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Rafting of benthic macrofauna: important factors determining the temporal succession of the assemblage on detached macroalgae

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Abstract

Rafting on biotic and abiotic substrata has been reported for many benthic marine invertebrates. Here, I describe important characteristics of common floating substrata and review published studies examining the succession of the assemblage on detached macroalgae to identify the most important factors determining this succession. Floating substrata differ in survival time (i.e. before they disintegrate) and in food value, with abiotic materials having high survival times but low food value and some biotic substrata (seagrasses, fresh wood) having high food values but short survival times. Large macroalgae with pneumatocysts may combine high survival times and high food values. Substratum survival and food value have consequences for the species composition of the rafting macrofauna. In general, suspension feeders dominate rafting assemblages on abiotic substrata, while grazing and boring species abound on macroalgae and wood. The succession of the rafting assemblage can be subdivided into three phases during which different processes predominate. During the initial phase some of the original colonizers (if present) disappear from the substratum, either due to active emigration or predation. This short, initial phase is followed immediately by the colonization phase, during which new organisms colonize the rafting substratum. Colonization may be rapid and intense in the beginning but then slows down. Towards the end of the colonization phase, some rafting organisms may reproduce and their offspring recruit within the parental raft. Results from two long-term studies confirmed that the proportion of species with direct development increased with duration of rafting. These successional changes will be most pronounced for large biotic substrata, rendering these particularly suitable for long-distance dispersal of organisms with direct development.

Introduction

Rafting on natural and anthropogenic floating material has been inferred as an important dispersal mechanism for many littoral marine invertebrates (Ingólfsson, 1995; Ó Foighil et al., 1999, 2001; Castilla & Guiñez, 2000). Organisms have been found rafting on a wide variety of different substrata of natural (wood, seagrasses, macroalgae, volcanic pumice, corals) and anthropogenic (plastics, tar balls, manufactured wood) origin. Floating substrata may differ not only in origin but also with respect to quality (food value, floatation potential, etc.). Some substrata may be much more suitable for rafting organisms than others. In particular, large macroalgae, which might continue to grow after detachment, combine a relatively high food value with high floatation potential.

Rafting assemblages may also be highly diverse (Hobday, 2000a), and strong competition for both space and food resources may exist among rafting organisms. Some species possess traits that make them much more suitable for rafting than others. For example, peracarid crustaceans, and other brooding marine invertebrates, are typically abundant on floating macroalgae (Hobday, 2000a; Castilla & Guiñez, 2000). These species may persist better than others during the voyage on floating substrata because their offspring may recruit directly to the parental raft, leading to successional changes of the rafting assemblage during the voyage. While many studies report the composition of the rafting assemblage at some moment after the start of the voyage (e.g. Helmuth et al., 1994; Ingólfsson, 1995; Hobday, 2000a), relatively little is known about the temporal succession of rafting assemblages. This succession depends not only on the biology of the rafting organisms, but also on the properties and history of the floating substrata. Since the outcome of the succession of the rafting assemblage during the voyage on floating substrata determines which species may arrive in new habitats, this process is of crucial importance when discussing rafting as a dispersal mechanism. Here, I identify some characteristics of the main substrata commonly harbouring rafting organisms and review several studies that report the temporal succession of the rafting assemblage. Rather than serve as an exhaustive review, this contribution represents a step in identifying some of the important processes and mechanisms involved in the succession of rafting assemblages.

Materials and methods

Recent publications were reviewed to identify and characterize the most ubiquitous floating substrata in the world's oceans. Particular emphasis was placed on characteristics of importance for potential rafting organisms. Species succession on abiotic floating substrata has been examined in a variety of different studies, but relatively little is known about this process on floating macroalgae. To obtain an estimate of successional changes of the rafting assemblage, three experimental studies, which investigated the succession of associated organisms on macroalgae after detachment from the primary substratum, were evaluated and examined for the existence of common patterns. All three studies were conducted with algal species that possess pneumatocysts and are commonly found floating at the sea surface. The first (Ingólfsson, 1998) examined the temporal succession of organisms associated with fronds of *Ascophyllum nodosum* (L.), while the second (Edgar, 1987) and third (Vásquez, 1993) examined the fauna associated with holdfasts of the giant kelp *Macrocystis pyrifera* (L.) (Table 1). I have evaluated these studies with respect to the total abundance of organisms associated with the detached macroalgae and the proportion of individuals with direct development. Furthermore, I mention briefly some of the important observations on the successional changes made by these authors.

Results and discussion

Floating substrata

A wide diversity of floating materials originating from human activities is found in the world's oceans. These items are reported frequently from seashores, even on remote islands (e.g. Barnes, 2002). Surveys have revealed that plastic items usually dominate floating marine debris, but glass bottles or metal containers are also found commonly in shore-based surveys (e.g. Garrity & Levings, 1993; Williams & Tudor, 2001). Besides these packaging materials, various other substrata originating from human activities have been reported, including tar balls and manufactured wood (Table 2). Sea-based surveys report similar materials, but plastic bags and fishing gear appear less abundant in shore-based surveys. Floating marine litter is most common at mid and low latitudes, close to major human populations (Matsumura & Nasu, 1997). Typically, these items are most abundant in coastal waters, but are also found in the open ocean. Among the most important biotic substrata are macroalgae, which are commonly reported from coastal areas, but have also been observed in the open ocean (Kingsford, 1992, 1995; Helmuth et al., 1994; Ingólfsson, 1995, 2000; Hobday, 2000b, c; Hirata et al., 2001).

Floating substrata differ widely in their nutritive value for rafting organisms. Macroalgae and seagrasses may be of high nutritional value for grazers, and animal remains may also be of high nutritional value depending on the proportion of organic tissue. Most floating litter (except for manufactured wood or other organic litter) present no nutritive value for rafting organisms, which is also true for other abiotic substrata such as volcanic pumice or buoyant coral (Table 2).

Survival estimates for floating items differ widely. Some abiotic substrata, such as pumice or some plastic litter, may float for years (Jokiel, 1989; Ebbesmeyer & Ingraham, 1992). Floating kelp has been inferred to remain afloat for more than 1 y (e.g. Dayton et al., 1984), while other authors suggest a lifetime of only a few days (Harrold & Lisin, 1989). Water temperatures and nutrient availability may play an important role in determining longevity of floating macroalgae (e.g. Edgar, 1987). Hobday (2000b) examined the aging rates of *M. pyrifera* in tethered plants and concluded that most rafts would disintegrate after <100 d, at least at water temperatures $>20\,°C$. Surprisingly little is known about floating times of wood,

Table 1. Data of the three studies examining the fauna associated with macroalgae detached from the primary substratum and tethered at the sea surface or in the water column

Macroalgal species	Algal part	Study site	Water depth (m)	Duration (d)	Reference
Ascophyllum nodosum	fronds	Iceland	0	20	Ingólfsson (1998)
Macrocystis pyrifera	holdfast	Tasmania	15	191	Edgar (1987)
Macrocystis pyrifera	holdfast	California	5–10	110	Vásquez (1993)

Table 2. Common floating substrata and some important properties, relevant to rafting; information on food value and floating potential inferred from primary literature (see 'Reference' section)

Substratum	Sources	Biotic/abiotic	Food value	Floating potential
Macroalgae*	natural	biotic	high	high
Seagrass plants	natural	biotic	high	low
Sea beans	natural	biotic	intermediate	very high
Natural wood*	natural	biotic	intermediate	high
Animal remains	natural	biotic/abiotic	high/low	low
Volcanic pumice	natural	abiotic	low	very high
Buoyant coral	natural	abiotic	low	very high
Plastic*	anthropogenic	abiotic	none	high
Glass	anthropogenic	abiotic	none	intermediate
Metal	anthropogenic	abiotic	none	intermediate
Manufactured wood	anthropogenic	biotic	intermediate	high
Organic litter	anthropogenic	biotic	intermediate/low	low
Tar balls	natural/anthrop.	abiotic	low	intermediate

* Most commonly reported floating substrata.

but anecdotal information and dense accumulations of adult-sized marine invertebrates on wooden items, indicate that these can float for a long time. Since some floating items may remain afloat for long time periods (months), there exists a potential for the rafting assemblage to undergo successional change.

Floating substrata can be divided into two major categories: substrata that carry abundant and diverse epibiota before starting their voyage, and substrata that start out without any epibiota. The former comprises substrata that previously had been attached in coastal habitats where they may have become colonized by a wide variety of benthic organisms. Among these substrata, macroalgae, which may become detached during storms (e.g. Witman, 1987; Seymour et al., 1989), typically predominate. Substrata originating from anchored installations, such as harbours or aquaculture materials (e.g. buoys), may also be inhabited by fouling organisms at the moment of detachment. In contrast to these substrata, most marine litter, volcanic pumice and wood are not colonized by marine fauna before starting their voyage. In summary, biotic substrata tend to start their voyage with passengers from many different faunal and floral taxa, while most abiotic substrata start in a 'clean' state.

Temporal succession of the rafting assemblage

Although the succession of rafting assemblages is best studied by following floating items in time and space, tracking free-floating items across the ocean surface imposes considerable logistical constraints (see e.g. Harrold & Lisin, 1989). Consequently, most studies that follow the succession of rafting assemblages over long time periods ($>$ a few days) use tethered substrata, except for two studies of free-floating macroalgae during the first few hours after detachment (Kingsford & Choat, 1985; Kingsford, 1992). Usually, tethering is done by tying floating items to weights, typically anchored in coastal habitats close to potential source populations. Furthermore, these experiments are conducted in sheltered bays to reduce the risk of losing tethered items.

There exists a vast literature on the species succession of the fouling assemblage on abiotic (typically artificial) substrata (for recent reviews see e.g. Wahl, 1997; Svane & Petersen, 2001). In general, these substrata become colonized by suspension-feeding organisms such as sponges, hydrozoans, bryozoans and ascidians together with a diverse associated fauna (e.g. Greene & Schoener, 1982; Relini et al., 2000; Holloway & Connell, 2002). This pattern, with a dominance of clonal suspension feeders, is in accordance with the results obtained from abiotic floating substrata collected in the flotsam (Winston et al., 1997; Barnes & Sanderson, 2000). While the main pattern of the successional changes on abiotic substrata (e.g. marine litter) is relatively well known, little is known about the species succession on floating biotic substrata. Some studies describe the successional changes in wood (e.g. Si et al., 2000; Tuente et al., 2002), but the succession of the rafting assemblages on macroalgae has been little studied despite their abundance and importance as floating substrata (e.g. Helmuth et al., 1994; Ingólfsson, 1995, 2000; Hobday, 2000c; Hirata et al., 2001; Smith, 2002).

In the three studies that examined the succession of the macrofauna organisms on macroalgae after detachment, some general trends were observed. The macroalgae remained intact for the duration of the respective experiments, but Vásquez (1993) and Edgar (1987) remarked that kelp holdfasts started to disintegrate after 110 d and 191 d, respectively. Edgar (1987) attributed this to the destructive activity of boring isopods, which increased in abundance during the experiment.

The temporal succession of the macrofaunal assemblage on detached macroalgae followed some general patterns. Numbers of species and total individuals remained very high or even increased after detachment (Fig. 1). In the *Ascophyllum*-study, abundance of associated organisms increased rapidly (Fig. 1A), primarily due to colonization by blue mussels and harpacticoid copepods via the water column (Ingólfsson, 1998). In the two holdfast studies, a small initial decrease in individual abundance was observed but, after approximately 10 d, numbers of associated organisms remained stable (Fig. 1B, C). In general, total species and individual numbers remained relatively high throughout the duration of the experiments, but some species and individual exchange occurred after deployment in the water column. The associated fauna of the kelp holdfasts comprised species from all major phyla (Arthropoda, Mollusca, Echinodermata and Annelida). Shortly after becoming detached, some of the original inhabitants disappeared from the substratum. Vásquez (1993) observed that, initially, ophiurids dominated the associated fauna, but their densities decreased strongly after deployment of the holdfasts in the water column. Molluscs and polychaetes also decreased in abundance shortly after deployment. This may be an active process where animals leave the floating substratum to fall or swim back to benthic habitats, or it may be a passive process where some organisms are selectively preyed upon by fish (Kingsford & Choat, 1985; Davenport & Rees, 1993; Shaffer et al., 1995; Deudero & Morales-Nin, 2000; Ingólfsson & Kristjánsson, 2002). Following this initial loss, either a strong increase of individual numbers on substrata can be observed or a stable phase occurs where eventual losses are balanced by new colonization. When substrata remain in the water column for relatively long time periods (>40 d), local reproduction and recruitment may occur, leading to a dominance of organisms with direct development on the floating substrata. Peracarid crustaceans were among the most abundant macrofauna organisms in the holdfasts and occurred also on the *Ascophyllum* fronds. In the study by Vásquez (1993), peracarids increased dramatically towards the end of the experiment, comprising >90% of all associated organisms at the final sampling date (110 d after deployment). He remarked that "it is interesting to note that both of these groups (isopods and amphipods) are brooders and reproduce inside the holdfasts". Similarly, Edgar (1987) mentioned that "the gradual population increases of holdfast species without pelagic larval stages during the first three months furthermore indicate that much of the fauna can complete all stages of their life cycles without leaving holdfasts". Many organisms that established strong local populations after considerable time periods were the original inhabitants of these biotic substrata. In all three studies, species numbers remained relatively stable during the experiment, suggesting a balance between immigration and extinction events.

As the kelp holdfasts (Edgar, 1987; Vásquez, 1993) were deployed at some depth below the sea surface, this may diminish substantially the possibility of encounter with other substrata and organisms floating at or near the water surface. Colonization by new inhabitants as reported in these two studies may, therefore, be substantially lower than that experienced by kelp plants floating at the sea surface. Ingólfsson (1998) remarked that tethered algal fronds frequently caught other free-floating algae, suggesting

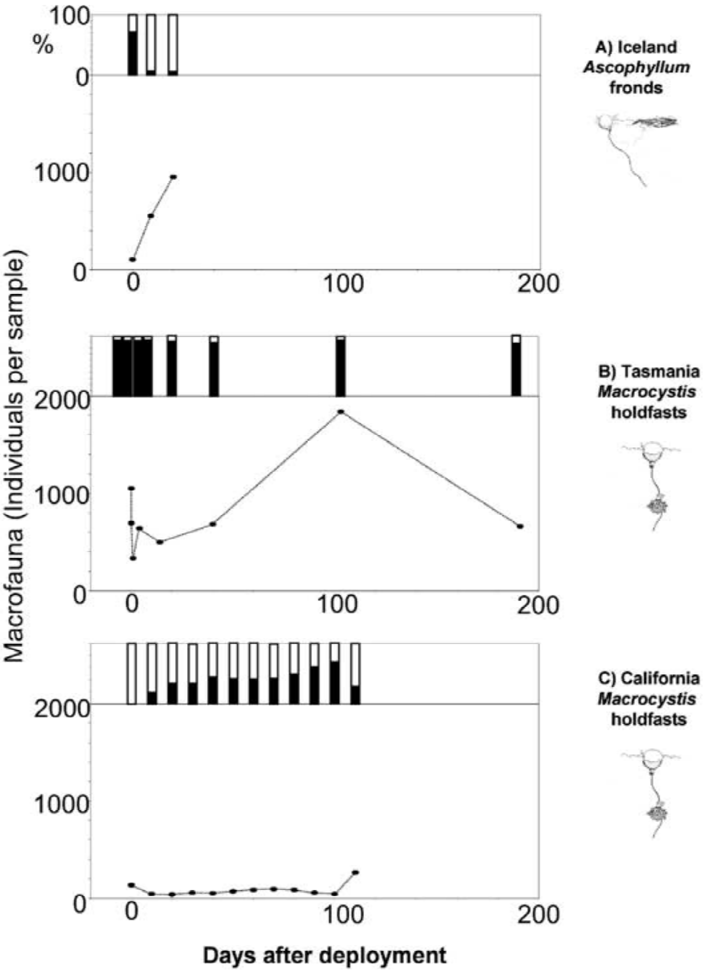

Figure 1. Abundance of macroinvertebrates in macroalgae separated from benthic habitats and exposed in the water column; columns in top figures show percentage of organisms with direct development (black) and with pelagic or unknown developmental mode (white); data taken from (A) Ingólfsson (1998); (B) Edgar (1987); (C) Vásquez (1993).

that some exchange between associated macrofauna from tethered algae and from free-floating algae may have occurred. These observations indicate that colonization of floating substrata via contact with other substrata may be important – a process inferred by other authors (Gutow & Franke, 2003). Nevertheless, the holdfast studies showed clearly the importance of local reproduction and recruitment in floating substrata. Other studies have also demonstrated that some organisms can complete their life cycle on floating substrata (e.g. Gutow & Franke, 2001).

General model for the temporal succession of rafting assemblages

Based on the results from the three studies reviewed, the successional changes of the associated fauna on any floating substratum may be subdivided into three distinct phases of different duration (Fig. 2).

Initial phase of floating

Substrata attached in coastal habitats before detachment (macroalgae, mangrove trees, buoys and anthropogenic installations) may harbour a diverse assemblage of associated fauna. After detachment, these substrata lose some of the original inhabitants because they either are not capable of holding onto floating items or because they are selectively eaten by predat-

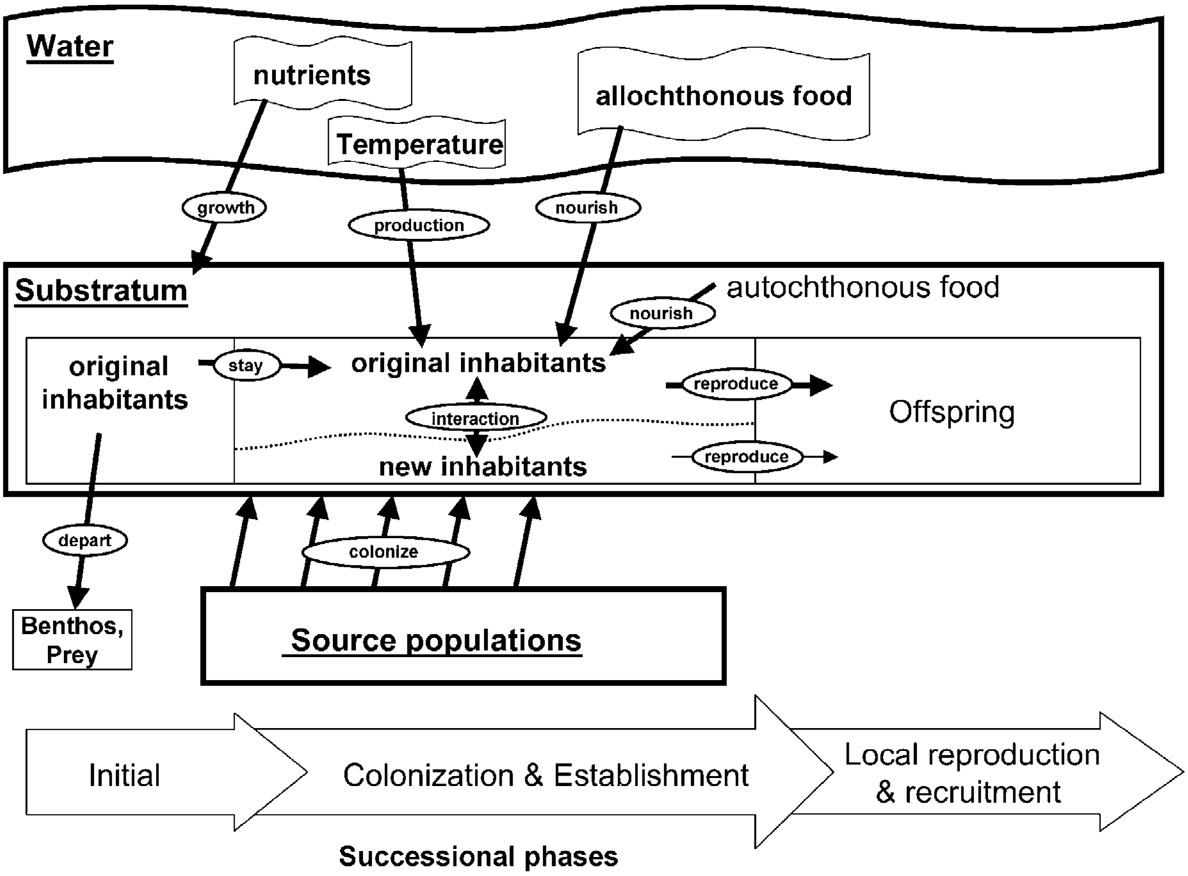

Figure 2. Schematic representation of the main factors and processes involved in the temporal succession of the rafting assemblage. Three distinct phases distinguished during the succession are indicated in the lower part of the figure.

ors (Fig. 2). Kingsford & Choat (1985) observed that many organisms, such as large, mobile invertebrates, actively abandoned kelp plants either immediately or soon after these had detached from the bottom and ascended to the water surface. Other organisms that live permanently attached to these substrata, or that inhabit protected structures such as burrows, will remain on these substrata. Many species of intermediate sizes (polychaetes, small bivalves, peracarid crustaceans) remain on the substrata after this initial phase.

Colonization and establishment phase of rafting fauna

Shortly after the start of the voyage, floating substrata become colonized by many different organisms, either arriving as larvae or as subadult stages. Following settlement on a floating item, a wide variety of biotic interactions are possible among rafting organisms, many of which might compete directly or indirectly for space and food. Species with a size advantage (e.g. original inhabitants) may suppress, or actively eliminate, small stages of other species. In contrast to these negative interactions, some species (e.g. settling macroalgae) may provide a habitat or food, thereby facilitating establishment of other organisms. The successional changes of the rafting assemblage will depend upon two main factors related to the characteristics of the surrounding water body: (1) the vicinity of floating material to source populations of potential colonizers, and (2) the dependence of colonizers on allochthonous food resources (Fig. 2).

Many studies of the colonization of benthic assemblages demonstrated the importance of larval supply (Roughgarden et al., 1987; Morgan, 2001). Similar mechanisms can be expected for floating substrata, but the influence of larval supply on the succession of the rafting assemblage is unknown. Other species colonize floating substrata in the subadult and adult stage.

For example, Brooks & Bell (2001) reported that floating algae that passed through a seagrass meadow were rapidly colonized by mobile peracarids. In coastal habitats, free-floating algae become quickly colonized by a variety of marine invertebrates (Kingsford & Choat, 1985). With increasing distances from suitable source populations (i.e. away from coastal habitats), floating substrata may be less prone to becoming colonized by littoral macrofauna.

Availability of food resources for new colonizers will also play an important role during the successional process. If the substratum itself does not provide food for colonizers (as is the case with abiotic substrata), colonizers will depend on food resources available in the surrounding water or growing on the raft. Therefore, suspension-feeding organisms (barnacles, bryozoans, hydrozoans) typically dominate abiotic substrata (Winston, 1982; Ye & Andrady, 1991; Minchin, 1996; Barnes & Sanderson, 2000). On biotic substrata, particularly those that continue to grow after detachment, colonizers may also feed on their substratum, i.e. on autochthonous food resources (e.g. Gutow, 2003). These substrata are more prone to destruction by their inhabitants than abiotic substrata. For example, rafting organisms that feed on their substratum may substantially contribute to the destruction of their home (Gutow & Franke, 2003; Gutow, this issue).

During this colonization and establishment phase, the importance of biotic interactions amongst rafting organisms is likely to increase. Colonizers may compete for space and food resources, or they may prey on each other. Nudibranch gastropods may feed on bryozoans or hydrozoans, omnivorous crustaceans may prey on larval or juvenile stages of other invertebrates and fish attracted to floating items may feed on associated macroinvertebrates (Hunter & Mitchell, 1967; Safran & Omori, 1990; Kingsford, 1992, 1995; Ingólfsson & Kristjánsson, 2002). The outcome of these biotic interactions during the colonization and establishment phase will determine which organisms persist on floating substrata. Successful raft organisms should be competitively superior to others, have only minor food requirements from their substratum, and be defended from predators (chemically or by crypsis).

Local reproduction and recruitment

The floating time of some substrata exceeds the life time of many of their invertebrate passengers. Some organisms may overcome this hurdle by reproducing within their floating habitat. In particular, species that produce propagules that can immediately colonize the natal float will gain important advantages over organisms that depend on pelagic larval stages, since the former are capable of establishing stable populations on floating substrata. Species with asexual reproduction (fission) or with direct development should, thus, be favoured during this later phase of rafting. Local reproduction and recruitment may gain particular importance on substrata that harbour original inhabitants with direct development and float away from potential coastal source populations. This late successional phase (sensu Tsikhon-Lukanina et al., 2001) may not be reached when floating substrata lack species with direct development, because they started their journey in a clean state and could only be colonized by species with pelagic larvae.

Outlook

Studies reviewed provide important insights into the successional changes occurring on macroalgae after detachment from the primary substratum. Due to logistic constraints, results are based on substrata anchored in coastal habitats, often in close vicinity to potential source populations. To achieve a sound understanding of the dynamics of rafting assemblages, it appears essential to track floating substrata during their voyage. Experiments investigating whether competition for food or space among rafting organisms is important could be conducted in the laboratory or in the field. Furthermore, it is important to establish whether rafting organisms arriving in new habitats are capable of successful colonization. Finally, biogeographic and molecular studies should be conducted to reveal whether rafting is an important process shaping the distributional pattern and genetic structure of the populations of coastal organisms (see e.g. Sponer & Roy, 2002).

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