

Rapid changes in the epifaunal community after detachment of buoyant benthic macroalgae

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*Rafting on floating macroalgae is a common dispersal mechanism of marine benthic invertebrates. Most benthic macroalgae are inhabited by diverse epifaunal communities but not all organisms may be adapted to live on floating algae. In particular, knowledge about the immediate effects of algal detachment on the associated biota is limited. Herein, we studied the composition of the communities of mobile invertebrates on benthic thalli of *Ascophyllum nodosum* and compared it with detached thalli that had floated for short periods. The community of the mobile invertebrates changed significantly within the first minute after detachment of the algae and showed decreased diversity and a tendency towards reduced abundances in most taxa. However, during the subsequent two hours of floating at the sea surface the species composition did not change further. A comparison of the size-spectra of the gastropod *Littorina obtusata* from attached and detached algae did not reveal differential migratory activity among size-classes of these gastropods. Most of the species encountered in this study are common rafters in coastal and offshore waters, which are well capable of holding onto floating seaweeds. Therefore, our results indicate that the animals actively abandoned the macroalgae immediately after detachment. A benefit of this behaviour may be to avoid increased predation risk in the open water. The fact that individuals remain associated with their algal host after detachment indicates the importance of rafting dispersal for a great variety of phytal species that might lead to range expansion and regional population persistence through metapopulation effects.*

Keywords: active migration, passive dispersal, phytal invertebrates, rafting

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INTRODUCTION

Rafting on objects which are floating at the sea surface is a common mechanism for the dispersal of marine species. Rafting dispersal is supported by a great variety of natural and anthropogenic floating items in the world's oceans. The most common floating objects in temperate waters are buoyant macroalgae (Thiel & Gutow, 2005a, b). Many seaweed species (mainly Phaeophyceae) possess pneumatocysts that keep submerged algal fronds in an upright position and allow them to float after detachment. When detached from their substratum by wave action (Seymour *et al.*, 1989), herbivorous feeding activity (Duggins *et al.*, 2001), or as a natural event in the alga's life cycle (Thomsen *et al.*, 2004) buoyant macroalgae rise up to the sea surface and carry with them a diverse epifaunal community from the benthic habitat.

The associated organisms can experience severe changes in their living conditions after detachment of their benthic algal substratum. Pressure and light conditions change during the ascent to the sea surface. At the surface, organisms are exposed to harmful UV-radiation and strong temperature

fluctuations (Cheng, 1975). Floating patches of macroalgae attract seabirds and predatory fish that forage intensively on associated organisms (Vandendriessche *et al.*, 2007a, b). Many algae are washed onto nearby shores quickly after detachment (Harrold & Lisin, 1989). While sessile epifaunal organisms are unable to leave their algal substratum mobile animals can rapidly abandon detached macroalgae. Kingsford & Choat (1985) observed that 'invertebrates streamed off and fish darted away from the plants as they began their ascent'. Caprellid amphipods have been seen to leave detached *Sargassum* sp. and descend back to the sea floor when the algae started to float (Takeuchi & Sawamoto, 1998). Boring limnoriid isopods quickly leave their holdfast burrows after experimental detachment of kelp holdfasts from the benthic substratum (Miranda & Thiel, 2008). Based on reports of low numbers of echinoderms, decapod crustaceans and gastropods on detached algae (Kingsford & Choat, 1985), Thiel & Gutow (2005b) suggested that particularly large organisms fall off quickly due to their incapability of holding onto floating objects. As a consequence, total densities of epifaunal invertebrates on macroalgae may significantly decrease during the first few minutes after detachment (Kingsford & Choat, 1985) resulting in substantial changes in the composition of the epifaunal community.

The composition of rafting communities on macroalgae collected from the sea surface after extended floating periods

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has been studied by Stoner & Greening (1984), Hobday (2000) and Tsikhon-Lukanina *et al.* (2001). Similarly, experimental investigations have focused on later successional stages of the rafting community on detached and tethered macroalgae that had been suspended in the water column or at the sea surface for weeks to months (Edgar, 1987; Vásquez, 1993; Ingólfsson, 1998). However, there is a lack of knowledge about changes in the epifaunal community of macroalgae immediately after detachment. We, therefore, investigated the immediate effects of algal detachment on the composition of the mobile epifauna in an intertidal kelp bed at the south-west coast of Iceland. We hypothesized that substantial changes in the rafting community occur immediately after algal detachment. In order to test whether particular size-classes or life history stages react to the detachment of their algal host, the size spectra of a common rafter on macroalgae in waters around Iceland, the gastropod *Littorina obtusata*, were compared between attached and floating macroalgae.

MATERIALS AND METHODS

Experiments were carried out in August 2004 on two successive days of calm weather in the intertidal at the Sandgerði Marine Station located at the exposed west coast of Reykjanes peninsula (south-western Iceland). The sandy intertidal at Sandgerði is interspersed with extensive rocky lava fields (Figure 1) covered by dense canopies of fucoid brown algae, mainly *Ascophyllum nodosum* (L.) Le Jol. 1863. According to Espinosa & Guerra-García (2005) the study site is largely controlled by natural biological and physical factors without significant effects of pollution. The tides around Iceland are semi-diurnal (Anonymous, 1993 cited in Ingólfsson 1996) and the tidal range at the south and south-west coast varies between 2.5 and 3.8 m (Ingólfsson, 1996). Water temperatures during the study period were about 12°C (data kindly provided by Heðinn Valdimarsson, Marine Research Institute, Reykjavik).

Randomly chosen complete thalli of the brown alga *A. nodosum* were cautiously detached from their rocky substratum in about 1.5 m depth by a person standing in the

submerged kelp bed. Each thallus was detached by a careful and quick cut with a knife immediately above the substratum keeping physical disturbance at a minimum. After one minute of floating freely (treatment: 1 minute) the detached algae were enclosed in plastic bags. We used plastic bags which were open at both ends. The bags were unfolded in the water and each alga was slowly dragged into a bag. When the alga was inside the bag the ends were closed quickly and tied with rubber bands. No organisms were observed to escape while the algae were enclosed in the bags. Following the procedure applied in previous studies on the succession of the epifaunal communities on floating macroalgae (Edgar, 1987; Vásquez, 1993; Ingólfsson, 1998), individuals of *A. nodosum* were tethered with ropes and were left floating at the surface for two hours after detachment (treatment: 120 minutes). In contrast to previous studies, however, detached algae were not tethered to bottom weights but to attached conspecifics by thin ropes which were 3–4 m long. As a control, algae were placed in plastic bags before detachment. Control and 1 minute algae were collected at high tide. In order to perform the 120 minute treatment evenly around high tide, the algae were detached one hour before high tide and the experiment was finished 1 hour after high tide. For each treatment five individual algae served as replicates.

The plastic bags containing the algae and enclosed seawater were immediately transferred to the laboratories of Sandgerði Marine Station. There the mobile epifauna was carefully washed from the fronds with warm tap water and collected over a 0.5 mm sieve. After removal of excess water by shaking the fronds the algal wet weight (WW) was determined to 10 g accuracy. Algal wet weight ranged from 160 g to 1780 g. Due to the large variability within the treatments, however, the average algal WW did not differ significantly between treatments (one-way ANOVA: $F_{2,12} = 0.52$, $P = 0.61$). All animals were identified to species level when possible. Numbers of epifaunal individuals were standardized to 1 kg of algal WW. As the number of species is likely to vary with sample size, diversity was calculated as expected number of species per 20 individuals (ES(20)) to account for variations in algal WW among replicates (Hurlbert, 1971). This parameter calculates the number of species that would be expected on larger samples that are scaled down to the size of the smallest sample taken.

To test if particular life history stages of associated species react differently to the detachment of their algal host we measured the size of each individual of the gastropod *Littorina obtusata* (Linnaeus, 1758). As the apex of the shell of *L. obtusata* is flattened and does not clearly protrude, we measured shell diameter instead of shell height. The maximum shell diameter as viewed from the apex was measured by a ruler to 0.5 mm accuracy and rounded down to the lower 0.5 mm.

Statistical analysis

For all tests we considered the effect of the fixed factor 'time since algal detachment' with three levels (control, 1 minute and 120 minutes). We tested for treatment effects on the macro-zoobenthic assemblage using a PERMANOVA (permutation-based multivariate analysis of variance: Anderson, 2001, 2005) with 4999 permutations. Weight of the algal fronds served as covariate. Additionally, a canonical analysis of principal coordinates (CAP: Anderson, 2003;

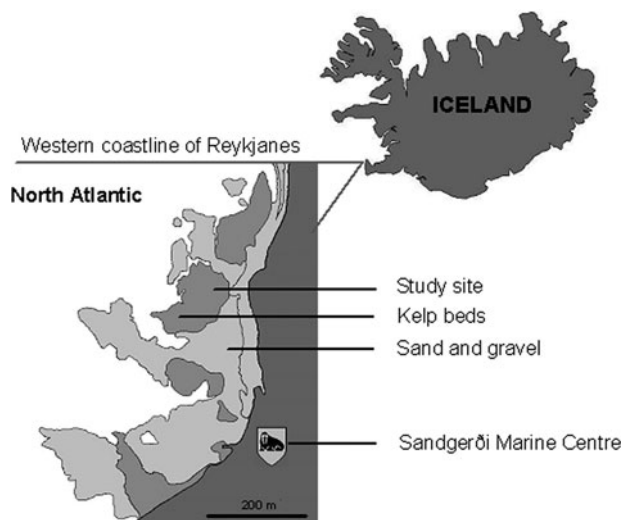


Fig. 1. Structure of the coast and location of the intertidal study site at Sandgerði on the west coast of Reykjanes peninsula (south-western Iceland).

Anderson & Willis, 2003) was performed. Multivariate tests were based on Bray–Curtis similarities (Legendre & Legendre, 1998) of previously fourth root transformed data. A test of heterogeneity in dispersion was applied with the test of multivariate dispersion using the PERMDISP program by Anderson (2004) proving multivariate dispersion to be not significantly heterogeneous ($P > 0.05$). Treatment effects on the total number of individuals and the expected number of species ($E(20)$) were evaluated by a one-way ANOVA followed by a Student–Newman–Keuls (SNK) post-hoc test.

The individuals of *L. obtusata* of each treatment were classified in three size-classes (0–4, 4.5–8 and 8.5–12 mm). Size-class distributions were compared among the treatments by a 3×3 contingency table.

RESULTS

A total of 16 taxa occurred on the thalli of *Ascophyllum nodosum* (Table 1). All of these taxa were present on attached as well as on detached algae. The only exception was the isopod *Idotea baltica* of which only a single individual was found on a detached thallus of the 120 minute-treatment. The most abundant species on

Table 1. Mean abundance \pm SD ($N = 5$) of mobile epifauna taxa on attached *Ascophyllum nodosum* (control) and on thalli that had been floating for 1 minute and for 120 minutes after detachment. Bold values denote significantly higher abundances evaluated by Student–Newman–Keuls test at $\alpha = 0.05$ after one-way ANOVA. Other significant treatment effects were not detected on the species level.

Taxon	Control	1 minute	120 minutes
Plathelminthes	7.9 \pm 6.6	9.1 \pm 5.5	6.7 \pm 3.1
Nematoda	2.8 \pm 4.3	1.2 \pm 2.6	1.5 \pm 2.0
Nemertea	3.2 \pm 3.1	0.0 \pm 0.0	0.6 \pm 1.4
Gastropoda			
<i>Lacuna vincta</i> (Montagu, 1803)	1.2 \pm 2.7	0.7 \pm 1.7	0.0 \pm 0.0
<i>Littorina littorea</i> (Linnaeus, 1758)	0.7 \pm 1.3	0.0 \pm 0.0	0.4 \pm 0.9
<i>Littorina obtusata</i> (Linnaeus, 1758)	72.8 \pm 57.1	86.9 \pm 22.7	96.9 \pm 101.7
<i>Nucella lapillus</i> (Linnaeus, 1758)	0.5 \pm 1.0	0.0 \pm 0.0	0.0 \pm 0.0
Oligochaeta	10.7 \pm 7.3	40.5 \pm 51.4	196.5 \pm 239.8
Polychaeta			
<i>Fabricia sabella</i> (Ehrenberg, 1836)	1.7 \pm 3.9	0.0 \pm 0.0	1.7 \pm 1.6
Crustacea			
<i>Calliopius laevisculus</i> (Krøyer, 1838)	0.6 \pm 1.3	0.0 \pm 0.0	0.0 \pm 0.0
<i>Gammarus stoerensis</i> (Reid, 1938)	10.3 \pm 8.1	0.7 \pm 1.0	0.3 \pm 0.7
<i>Idotea baltica</i> (Pallas, 1772)	0.0 \pm 0.0	0.0 \pm 0.0	0.4 \pm 0.9
<i>Idotea granulosa</i> Rathke, 1843	19.8 \pm 18.3	5.1 \pm 5.8	2.0 \pm 2.1
<i>Jaera</i> sp.	19.1 \pm 17.5	0.0 \pm 0.0	0.4 \pm 0.9
Acari	22.4 \pm 21.5	2.8 \pm 2.1	6.2 \pm 6.3
Insecta			
<i>Halocladus variabilis</i> (Saeger, 1839)	62.6 \pm 132.7	8.8 \pm 16.2	2.2 \pm 4.1

attached *A. nodosum* was the gastropod *Littorina obtusata* followed by larvae of the chironomid *Halocladus variabilis*. *Littorina obtusata* dominated also on detached fronds together with an unidentified oligochaete species.

The effect of algal detachment was significant at the community level (PERMANOVA $F_{2,11} = 2.33$, $P < 0.05$) with the control treatment differing from the detachment treatments. Weight of algal fronds (covariable) did not significantly affect the composition of the faunal assemblage (PERMANOVA $F_{1,11} = 1.50$, $P > 0.05$). Abundance was correlated with clump size only in the isopod *Idotea granulosa* in the control treatment ($r = 0.96$, $P < 0.05$). The ordination given by CAP showed that 73% of the replicates were correctly classified into their groups: all replicates of attached algae were grouped while the detached replicates were less clearly separated. Control and detachment treatments were clearly separated in the CAP plot (Figure 2): control replicates grouped in the positive section of the first canonical axis while the detached replicates grouped in the negative section of this axis. Most taxa correlated positively with the first canonical axis indicating a reduction in abundance after detachment. This was particularly evident for *Jaera* sp., Nemertea and *Gammarus stoerensis* that showed the highest correlations with the first canonical axis (Figure 2). These were the only taxa that were significantly less abundant on detached algae (Table 1). Other taxa such as *H. variabilis*, *I. granulosa*, and Acari also decreased strongly in abundance after detachment of the algae. Due to strong variations among replicates, however, these changes were statistically not significant.

Few taxa were negatively correlated with the first canonical axis, but the absolute values of the correlation were low ($r < 0.40$). The average number of oligochaetes was four times higher on 1 minute algae than on control algae and 20 times higher on 120 minute algae. Similarly, the density of *L. obtusata* was 15 to 25% higher on detached algae. But again, for both species the differences were statistically not significant because of strong variations among the replicates.

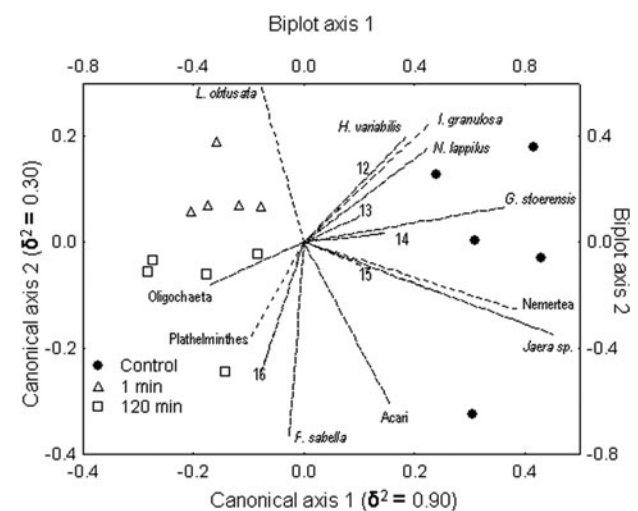


Fig. 2. Canonical analysis of principal coordinates (CAP) ordination with projection of individual taxa onto the ordination axes. The analysis was performed after Bray–Curtis distance of fourth root transformed data. CAP selected the first four principal coordinates that explained 79% of the total variation. Individual taxa with low correlation coefficients are given as numbers as follows: 12, *Calliopius laevisculus*; 13, *Lacuna vincta*; 14, *Littorina littorea*; 15, Nematoda; 16, *Idotea baltica*.

Due to the high number of oligochaetes on the floating algae, detachment and subsequent floating of *A. nodosum* had no significant effect on the total abundance of the epifaunal organisms (ANOVA: $F_{2,12} = 0.72$, $P > 0.05$) (Figure 3). The expected number of species was reduced by algal detachment (ANOVA: $F_{2,12} = 6.69$, $P < 0.05$) (Figure 4). ES(20) was higher on attached *A. nodosum* than on 1 minute algae (SNK test: $q = 3.94$, $P < 0.05$) and on 120 minute algae (SNK test: $q = 4.87$, $P < 0.05$). ES(20) remained constant during subsequent floating of the algae (SNK test: $q = 0.92$, $P > 0.05$).

The size of *L. obtusata* ranged from 0.5 to 12 mm. In each treatment more than 90% of the individuals were ≤ 4 mm (Figure 5). The size-class distributions did not differ significantly among the treatments ($P = 0.058$, $\chi^2 = 9.109$, $df = 4$). The proportion of individuals with a shell diameter > 4 mm, however, tended to decrease after algal detachment and during subsequent floating.

DISCUSSION

The detachment of benthic *Ascophyllum nodosum* was accompanied by a significant change in the community composition of the associated mobile epifauna. During the subsequent two hours of floating at the surface, however, the community composition remained stable. Although the total abundance of associated organisms was not affected by algal detachment the tendency towards lower abundances on detached algae, as previously observed by Kingsford & Choat (1985), was evident in most taxa. These results confirm our hypothesis that substantial changes in the community of mobile organisms occur immediately after detachment of benthic algae.

Emigration from detached algae

The strongest decrease in abundance was observed in peracarid crustaceans such as *Gammarus stoeberensis*, *Jaera* sp. and *Idotea granulosa*. The densities of these species dropped from some tens of individuals per kg algal WW to almost zero after detachment of the algae. Kingsford & Choat (1985) observed a similar loss of phytal amphipods from macroalgae immediately after detachment. This observation was surprising since peracarids are among the most common rafting invertebrate species in the world's oceans

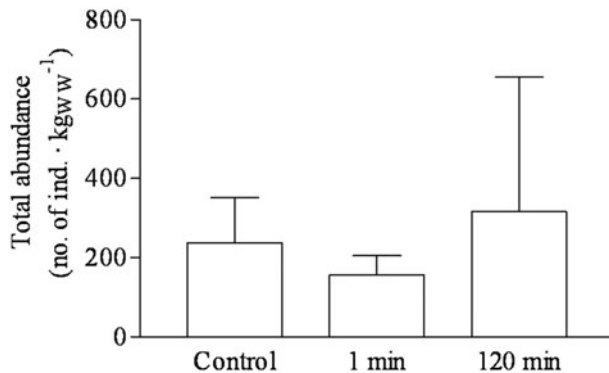


Fig. 3. Total abundance of mobile epifauna on attached *Ascophyllum nodosum* (control) and on thalli that had been floating for 1 minute and for 120 minutes after detachment. Error bars denote standard deviation ($N = 5$).

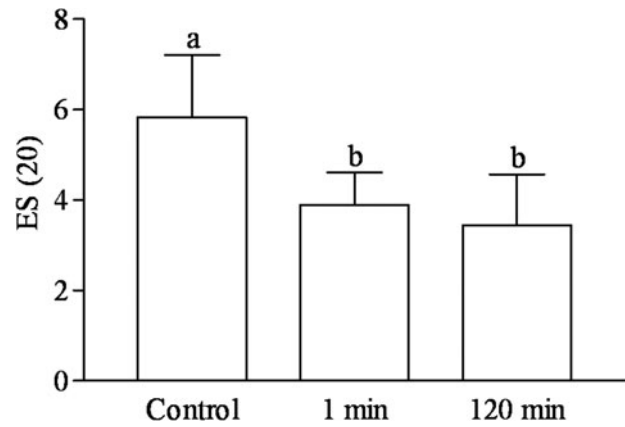


Fig. 4. Expected number of species (ES(20)) of mobile epifauna on attached *Ascophyllum nodosum* (control) and on thalli that had been floating for 1 minute and for 120 minutes after detachment. Different letters denote significant differences among treatments evaluated by Student–Newman–Keuls test at $\alpha = 0.05$ after one-way ANOVA. Error bars denote standard deviation ($N = 5$).

(Thiel & Gutow, 2005b) indicating their high potential for persistence on floating items. The number of peracarids decreased drastically after detachment of the algae despite their high capability of clinging efficiently to their algal host (Dommasnes, 1968). We, therefore, assume that these animals leave the algae actively immediately after detachment. A similar rapid and strong reaction was observed for holdfast-boring isopods *Limnoria* spp. in a Chilean kelp forest, which quickly abandoned their burrows after detachment of the holdfast from the substratum (Miranda & Thiel, 2008).

Edgar (1987) expected that organisms on floating holdfasts of the giant kelp *Macrocystis pyrifera* experience greater water motion than on attached holdfasts. Accordingly, Thiel & Gutow (2005b) suggested that some of the original inhabitants of the algae are lost from the community immediately after detachment because of their incapability of holding onto floating items. The majority of the taxa found in our study, however, have been repeatedly recorded as rafting organisms on macroalgae in coastal and offshore waters around Iceland (Ingólfsson, 1995, 1998), which confirms their general ability of clinging efficiently to floating algae. We, therefore, consider it unlikely that these animals are unable to hold onto detached algae especially under the calm weather conditions during the experimental period. Individuals of these taxa rather abandoned the algae actively after detachment, similar to the peracarids. Kingsford & Choat (1985) assumed that a large

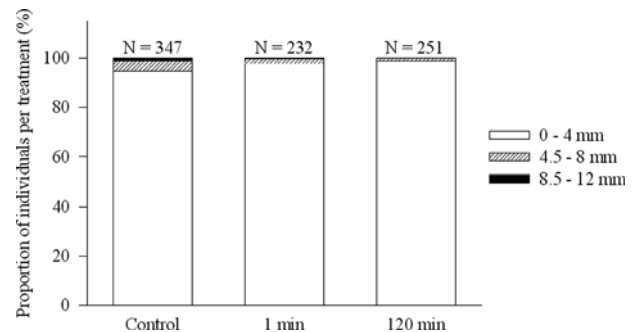


Fig. 5. *Littorina obtusata*. Proportions of individuals classified into one of three size-classes for each treatment.

number of organisms will probably be removed from their host under stormy conditions when the algae tumble over the rocky substratum after detachment. Particularly large organisms such as gastropods will be shaken off from their algal host under rough conditions. Our comparison of the shell size-distributions of the gastropod *L. obtusata* showed a tendency towards lower proportions of larger individuals, which was, however, statistically not significant. The overall very small proportion of large individuals even on attached *A. nodosum*, however, did not allow for reliable conclusions concerning size-specific clinging capacities.

Immigration onto floating algae

It might be possible that the observed slight increase in the proportion of small *L. obtusata* on detached *A. nodosum* was simply an experimental artefact. The density of *L. obtusata* increased after algal detachment and was highest after two hours of floating. An even stronger increase in density on detached algae was observed for the oligochaetes. Juveniles of various gastropod species perform tidal migrations by entering the water column by the use of mucus threads (Martel & Chia, 1991). It is unknown if small *L. obtusata* perform pelagic dispersal. Post-metamorphic drifting via mucus threads was, however, reported for the congener *Littorina sitkana* (Martel & Chia, 1991). Similarly, benthic oligochaetes suspend in the water column and use tidal currents for migrations between intertidal and subtidal habitats (Nilsson *et al.*, 2000). Suspended individuals might have been sieved out of the water column and become concentrated on the tethered algal fronds that were floating for one hour at the surface in the ebb tide.

Causes and implications of rapid migration after algal detachment

The exact signal, which induces the observed rapid reaction of the associated organisms is unclear. It is unlikely that the active escape from the detached plants was induced simply by the presence of a field investigator shadowing the algae like predatory fish or seabirds do. This effect should have been observed on attached algae as well. Phytoplankton animals avoid exposure to visually hunting predators by hiding on their algal host during daytime (Taylor, 1998). Migration is, thus, unlikely to be induced by the presence of a potential predator.

Phytoplankton organisms might be deterred by chemicals released by the algae after detachment. Indeed, wounded *A. nodosum* releases chemicals that attract predators. The release of such infochemicals is, however, induced by grazing herbivores and not by artificial damage of the alga (Coleman *et al.*, 2007).

The epifaunal organisms may perceive changes in their physical environment after the detachment of the benthic macroalgae. Due to the shallowness of the study site (i.e. ~1.5 m depth) the changes in light intensity and pressure during the ascent of the algae to the surface seem negligible. The altered movement pattern of the algae after detachment and the changed drag forces might form a signal of habitat modification that induces the reaction of the animals.

By escaping from the detached algae the animals avoid displacement from the structurally complex phytoplankton habitat that provides efficient shelter from visually hunting predators (Nelson, 1979). The isolation of a detached alga from the

benthic assemblage will affect the structural complexity of the floating habitat and reduce the protective efficiency. Many floating macroalgae end up on nearby beaches shortly after detachment (Harrold & Lysin, 1989). Therefore, Miranda & Thiel (2008) suggested that rapid emigration from detached macroalgae reduces the risk for associated organisms to become deposited on the shore.

For most species the decrease in abundance after detachment of the algal host was statistically not significant indicating that a substantial number of individuals remain associated with floating algae. Obviously conspecific individuals differ in their readiness for active migration. Differential migratory activity among life history stages has been described for various species including peracarids (Johnson & Menzies, 1956), bivalves (Lane *et al.*, 1985), and gastropods (Martel & Chia, 1991). The individuals that hold onto their algal raft after detachment have a considerable chance of being carried out of the local kelp forest and enter large scale offshore currents. Low migratory activity can, thus, increase the probability for long distance dispersal. Efficient rafting dispersal can result in natural range expansion (Johannesson, 1988), colonization of new areas (Ó Foighil *et al.*, 1999), and connectivity among local populations allowing for regional persistence of species through metapopulation effects (Thiel & Haye, 2006).

In conclusion, our experiments showed that the moment of detachment of benthic macroalgae has a substantial effect on the composition of the epifaunal community and, thus, the future succession of the rafting community.

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