast, planktonic larvae show diverse adaptations to select suitable habitats during settlement. They may settle only in a very restricted range across a gradient. Additionally, small, recently metamorphosed individuals may be highly susceptible to adverse environmental conditions. Rafting organisms, many of which feature direct development, release advanced developmental stages that may also survive in less favourable conditions. Consequently, rafters may initially survive over a wider range of environmental gradients than species with planktonic larvae. During subsequent population establishment, diverging selective pressures may result in genetic divergence of local populations, which is further enhanced by retention of lineages with favoured genes due to local recruitment of direct developers. Johannesson (2003) emphasised that: "The absence of pelagic larvae prevents rapid colonisation of habitats, but promotes local adaptation by subpopulations living generation after generation in the same habitat". In her excellent review on evolutionary processes in littorinid snails she concluded that "we have evidence both from morphological and molecular traits that directional selection can produce rapid evolutionary changes. If such changes create reproductive barriers either directly or as secondary effects, reproductive isolation (and thus speciation) might appear more or less instantaneously upon an ecological shift of a population". Interestingly, these rapid changes are most pronounced in those species with direct development, and rafting contributes to these microevolutionary processes. The interaction between rafting and direct development appears to play an important role in these processes, and it is suggested that future studies should *a priori* focus on this interaction. For species with planktonic larvae, Havenhand (1995) had stated: "Because the capacity for gene-flow between populations is frequently related to the dispersal potential of the larvae, the degree of larval dispersal may strongly mediate rates of evolution in marine species". Rates of evolution in some rafting-dispersed direct developers may be particularly fast due to the reasons discussed.

Isolation and secondary admixture

As emphasised above, LDD via rafting may often result in isolated local populations. In particular in populations established on episodic rafting routes, periods of isolation may be sufficiently long to result in significant population divergence. There are abundant examples in the literature suggesting isolated dispersal events (see above) that resulted in allopatric speciation. For example, for littorinid snails, Williams et al. (2003) suggested dispersal of ancestors of recent species from the genus *Austrolittorina* in the Southern Ocean between New Zealand and South America about 15–30 Mya, and due to the long distance and intermediate larval lifetime they invoked rafting as a potential dispersal mechanism. Williams & Reid (2004) also suggested transatlantic dispersal in the equatorial current system starting around 20 Mya ago, when oceanic currents became stronger. They inferred that dispersal has primarily taken place in an easterly direction, but they did not discuss the dispersal mechanism. Based on the phylogeography of the species-rich genus *Echinolittorina* they emphasised that "speciation may be predominantly allopatric in each case, but on long coastlines allopatry is more likely to be transient, because of greater opportunities for post-speciation range extension, whereas geographical isolation should be more complete in island settings" (Williams & Reid 2004). Donald et al. (2005) inferred rafting events to have played an important role in the phylogenetic evolution of snails from the family Trochidae. In a phylogenetic analysis of marine bivalves from the genus *Lasaea*, Ó Foighil et al. (2001) also suggested that rafting followed by isolation has repeatedly influenced evolutionary processes. Rafting may also affect evolution in species with planktonic larvae. For example, Waters & Roy (2003) stated with respect to a widespread seastar genus with planktonic larval development "that both rare dispersal (e.g., rafting) and recent vicariance (e.g., formation of the Benguela Current) may have promoted allopatric divergence and speciation in *Coscinasterias*".

Rafting dispersal followed by isolation has also led to allopatric speciation in many terrestrial species. Most recent evidence comes from phylogenetic studies on reptiles. Carranza et al. (2000) inferred that geckos from the genus *Neotarentula* colonised Cuba up to 23 Mya, coming from North Africa, most likely rafting in the North Equatorial Current. Glor et al. (2005) reported that Caribbean species from the genus *Anolis* have diverged on different islands following overwater dispersal (via rafting).

If isolation has not yet led to reproductive barriers, secondary contact via rafting may allow hybridisation of diverging clades. In general, founder effects, genetic bottlenecks, long periods of isolation and secondary admixture may result in a complex genetic pattern among local populations of many species. Possibly, the high degree of polymorphism among species commonly known as rafters is a consequence of various combinations of these processes. Occasional hybridisation between the different ecotypes of *Littorina saxatilis* may result in the observed polymorphism in this species (Pérez-Figueroa et al. 2005). Rafting may also allow exchange of similar ecotypes from different localities, further enhancing polymorphism in *L. saxatilis*. Another example might be found among the species of caprellid amphipods, which are commonly reported as rafters (Thiel & Gutow 2005b). Many of these species feature highly variable morphotypes (known as smooth and spinose forms). This group (and other peracarids) may prove in the future to be an excellent model to study evolutionary processes among common rafters with direct development.

Evolutionary processes influenced by rafting represent an exciting challenge for marine biologists. Rafting-mediated evolution shows some particularities that are the result of the fact that this dispersal process usually transports a limited number of individuals, which nevertheless have a high likelihood of successfully establishing populations in new habitats. This increases the probability of founder effects and population persistence, even in isolation from other populations. While this may also increase the risk of extinction (due to inbreeding and low genetic diversity), there is ample indication that many founder populations have persisted and spread successfully in new habitats. Arrival of conspecifics (or congeners) long after the arrival of early colonists may lead either to secondary admixture or to sympatric coexistence of closely related species.

In summary, evolutionary processes mediated by rafting can lead to species divergence, either in sympatry or in allopatry. Rafting thus contributes to local biodiversity, not only by importing colonisers to marine communities but also by facilitating speciation.

Implications for conservation of marine biodiversity

Connectivity and conservation

In accordance with conservation strategies applied in terrestrial systems, protected areas have been recognised as a powerful conservation tool in the marine environment also (Carr et al. 2003). Marine protected areas (MPA) and marine reserves are increasingly created in many regions of the world in order to provide refuges for over-exploited species or to protect biodiversity in general (Lubchenco et al. 2003, Palumbi 2004). Building on the metapopulation concept, it has been recognised that a single isolated MPA has only a limited potential for the protection of endangered species (Gerber et al. 2003). Isolated populations depend exclusively on local recruitment, making a population vulnerable to extinction if unpredictable climatic variations affect reproduction or survival (Figure 31).

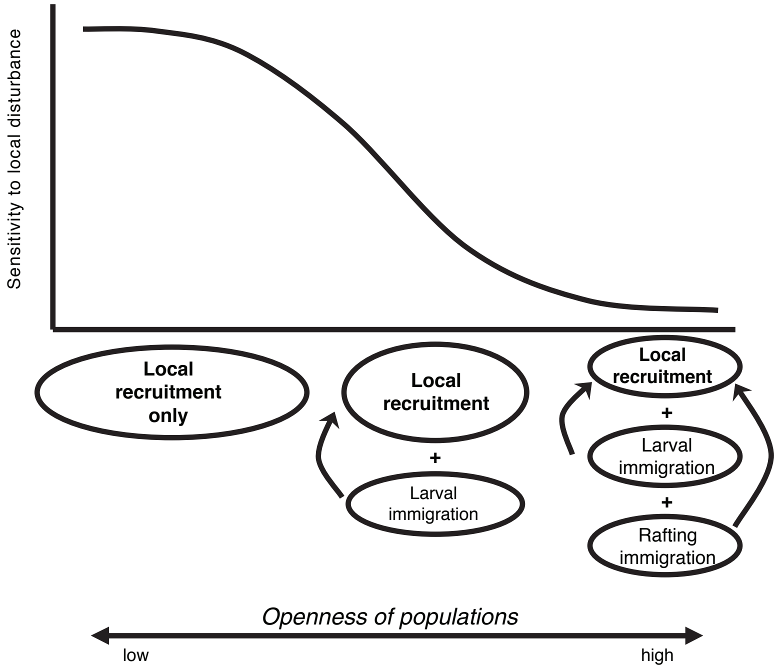

Figure 31 Relationship between the connectivity of local populations (via different mechanisms) and the sensitivity to disturbance. The openness or closed nature of populations makes them more or less dependent on local recruitment. Absolute dependence on local recruitment (closed population) leads to a high sensitivity to local disturbance, while populations open to the input of larval and/or rafting dispersal will be less sensitive to local disturbance.

Ensuring connectivity with other populations and immigration of propagules from other areas will alleviate failures in local recruitment and avoid extinctions of populations in an isolated reserve area. Consequently, networks of MPAs encompassing multiple local populations are required, because connected local populations are less vulnerable to local catastrophes (Figure 31). Resilience of a population to environmental changes can be expected to increase with the number of populations to which it is connected, because more connections result in a higher probability that at least some of the connections are not interrupted by environmental disturbances. Similarly, the larger the total area of a network, the higher is the probability that at least some of the local populations are not affected by local disturbances and maintain their function as a donor of individuals for affected populations (Allison et al. 2003, Halpern 2003). Rafting connections occur on a variety of spatial scales, and in particular those routes that connect local populations (frequent and intermittent rafting routes) need to be taken into account in the design of MPA networks.

The major challenge in the development of MPA networks is the appropriate spacing of the subunits of a network in order to allow for sufficient connectivity between local populations (Shanks et al. 2003). Consequently, the creation of efficient MPA networks requires detailed knowledge of the dispersal capacities of the species under protection. To date, most efforts have focused on species with planktonic larvae (e.g., Guichard et al. 2004) and/or active migration (e.g., swimming) (e.g., Rakitin & Kramer 1996). Even though empirical data for dispersal distances of commonly rafting organisms are rare, there is growing indication that this might substantially contribute to the connectivity among local populations (see above). In many regions, rafting and other alternative dispersal mechanisms may contribute to the connectivity among populations that appeared to be unconnected when accounting only for larval dispersal or active migration. Considering all relevant aspects in the assessment of the dispersal capacity of a species (including the possibility of rafting) will allow for an accurate estimate of the connectivity of populations, the relative importance of local recruitment vs. immigration processes, and the vulnerability of a population toward environmental variability (see, e.g., Gerber et al. 2005).

The development of efficient MPA networks requires a quantification of exchange processes of individuals between local populations. Even though complex behaviour (Yeung & Lee 2002) and physiological constraints of larvae (Anger 2003) complicate the modelling of dispersal, rafting dispersal is even more difficult to apprehend because it depends on multiple external variables and requires extensive empirical information from field investigations. The importance of external factors such as availability, quality, and longevity of rafts decreases the relative importance of intrinsic features of the organisms making exclusive laboratory investigations (as used for estimating the duration of larval development — see, e.g., Goffredo & Zaccanti 2004) insufficient in order to obtain reasonable estimates of rafting processes. The quantification of rafting opportunities and the assessment of the directionality of transport processes are basic aspects in the evaluation of the importance of rafting for the connectivity of populations in a given region.

In addition to the extrinsic factors depending on currents and floating substrata, the life history of organisms needs to be taken into account. For many of the taxa that have been found on floating substrata, relatively little is known about their population connectivity (Table 3). For example, even though amphipods are among the most abundant rafting species, only for very few species are data available about population connectivity. Despite this general lack of knowledge about rafting organisms, it can be mentioned that many species feature particular life-history characteristics. Many common rafting species are small, have a limited reproductive potential (individual clutch sizes usually <100 offspring) and feature direct development. Due to these characteristics, the inclusion of these organisms in effective conservation measures and the design of MPA networks require particular considerations.

Rafting connectivity is achieved via three important steps: (i) going onboard, (ii) surviving the voyage and (iii) disembarking and establishment. Only when all these steps are successfully completed can rafting be an efficient dispersal mechanism. The first two steps depend on both the organisms and the floating substrata, while the last step also depends to a high degree on the characteristics of the sink regions. Human activities are affecting the first two steps by changing the availability of floating substrata and the last step by modifying the characteristics of potential arrival sites.

Changes in rafting opportunities

In many regions of the world the frequency of rafting opportunities has changed significantly, often as a consequence of human activities affecting the spatial and temporal distribution of floating items. The introduction of large amounts of floating debris into the marine environment over the last decades has increased rafting opportunities (Winston 1982, Winston et al. 1997, Barnes 2002, Aliani & Molcard 2003, Masó et al. 2003) and, thus, is likely to have contributed to population connectivity for those species capable of rafting on artificial substrata. Even though floating anthropogenic debris might enhance population persistence by supporting species transport, its chronic presence may superimpose on natural dispersal patterns. The high longevity of plastics in the marine environment might result in transport of associated organisms over large distances, similar to that on pumice or other natural substrata that are available only sporadically. The ubiquitous and continuous presence of plastics may change the episodic character of LDD via rafting, thereby enhancing the frequency of rafting dispersal of many organisms across biogeographic barriers. This could lead to an enhanced globalisation of species transported on these long-lived substrata by raising the risk of species introductions (Barnes 2002). The introduction of

Table 3 Number of marine invertebrate species that have been reported or inferred as rafting in a previous review (Thiel & Gutow 2005b), and species for which data on the genetic population connectivity are available (see Table 1)

Taxon	Sum of rafting species	Sum of species with data for genetic population connectivity
Porifera	3	2
Cnidaria		
Hydrozoa	102	1
Anthozoa	28	27
Annelida		
Polychaeta	79	3
Arthropoda		
Cirripedia	22	2
Copepoda (Harpacticoida)	72	0
Hoplocarida	0	1
Eucarida	96	7
Peracarida (Amphipoda)	108	8
Peracarida (Isopoda)	38	7
Mollusca		
Gastropoda (Prosobranchia)	72	27
Gastropoda (Opisthobranchia)	44	2
Bivalvia	51	4
Cephalopoda	11	1
Echinodermata		
Asteroidea	16	7
Echinoidea	7	14
Holothuroidea	6	2
Ophiuroidea	11	1
Ectoprocta (Bryozoa)	96	5
Chordata		
Tunicata	11	3
Total	873	124

non-indigenous species into new regions has been recognised as a major threat to biodiversity (Carlton & Geller 1993). Especially polar regions, which are thought to be particularly vulnerable to the harmful effects of bioinvasions due to their high degree of endemism (Barnes & Fraser 2003), are expected to be threatened by an increasing amount of floating debris in the world's oceans (Barnes 2002). However, the role of plastics in the 'ecological roulette' of bioinvasions is discussed controversially and some scientists believe that the role of plastic rafting may be overestimated. In order to evaluate risks created by these substrata, the global distribution pattern of floating anthropogenic material has to be taken into consideration. In coastal waters near the centres of human activity at low and mid latitudes, floating marine debris is highly abundant (Thiel & Gutow 2005a), possibly contributing significantly to the transport of species (e.g., Winston et al. 1997, Masó et al. 2003, Aliani & Molcard 2003). At high latitudes, however, where densities of floating plastics are lower, the contribution of these items to the overall transport of marine species has not yet been evaluated thoroughly. Based on the finding of plastic-rafted organisms, Barnes & Fraser (2003) confirmed that some species could be successfully dispersed by rafting in Antarctic and subantarctic waters. Lewis et al. (2005) agree that floating plastics provide artificial surfaces for settlement of organisms but they consider fouling on ship hulls as a more imminent threat to polar biodiversity. Furthermore, due to the low abundances of floating plastics in polar waters, compared to naturally occurring substrata such as pumice or floating macroalgae, the authors expect floating plastics to simply supplement already existing natural pathways in Antarctic waters but produce no significant effects on biodiversity (Lewis et al. 2005). At lower latitudes, however, there is some indication that rafting on anthropogenic floating substrata has already led to significant niche expansions or to the spread of species into areas previously not colonised by them. Winston (1982) described how an increasing amount of floating plastics can facilitate the proliferation of species. The bryozoan *Electra tenella* was rare at the Atlantic coast of Florida, but its ability to colonise artificial substrata enabled this species to establish in the region and to persist in competition with indigenous species such as the bryozoan *Membranipora tuberculata*, usually competitively superior in the natural benthic environment. Similarly, range expansion via rafting has also been inferred for the Pacific oyster *Lopha cristagalli*, formerly known only from northernmost New Zealand. Individuals of this species have been found on stranded rope masses on a remote beach of the South Island of New Zealand (Winston et al. 1997). These examples indicate that an increasing amount of floating debris in the world's oceans results in an intensified transport of organisms potentially beyond existing distributional limits.

In addition to contributing directly to bioinvasions, rafting can also facilitate the local or regional spread of a non-indigenous species after these have been introduced by alternative dispersal mechanisms. The barnacle *Elminius modestus* was brought to European waters in the 1950s on ship hulls from the South Pacific (Crisp 1958). Within a few decades this species spread rapidly throughout the coastal regions of northwestern Europe. Rafting has never been discussed as a potential mechanism for regional dispersal of this species in European waters. Recent reports of *E. modestus* from floating debris in the North Atlantic (Barnes & Milner 2005) indicate that rafting on anthropogenic rafts cannot categorically be excluded as a possible mechanism for the extensive spread of this species in its new environment. Rafting has also been discussed as a possible mechanism for regional spread of the skeleton shrimp *Caprella mutica* in the North Sea where the species was co-introduced with the pacific oyster *Crassostrea gigas* (Buschbaum & Gutow 2005).

These examples indicate the potential of persistent anthropogenic rafts in facilitating species invasions that might be less likely under natural conditions of raft availability and quality. While the availability of anthropogenic flotsam has increased, naturally occurring types have, in turn, decreased in abundance in the marine environment, at least regionally. Logging activities have changed the supply of floating wood in many areas of the world during the past centuries (Maser & Sedell 1994). Damming of rivers has led to retention of floating wood, which is no longer delivered to the sea during flood events. Similarly, shoreline stabilisations such as dikings and embankments prevent seasonal flooding of coastal lowlands. Terrestrial plant material usually washed out during these events is retained and, consequently, not available for important seasonal dispersal events.

Modern coastlines and connectivity

There are numerous factors that influence the arrival process of rafters (Thiel & Gutow 2005b). Human activities may affect this process in two important ways, namely by modifying the filter efficiency of many habitats and the retention efficiency of coastlines.

The filter effect refers to the structure of many habitats where vascular plants or algae extend across the sea surface, effectively filtering out most floating substrata preventing these from being washed onto inhospitable beaches or higher shores. This filter effect is vividly described by Simberloff & Wilson (1969) for small mangrove islands: "Drifting wood usually hits an island, gets trapped temporarily among roots, and eventually floats away". Similar observations were made for kelp forests, where floating algae frequently entangle in kelp forests (Zobell 1971, Dayton et al.

Figure 32 Grazing has an important effect on the filter efficiency of salt marshes. (A) Ungrazed salt marsh showing that large quantities of floating debris are filtered out by the vegetation, and (B) grazed salt marsh showing that plant debris passes the salt marsh without being filtered out before ending up on the dike (photos courtesy of Martin Stock, Nationalparkamt Schleswig-Holsteinisches Wattenmeer, Germany).

1984, Dayton 1985). Any activity that leads to an elimination or length reduction in the plants/algae that constitute the filter will also reduce their efficiency in filtering out floating substrata at the sea surface. For example, mangrove clear-cutting, in particular on the seaward edge of mangrove forests, leads to a reduction of roots intersecting the sea surface. Similarly, industrial-scale kelp harvesting removes a large proportion of the surface canopy (California Department of Fish and Game 2000, Casas et al. 2003), reducing the filter efficiency of kelp beds. Intensive grazing of saltmarsh vegetation produces a very short lawn unable to filter floating detritus during high tides (Figure 32). These effects may cause most floating materials to end up directly on the high shore where living conditions are unsuitable for most marine rafters.

The retention efficiency of coastal areas depends on the geomorphology of the shore. Highly fragmented coastlines with many semienclosed bays and inlets facilitate the retention of floating items within such bays. Turbulent current and front systems and coastal eddies, characteristic for many irregular coastal areas, might prevent floating items from escaping to offshore waters (Largier 2003) and, thus, increase the probability of successful disembarking of rafting organisms. Harrold & Lisin (1989), for example, observed that the majority of *Macrocystis pyrifera* rafts in Monterey Bay (California) remained within the bay as a consequence of local current and wind conditions. This process is supported by internal waves and surface slicks that often transport floating objects toward the shore (Kingsford & Choat 1986, Shanks 2002). These coastlines thus provide ample opportunities for rafting organisms to disembark from floating items. In contrast, linear coastlines have only a limited retention efficiency because water movements are intensified along the entire shore. Human activities in many of the densely inhabited coastal regions of the world have significantly modified coastlines during the past centuries. For example, until the late 1700s, the North Sea coast of Germany was highly fragmented with long-stretching estuaries where tidal currents reached far inland (Figure 33). As a consequence of extensive diking during the past centuries, the shape of the coastline has been smoothed dramatically, and many of the smaller estuaries are now cut off from tidal influence. Canalisation of larger estuaries and intensified river runoff might lead to stronger seaward-directed currents preventing the arrival of rafts in up-estuary habitats. Consequences of all these changes are similar to those of the filter effect. Floating substrata are no longer retained in shallow waters but rather end up on inhospitable dikes. Coastlines of many tropical and subtropical regions have experienced similar modifications. For example, the Atlantic coast of Florida, which until the beginning of the twentieth century was highly fragmented, was artificially remodelled by raising the height of supratidal areas and simultaneously deepening

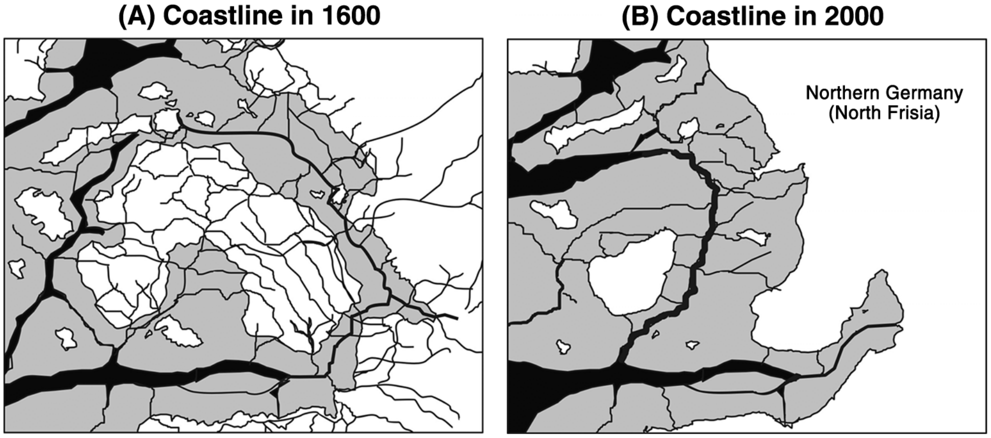

Figure 33 Maps of the North Sea coast of N Germany in the sixteenth century (A) and at present (B), showing the high degree of fragmentation in the sixteenth century and the rectilinear coastlines predominating since the twentieth century. Land (white), intertidal flats (shading) and subtidal streams and rivers (black) are shown.

shallow subtidal areas. The reduced extension of intertidal and low supratidal areas may have compromised the retention efficiency in many of these coastal regions. These changes usually lead to enhanced flow speeds in the remaining coastal waters. Davis et al. (2002) remarked that in highly modified bays "nutrients, food, and larvae in this water have a greater open-coast signal". While these modifications enhance exchange of water masses and thereby the transport of planktonic organisms (and larvae), they may result in a reduced connectivity via rafting dispersal. To the present authors' knowledge rafting-mediated dispersal has never been addressed in studies concerned with the modifications of coastlines. It is apparent that in addition to the loss of habitat and biodiversity, changes in the rafting dispersal processes and connectivity may be important secondary consequences of these human interventions of coastlines.

Other human activities may lead to enhanced population connectivity via rafting in coastal waters. Artificial hard substrata such as harbours, aquaculture installations, navigation buoys, platforms, wind energy towers or piers constitute settlement substrata for a great diversity of organisms (Davis et al. 2002, Bram et al. 2005). All these constructions intercept the sea surface and thus may also retain floating substrata. In fact, cleaning of entangled floating algae has been reported to produce major costs to aquaculture installations in Australia (Hodson et al. 1997). Other anthropogenic structures are also assumed to retain floating items. Already established algal communities on breakwaters, jetties and piers may filter out floating items from the sea surface, thereby facilitating successful arrival of rafting organisms. Johannesson & Warmoes (1990) reported rapid colonisation of breakwaters on the Belgian coast (where natural hard substrata are lacking) by *Littorina saxatilis*, which most likely had arrived via rafting. Similarly, Dethier et al. (2003) remarked that direct development and the lack of an autonomous dispersal stage is no impediment to successful colonisation of a rock jetty at considerable distance (>40 km) from potential source populations. These examples demonstrate that artificial structures can serve as intermediate stepping stones, not only for species with planktonic larvae, but also for those that are thought to arrive as rafters. Anthropogenic structures may not only act as filters for floating substrata, but also as retention areas. For example, harbour basins often represent zones of reduced current velocities (Bulleri & Chapman 2004), where floating items might linger for longer time periods increasing the probability of successful disembarkation of associated rafters. In addition to their action in filtering out or retaining floating items, anthropogenic structures may also serve as important stepping stones, leading to a higher connectivity among local populations. In this context, Pinn et al. (2005) remarked that artificial hard substrata may “influence the dispersal of sessile organisms, allowing species that are poor dispersers to cover greater distances by using these structures as stepping stones” (see also Thompson et al. 2002).

In general, human activities affect various stages of rafting journeys. Some activities may enhance connectivity between populations (introduction of plastics, construction of artificial filters and stepping stones), while others lead to a decreasing connectivity (retention of riverwood, elimination of filter habitats, coastline construction). Species that depend almost exclusively on rafting for dispersal can be expected to be most affected by these changes.

Outlook

Some of the expressions most commonly used in this review are ‘may be’ or ‘suggest’. This demonstrates the high degree of uncertainty with respect to rafting as a dispersal process in the sea. However, the abundance of cases where authors are left with rafting as the only reasonable explanation for a certain pattern, is giving a clear signal. Rafting does occur and it connects populations of many species, or it transports organisms to new habitats where they may establish new populations. Based on the accumulated evidence the present authors believe that it is high time to move beyond the suggestive phase. Rafting plays an important role over most spatial and temporal scales operating in present-day oceans. The urgent need for effective and representative conservation measures in the marine environment requires that rafting be taken into account.

The directionality of rafting dispersal, similar to the situation for larval dispersal, is crucial for the spatial arrangement of marine reserve networks. Accordingly, marine network reserves need to consider connectivity including rafting-mediated dispersal, which requires understanding the rafting dynamics of marine metapopulations (i.e., source-sink dynamics, sources of floating substrata). For example, if populations persist in a source-sink system with down-current sink populations being supplied from a large up-current source population, it is important to define adequate up-current reserve areas. The up-current area must not only provide supply of individuals but also sufficient rafts necessary for appropriate transport of organisms. The identification of relevant natural raft sources such as macroalgal belts, mangrove forests, salt marshes, or seagrass beds (see above) are, thus, obligatory for the development of efficient management programmes. Recognition of source areas might be complicated when rafts originate from distant sources without any obvious spatial relation to the actual conservation area. Rafts themselves (or the rafting organisms) may carry signals that allow the identification of source areas. Jokiel (1989), for example, collected rafting colonies of corals from floating pumice at Hawaii: the chemical composition of pumice can be utilised to identify source regions (Frick & Kent 1984, Jokiel & Cox 2003). Other characteristics of floating items (or size of rafting organisms) could also be used to infer their origin. Some of the most powerful tools to identify potential source regions are the genetic signals of the organisms themselves as has been demonstrated by several of the studies presented herein.

Rafting not only poses challenges to conservation biologists, it also offers opportunities. One of the main questions in the study of marine reserve design is the question for source and sink regions: where do the organisms living in a marine reserve actually come from? Also one of the principal questions related to rafters observed on the high seas (or arriving in coastal habitats) is, where do they come from? Rafters can be traced back to the source regions by a variety of methods (see above). However, in contrast to tiny planktonic larvae, where evidence for source regions usually is inferential (e.g., Becker et al. 2005, Zacherl 2005), rafts can also be followed at sea and tracked during the rafting journey. Following dispersing organisms would also provide an understanding of the processes leading to the survival or demise of rafters. In a previous review (Thiel & Gutow 2005b), it was argued that long-distance rafters may reproduce during the journey, and in the present review it is suggested that this may lead to founder effects within rafts. These processes may also influence the viability and genetic structure of groups of colonisers in new habitats. In order to understand these processes satisfactorily it is necessary not only to examine populations in source and sink regions, but also groups of travellers. It is therefore suggested that molecular studies that examine the population connectivity of coastal organisms should also incorporate rafting individuals whenever possible and feasible. It appears that the study by Reusch (2002) is the only one that sampled rafting individuals in an attempt to identify their source of origin with the aid of molecular markers.

While rafting on the one hand offers unique opportunities in tracking organisms, on the other hand, direct testimony of arrival is much less likely than for species with planktonic larvae. Numerous studies have examined settlement in planktonic larvae, and many more have monitored recruitment events (for synthesis see, e.g., Eckert 2003). In contrast, very few investigators were actually present during the arrival of rafters. Successful colonisations by rafters are often only detected a long time after the arrival event. This is not very different from the arrival of species transported by other dispersal agents (e.g., birds, fish or humans). In these cases, the appearance of invaders often is noticed many years or decades after the first arrival. Not surprisingly, very little is known about the arrival process and initial colonisation in both categories. Consequently, in many cases it is difficult to infer whether an organism has arrived in a new area via rafting or via other agent-mediated transport mechanisms. Molecular studies can help to answer this question, because they permit an estimation of whether arrival has happened very recently or far back in time. For example, in a series of studies Duran et al. (2004a,b,c) have examined the present geographic distribution of the marine sponge *Crambe crambe* (which has short-lived lecitotrophic larvae) around the coasts of the Mediterranean and the North Atlantic (Madeira and Canary islands). At a scale of 3000 km, Duran et al. (2004a,b) found high genetic structure of populations following an IBD pattern based on microsatellites and nuclear DNA. The shallow divergence among sequence types in this study, led the authors to propose that *C. crambe* either is a young species (with no time to generate large sequence divergence) or an old species that has suffered demographic changes or a low mutation rate (Duran et al. 2004b). Duran et al. (2004b) elaborated on potential demographic changes as being "a strong recent bottleneck that has reduced its former genetic diversity, followed by a new expansion and accumulation of new mutations". The authors offered human-mediated dispersal as the most likely explanation for recent exchange among populations of *C. crambe*, but they did not completely discount rafting as a possibility, which could result in a similar genetic pattern.

Molecular studies have also helped to reveal that the present-day distribution of many organisms is due to historic dispersal events, most likely via rafting. In the wake of these studies it has been increasingly recognised that rafting may have contributed significantly to the species succession and biodiversity of coastal ecosystems and island communities. More species may have reached these habitats via rafting than previously assumed. For example, in an extensive review (Thiel & Gutow 2005b) reported a total of 17 invertebrate species for which rafting was inferred based on genetic data. Twelve of these species have never been observed on or near a raft, but based on all available evidence the authors of the respective studies offered rafting as the most probable explanation for the observed genetic patterns. It is likely that in the future the number of species for which rafting is inferred based on genetic evidence will be increasing.

Extensive evidence has been provided that rafting is an important mechanism that affects biodiversity at a local and global level. From frequent to episodic rafting routes there exists a continuum of rafting intensity, distance and selective pressures (= filters) posed to rafters, which influences processes from population dynamics to allopatric speciation. It has been shown that different rafting routes provide varying degrees of connectivity for populations. Also, that organisms with direct development can achieve LDD via rafting and that the Rockall Paradox is no longer a paradox. Based on the evidence and examples presented herein, it becomes clear that rafting-mediated dispersal of organisms is yet another process that needs to be taken into account when studying and interpreting the biogeography and evolution of coastal organisms.

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