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# Soft bottom versus hard rock: Community ecology of macroalgae on intertidal mussel beds in the Wadden Sea

Annelise S. Albrecht[1]

*Dalhousie University, Biology Department, Halifax, Nova Scotia B3H 4J1, Canada*

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## Abstract

On the extensive mud and sand flats of the Wadden Sea, intertidal mussel beds (*Mytilus edulis* L.) represent one of few secondary hard substrata and thus potentially serve as attachment surfaces for macroalgae in an environment which is largely dominated by sediments. However, the only abundant colonizing seaweed on mussel beds is a special form of rockweed, *Fucus vesiculosus* forma *mytili* (Nienburg), which lacks a holdfast and reproduces only vegetatively. Ephemeral macroalgae are absent from mussel beds, and large mussel patches remain completely uncolonized by seaweeds. I tested the effect of grazing by periwinkles, *Littorina littorea* L., on algal cover through experimental exclusion of snails. Under reduced grazing pressure, ephemeral green and red algae (*Enteromorpha*, *Ulva* and *Porphyra*) developed and either partially or completely covered the surface on mussel bed plots, but only in the absence of *Fucus*. Additional experiments showed that *Fucus* dispersal from fertile populations to mussel beds is possible within a range of at least 25 m. Between 5 and 25 m from a fertile population on rocky substratum *F. vesiculosus* recruited successfully on artificial settlement surfaces, in the absence and to a lesser extent also in the presence, of littorinid grazing. If *F. vesiculosus* zygotes settle on mussel surfaces, they are subject to very high post-settlement mortality. Field experiments showed that survival of *Fucus* zygotes inoculated onto live mussels was close to zero, under high and low grazing intensities. Survival was elevated on mortar-filled mussel valves when snail grazing pressure was reduced, and especially if barnacles were present. As demonstrated in laboratory experiments, the recruitment failure on live mussels was due to the accumulation of faeces and pseudofaeces which shade, bury and eventually kill *Fucus* zygotes underneath. Adult thalli are either not susceptible to these adverse effects of mussel biodeposition or can counterbalance them by growth. Since propagation can occur through fragmentation of adults, sexual reproduction is unnecessary for the survival of the *Fucus* population. Just as on rocky shores, the abundance of ephemeral seaweeds on mussel beds of the Wadden Sea tidal flats is controlled by grazing. With opportunistic life strategies ephemerals are characterized by high growth rates and reproductive capabilities which

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[1] Present address: University of Plymouth, Dept. of Biological Sciences, Drake Circus, Plymouth, Devon PL4 8AA, UK. E-mail: Lise@codium.clara.net

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allow them to respond rapidly to spatial and temporal reductions in grazing pressure. In contrast, adults of the long-lived perennial seaweed, *Fucus*, are largely unaffected by grazing, and juvenile stages, which would be subject to herbivory as well as strong biodeposition on Wadden Sea mussel beds, are omitted from the life cycle of *Fucus* in this environment.

*Keywords:* Fucoid microalgae; *Fucus vesiculosus*; Dispersal; Recruitment; *Littorina littorea*; Grazing; *Mytilus edulis*; Biodeposition; Sediment dynamics

## 1. Introduction

As one of the largest coastal softbottom habitats in the world, the Wadden Sea is dominated by mobile sediments. In contrast to rocky shores, primary substrata for colonization of sessile epifauna and macroalgae are generally missing. Extensive mussel beds (*Mytilus edulis* L.) constitute the only widely available alternative substratum to mobile sediment surfaces for these epibionts. As an aggregation of live blue mussels, shell fragments and accumulated debris, they represent firm three-dimensional structures on otherwise largely unstructured mud and sandflats.

The diversity and abundance of benthic macrofauna in Wadden Sea mussel beds reflects these features: mussel beds are utilized by sessile epifauna (e.g., barnacles, anthozoa and hydrozoa, Sebens, 1982) as well as by many vagile species which find hiding spaces from predators or profit from the comparatively stable microclimate within the bed (Wohlenberg, 1937; Scherer and Reise, 1981; Riesen and Reise, 1982). Consequently, faunal species richness is always higher in mussel beds than on surrounding flats.

In contrast, the distribution of macroalgae on intertidal mussel beds in the Wadden Sea is limited: although ephemeral green algae in particular have become very abundant in the Wadden Sea and often form thick mats (Reise and Siebert, 1994), they are rarely found attached to blue mussel aggregations. Similarly, the growth of various red and brown algal species on mussel beds is occasional, although they occur regularly in the Wadden Sea intertidal zone (van den Hoek et al., 1979).

Thus, in spite of their apparent suitability as attachment surfaces, large areas of mussel beds in the Wadden Sea often remain completely uncolonized by macroalgae. The only exception to this pattern is a specific form of bladder wrack – [*Fucus vesiculosus* forma *mytili* (Nienburg) Nienhuis, Phaeophyceae] – which may cover mussel beds either partially or completely as a thick blanket. This "mussel bed *Fucus*" (hereafter "*Fucus*") always lacks a holdfast and the typical air vesicles and does not become fertile. No sexual recruits of *Fucus* are ever found on mussel beds in this environment. In contrast to *Fucus* spp. growing attached to mussels in the rocky shore intertidal zone (Janke, 1990), *Fucus* on Wadden Sea mussel beds is fastened to the substratum by *M. edulis*' byssal threads. The specific association between mussels and *Fucus* is common all over the Wadden Sea (Nienburg, 1925, 1927; Kuenen, 1942; den Hartog, 1959; Nienhuis, 1970; van den Hoek et al., 1979), and *F. vesiculosus* forma *mytili* now represents the third-most abundant macrophyte in this environment, after seagrasses and green algal mats (Reise et al., 1994).

Whereas the population and community dynamics of seaweeds on rocky shores have been widely studied and are well understood (e.g., Burrows and Lodge, 1950; Dayton, 1975; Lubchenco, 1978, 1980, 1983; Lubchenco and Menge, 1978; Lein, 1980; Gaines, 1985; van Alstyne, 1988; Buschmann, 1990; Duffy, 1990; McCook and Chapman, 1992, 1993; Parker et al., 1993; Chapman, 1995), it is unclear how processes like competition, facilitation, herbivory and succession operate on macroalgae in soft sediments. The epifaunal species composition of mussel beds may be conspicuously similar on both rocky and soft sediment shores within the same geographical range (compare Reise, 1985; Dittmann, 1987; Janke, 1990). Also, mussels serve as secondary substrata for epibionts in these environments. However, colonization patterns of macroalgae appear to be fundamentally different on rocky shore vs. Wadden Sea mussel beds (Lohse, 1993; Albrecht and Reise, 1994) which invokes the question of the underlying processes differentiating both environments.

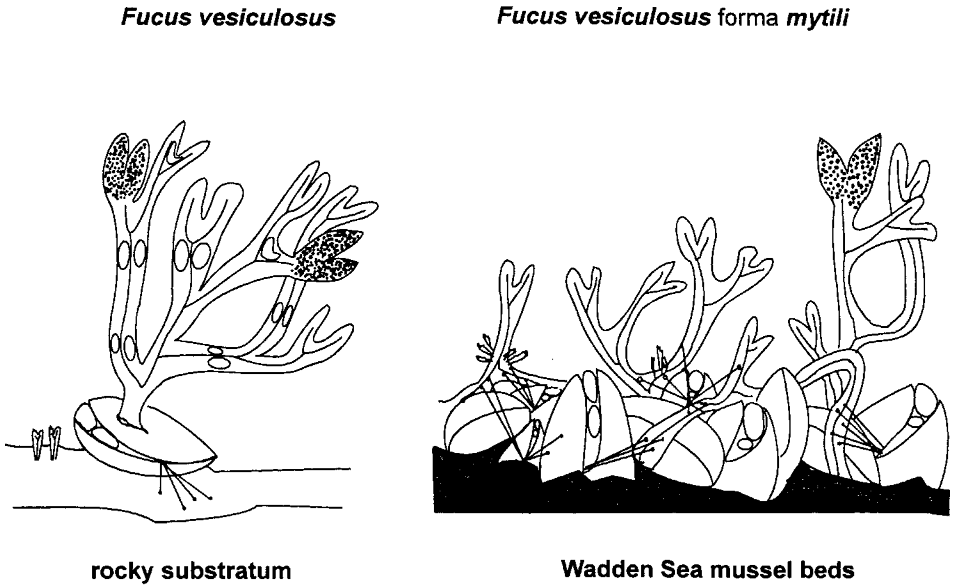
The objective of this study was to explain the distribution pattern of ephemeral macroalgae and *Fucus* on intertidal mussel beds in the Wadden Sea in comparison to rocky intertidal mussel beds. I tested the hypothesis that periwinkles (*Littorina littorea* L.), which occur in densities of hundreds of adults per $m^2$ on Wadden Sea mussel beds (Wilhelmsen and Reise, 1994), prevented growth of ephemeral macroalgae at microscopic stages through intensive grazing pressure. The complete absence of sexual recruits of *Fucus* on Wadden Sea mussel beds may be a consequence of mortality of zygotes from fertile *F. vesiculosus* populations on artificial hard substrata. Such populations represent the only natural source of gametes and potentially supply recruits to mussel beds. Therefore, I investigated the dispersal of *Fucus* from fertile hard substratum populations and tested whether post-settlement mortality of *F. vesiculosus* zygotes, which were experimentally introduced to mussel beds, was high.

The low survival of zygotes on live mussels in contrast to artificial shell substrata during a field experiment was investigated further in the laboratory. I identified the relative significance of two potentially important mechanisms of zygote mortality after settlement on live *M. edulis* when grazing was reduced. One process is the shell cleaning of mussels with their foot (Theisen, 1972) which would remove newly settled zygotes; the other one is the accumulation of faeces and pseudofaeces of mussels on the shell surface which would bury *F. vesiculosus* zygotes underneath.

The results suggest that the unusual life history of *Fucus vesiculosus* forma *mytili* has adaptive significance in the Wadden Sea environment. Does the omission of juvenile life stages, which, in many respects, are most susceptible to biological and environmental stresses, relate to any factors which are specific to this soft sediment system?

## 2. Algal natural history and study sites

The association of *Fucus* with *M. edulis* on mussel beds in the Wadden Sea was first described in the 1920s by Nienburg (1925), (1927) who identified the ''mussel *Fucus*''



***Fucus vesiculosus***

***Fucus vesiculosus* forma *mytili***

**rocky substratum**

**Wadden Sea mussel beds**

Fig. 1. Growth habit and morphology of fertile *F. vesiculosus* on rocky substratum (left) and sterile *F. vesiculosus* forma *mytili* (Nienburg) Nienhuis from Wadden Sea mussel beds (right).

as a distinct species (*F. mytili*), the status of which was later revised and is now considered a form of *F. vesiculosus*: *F. vesiculosus* forma *mytili* (Nienburg) Nienhuis.

In the association with mussel beds in the Wadden Sea *Fucus* is always lacking a holdfast (Fig. 1). Thalli are attached to the substratum by byssal threads of *M. edulis.* Individual thalli are tied down by several mussels and, simultaneously, single mussels can connect to different *Fucus* thalli, thus forming a dense mussel–seaweed matrix. Through continual sediment accumulation on the mussel bed (which, in the presence of *Fucus* is enhanced as a consequence of reduced current speeds, Albrecht and Reise, 1994) *Fucus* is gradually buried by mud and is subject to deterioration at its basal parts. Distally, it continues growth towards the water column. Mussel bed *Fucus* often exhibits a slight spirality of the thallus and generally lacks the air vesicles typical for *F. vesiculosus.* Most of the thalli do not form receptacles, but if reproductive structures are found they always contain only oogonia which are underdeveloped in comparison to conspecifics from rocky substratum; antheridia never occur. Reproduction of mussel bed *Fucus* is purely vegetative by means of drifting fragments of adult thalli.

## 3. Study sites

All experimental work was carried out on intertidal mussel beds in ''Königshafen'', a shallow tidal bay at the north of the island of Sylt (North Sea, Germany), Fig. 2. Königshafen Bay covers an area of approximately 6.2 km$^2$ and is open to the East (55°02′N, 08°06′E). A peninsula divides the bay into two areas, the ''inner bay'' – a

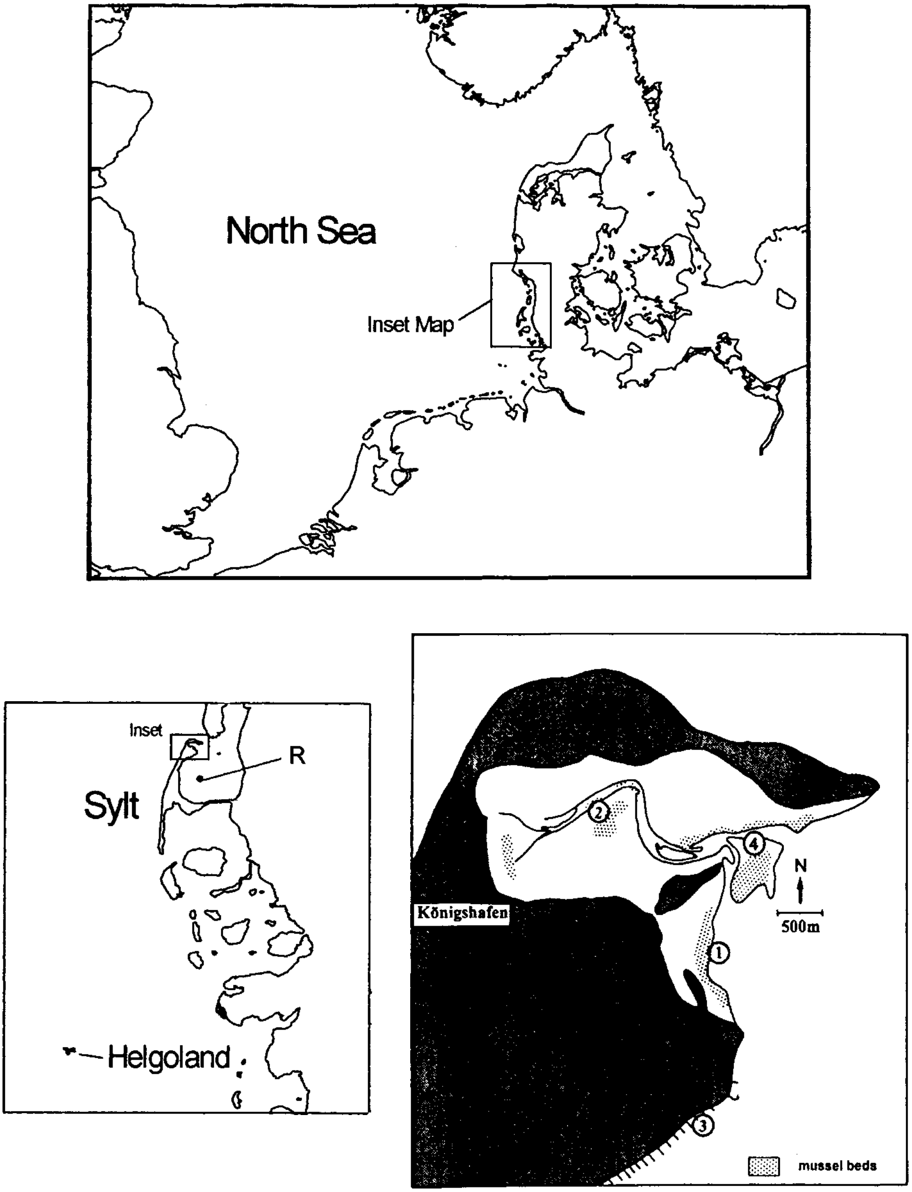


Fig. 2. Investigation area in the Wadden Sea at the island of Sylt, North Sea, Germany. Above: overview of North Sea, location of the island of Sylt (modified from the "General Bathymetric Chart of the Oceans", GEBCO, digital atlas by the British Oceanographic Data Centre). Below left: coastal islands in the North Frisian Wadden Sea and the rocky island of Helgoland in the German Bight (modified from GEBCO, see above). Below right: Königshafen Bay. Investigation sites: (1) Oddewatt, (2) Möwenbergwatt, (3) rocky breakwater, (4) outer Königshafen, (R) Rauling Sand. Distribution of mussel beds in the bay between 1992 and 1994.

very protected part in the west, and the "outer bay" at the open side. Most water transport occurs through a tidal channel running East–West. The mean tidal range of Königshafen Bay is 1.8 m, average salinity is 30‰ and mean water temperature is 15°C in summer and 5°C in winter. The surface sediments of the area are coarser than on most other tidal flats along the North German coast (Figge et al., 1980; Austen, 1992). Moving from East to West inside the bay, the sediment becomes increasingly muddy; thus the "outer Bay" and "Oddewatt" with their exposed position consist of very coarse sands and the "Möwenbergwatt" is characterized by mixed sediments (Austen, 1992). East of the island of Sylt yet another intertidal sandy site, "Rauling Sand" of 3.5 $km^2$, carries a group of large mussel beds along its southeastern edge. This site was included in the mapping of ephemeral seaweed vs. snail abundances (see below).

On mussel beds, biodeposits of the benthic macrofauna, particularly *M. edulis*, dominate the sediment composition. Thus, irrespective of site specific differences, mussel beds always contain a higher proportion of fine grained sediments than surrounding tidal flats (Dittmann, 1987).

Several fertile populations of hard substratum *F. vesiculosus* grow on a series of rocky breakwaters (80 m long, interspersed by ~100 m) south of the bay. One of the breakwaters was the site of the dispersal experiment and will be referred to as the major comparative hard substratum site in the area. The breakwaters are also colonized by *M. edulis* and other benthic macrofauna and have a similar epibenthic species composition as intertidal mussel bed assemblages.

## 4. Materials and methods

### 4.1. Grazing of *Littorina littorea* on mussel beds

The influence of periwinkles on the growth of ephemeral macroalgae on mussel beds was investigated (a) by correlative measurements of snail and algal abundances on mussel beds without *Fucus* cover (as ephemeral seaweeds never occurred in any abundances on *Fucus* covered mussel beds) and (b) by grazer exclusion experiments.

On June 26/27 1995 abundances of *L. littorea* were mapped together with abundance of ephemeral macroalgae at four different mussel bed sites, one of which ("Rauling Sand") had appeared – atypically – completely covered with green algae in an areal view. Mussel beds without *Fucus* at "Oddewatt", "Möwenbergwatt", "outer Bay" and "Rauling Sand" were sampled randomly, using a counting frame of $0.5 \times 0.5$ $m^2$, divided into 25 subsections of 100 $cm^2$. On each one of between 7 and 14 0.25 $m^2$ plots per site (depending on the total area of the mussel bed) two variables were measured within seven 100 $cm^2$ subplots per frame: (a) abundance of adult *L. littorea* ($>1$ cm shell height) was recorded as ind. 100 $cm^{-2}$, and (b) surface cover of ephemeral green and red algae (*Enteromorpha* spp. and *Porphyra* spp.) was estimated categorically (1: 0–25% cover, 2: 26–50%, 3: 51–75%, 4: 76–100%). Subplot readings were then pooled.

Preliminary cage exclusions of *L. littorea* from mussel beds without *Fucus* cover at the inner Königshafen Bay (1992, unpubl. data) had shown that ephemeral green algae were beginning to grow on mussel shells if *L. littorea* abundances were reduced to approximately one third of natural densities. From April to July 1993 the effect of grazing by *L. littorea* on the growth of ephemeral macroalgae was tested experimentally on mussel beds with and without a *Fucus* cover at ''Oddewatt'', where average snail densities were as high as 500 to 1000 ind. $m^{-2}$. Snail exclusion was achieved by installation of square $0.5 \times 0.5$ $m^2$ fences, which consisted of a wooden inner frame and a surrounding wire fence of rust-resistant $6 \times 6$ $mm^2$ mesh. The maximum shell height of snails capable of passing through this mesh was 8.5 mm. The height of the fences was 35–40 cm above ground and 20 cm below the sediment/mussel surface. The top 5 cm of mesh wire were folded outwards in a 135° angle in order to further ensure exclusion of periwinkles. I did not use roofed cages in order to limit artifacts of flow alteration. Fences which left a 5-cm space above the ground so that snails could freely pass into and out of the sampling area served as procedural controls and were afterwards compared to artifact control plots without fences. Snail exclusions were applied accordingly on *Fucus* covered and uncovered plots. Thus, the design was orthogonal, two-factorial (snail grazing, *Fucus* cover) with two levels of each factor. Each treatment combination was replicated five-fold. The experiment was installed between April 7 and 12, 1993, a period over which snails were removed continually from exclusion treatments after appearing on the surface from within the mussel matrix. Over the experimental period exclusions were attended to regularly to remove newly entered snails. Since snail exclusions were not 100% effective they will be referred to as ''reduction treatments''. The experiment was terminated in mid July 1993. Between July 14 and 27 the central areas (500 $cm^2$) of each of five plots per day (different treatments) were sampled destructively: all macroalgae were removed and their fresh weight determined after rinsing in fresh water and blotting. The plants were then dried (3 days, 80°C), re-weighed and subsequently combusted (12 h, 520°C). Ash free dry weight was calculated as the difference between dry weight and ash weight. Simultaneous with algal sampling, abundances of periwinkles (*L. littorea* and *L. mariae* Sacchi et Rastelli) were determined on the experimental plots.

### *4.2. Dispersal and sexual recruitment of F. vesiculosus*

In the Wadden Sea *F. vesiculosus* in its fertile (''normal'') form is not only found near shore but occasionally also on spatially isolated hard substrata such as wrecks, navigation marks, etc. (pers. obs.). This indicates the potential for wide dispersal of propagules by drift from fertile parental populations. I conducted a field experiment to test whether *F. vesiculosus* propagules (gametes and zygotes) were potentially able to reach mussel beds in Königshafen Bay through drift from the rocky breakwater as the main source of fertile *F. vesiculosus* in the investigation area, or whether pre-settlement mortality, and post-settlement grazing in particular, were too high to allow recruitment within this range. The maximum distance investigated was 25 m, because it was on this spatial scale that the nearest mussel aggregations were found regularly and would potentially allow gradual dispersal of *F. vesiculosus* to larger mussel fields in Königshafen Bay. Although such smaller mussel aggregations (up to several square metres) persist on a smaller time scale than larger beds (months to several years as opposed to decades), they are abundant and thus could theoretically provide stepping stones for colonization of perennial mussel beds. Recruitment of *F. vesiculosus* was measured over increasing distances from the fertile population by using wooden poles as artificial settlement substrata. The breakwaters extended perpendicularly from the shore. Six poles (1 m total length, 50 cm above ground, 10 cm circular diameter) were placed randomly on each of three imaginary lines running parallel to one breakwater at 5, 10 and 25 m distance, and perpendicular to tidal currents. Alternating poles on each line were either supplied with a wire brim (15 cm wide, 15 cm above surface at a 45° angle) to prevent snail grazing on the upper part or had no such devices and allowed access of *L. littorea* to all parts of the pole. The experiment was started on April 10, 1994 and was terminated on November 24, 1994 at which time the number of *F. vesiculosus* individuals per pole was determined. Thus, I measured long term recruitment of juveniles which is likely to have more relevance for the previously described stepwise colonization of mussel beds than short term processes because it integrates post-settlement mortality on a larger time scale.

### *4.3. Post-settlement mortality of F. vesiculosus sexual recruits on mussel beds (see Fig.* 3 *for experimental design)*

Reproduction of *Fucus* on mussel beds in the Wadden Sea is strictly vegetative, and germlings or juveniles do not appear in the life history. In rocky shore populations, these stages are the most susceptible to grazing by periwinkles whereas adult thalli are better protected mechanically and chemically (Geiselman and McConnell, 1981). It was tested experimentally if grazing prevented sexual recruitment of *F. vesiculosus* on *M. edulis*

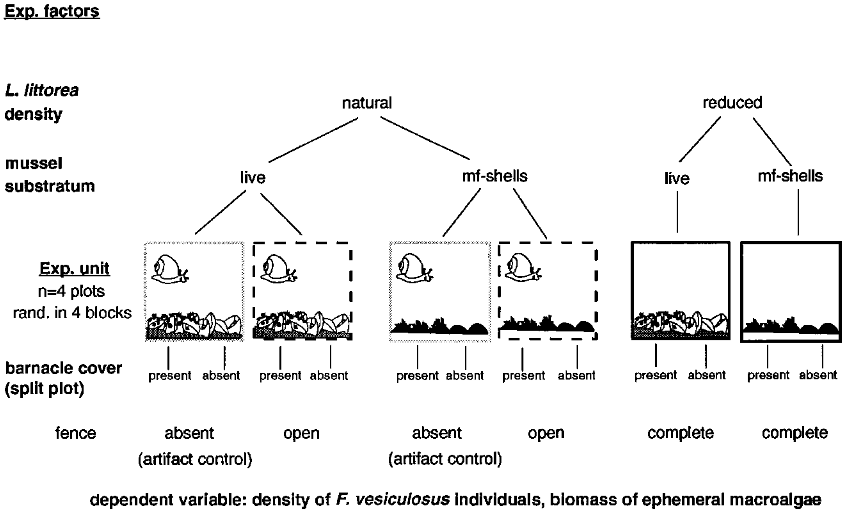


Fig. 3. Experimental design for field experiment on post-settlement mortality of *F. vesiculosus* zygotes on mussel beds. "mf-Shells" = mortar-filled shells.

beds, in which case the specific form of growth and reproduction of *Fucus* in this habitat might have an adaptive value with respect to the high grazing pressure by periwinkles. Secondly, barnacle cover of the substratum was manipulated because it has been shown to affect grazing efficiency of littorines in other habitats (Petraitis and Sayigh, 1987). Thus, half of the mussels on each substratum plot were selected with a dense barnacle cover, the other half was barnacle free at the beginning of the experiment. Thirdly, the significance of live *Mytilus edulis* as substratum for *Fucus* zygotes was investigated by comparing it to stabilized empty mussel shells as attachment surfaces. This precluded filtration and biodeposition of live mussels and the potential effects of these activities on epibionts after settlement, while providing the same topographical substratum properties. All experimental mussel substrata were also free of adult *Fucus*.

The ‘‘artificial’’ mussel substrata ($0.3 \times 0.3$ m$^2$) were manufactured by attaching shell pairs of *M. edulis* individuals from a wide size range to the top and bottom of a fishing net ($1 \times 1$ cm$^2$ mesh size). The space between shell pairs was filled with mortar and then left to dry (mortar-filled shells will be referred to ‘‘mf-shells’’ hereafter). This produced a flexible, but over the experimental period persistent, shell matrix which closely resembled natural mussel substratum. Initial manipulation of substrata (live mussels and mf-shells) took place in the laboratory: live mussels were collected as matrices (similar size range and density as mf-shells on $0.3 \times 0.3$ m$^2$ meshes), washed, cleared of associated macrofauna – except for barnacles where applicable (see above) – and kept in aquaria with filtered seawater for several days to guarantee matrix stability. Subsequently, zygotes from the fertile breakwater population of *F. vesiculosus* were inoculated onto the different substrata (gamete release was performed as described by Quatrano, 1980). In case of mf-shell substrata, the matrices were placed in 25 l aquaria immersed in seawater. Suspensions of antheridia and oogonia which had been mixed 15 min before to allow fertilization were then added to the water. Uninterrupted settlement and attachment of zygotes was allowed to occur over a 24 h period. Live *M. edulis* matrices were inoculated by pipetting the gamete suspension onto emersed mussels in order to avoid gamete filtration and digestion. Substrata were re-immersed in seawater (25 l aquaria) after 3 h and remained in the laboratory for an additional 21 h as the other substrata. Preliminary experiments had shown that settlement of zygotes was equally successful on emersed and immersed mussel substrata, justifying the use of two inoculation methods for live mussels and mf-shells.

Experimental plots ($0.5 \times 0.5$ m$^2$) were set up in May 1994. As in the previous experiment, complete fences served as *L. littorea* exclusions, lifted fences as procedural controls and fenceless plots as artifact controls. Snails were removed regularly from the exclusion treatments and their densities recorded as often as possible on these occasions. Treatment combinations of the two main experimental factors (*L. littorea* presence or absence) and substratum type (live mussels or mf-shells) were orthogonal in an unreplicated randomized block design with four different mussel beds along the low tide line of ‘‘Oddewatt’’ as blocks. ‘‘Barnacle cover’’ was introduced as a split plot factor in all treatment combinations (Fig. 3). Between May 25 and June 3, 1994 mussels were removed from all plots. Inoculated mussel substrata were transferred to the field within one day of inoculation to ensure the smallest possible growth stage of *F. vesiculosus* juveniles at the start of the experiment. Because of the small size (approximately 100 μm) and the dark green colour of zygotes, it was impossible to quantify their densities on the blue mussels at this stage. Different inoculation batches were therefore distributed across treatment combinations to avoid systematic error due to variation between batches. On July 12 and August 16, 1994 the number of *F. vesiculosus* individuals was determined on previously marked circular areas (3 $\mathrm{cm}^2$) from each of 10 mussels per plot, five with and five without barnacle cover. Data from five mussels were pooled to obtain a mean value of *F. vesiculosus* density per split plot. Percent cover of ephemeral macroalgae was recorded on July 12, 1994 at the peak of their abundance.

### *4.4. Impact of sedimentation on growth success of F. vesiculosus recruits on mussels (see Fig. 4 for experimental design)*

A laboratory experiment was designed to differentiate between two mechanisms that potentially affect survival of newly settled *F. vesiculosus* zygotes on mussels in the absence of grazing: (1) juvenile mussels, especially, clean their shell surface with their foot (Theisen, 1972) and could remove zygotes as well as other particles. (2) High filtration activity of mussels leads to the production of large amounts of faeces and pseudofaeces which are accumulated on the shell surface where they initially shade zygotes of *F. vesiculosus* and eventually cause their deterioration.

In October 1994, nine 10 l aquaria were supplied with different combinations of live and artificial mussels as substrata for *F. vesiculosus* zygotes: Group 1 contained 25 live *M. edulis* and five mf-shells, group 2 contained 15 live mussels and 15 mf-shells, and group 3 contained five live mussels and 25 mf-shells. Each group was represented in three replicate aquaria (single-factor design with three levels).

The production of faeces and pseudofaeces by mussels would affect zygotes equally on live mussels and on mf-shells within one aquarium because released particles would accumulate eventually on either shell surface. This effect should become more pronounced with increasing proportion of live mussels in an aquarium. In contrast, shell cleaning activity would affect *F. vesiculosus* recruits almost exclusively on live mussels (Theisen, 1972), because cleaning of neighbouring individuals (live or artificial) is most

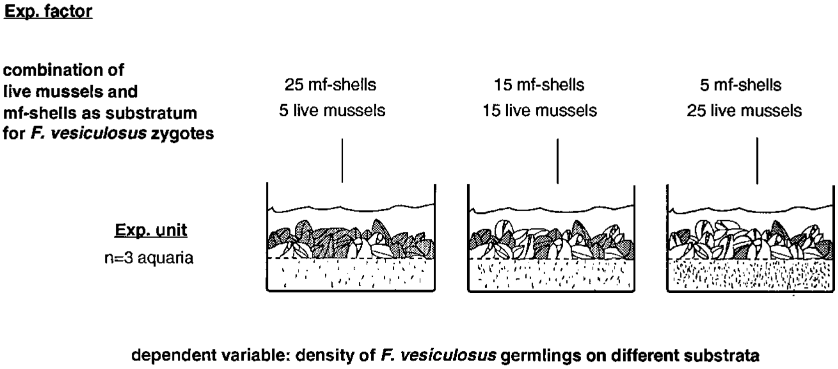


Fig. 4. Experimental design for laboratory experiment. "mf-Shells" = mortar-filled shells.

likely restricted to accidental encounters in densely packed assemblages (not the case in this experiment).

The experiment was designed to distinguish between the two processes by either finding only mortality of *F. vesiculosus* zygotes on live mussels, or to observe zygote mortality on both live and mf-shells. Therefore, the densities of live mussels used in the experiment (between five and 25 individuals per treatment) were chosen low enough to avoid the production of lethal levels of biodeposits for all epibiontic zygotes. (In comparison: natural densities of mussels from a mussel bed of the same area, 0.04 $m^2$, are often at least five-times as high, i.e., 130–160 ind. 0.04 $m^{-2}$, Albrecht and Reise, 1994).

For this experiment, mf-shells were individually filled with mortar and not attached to a mesh. All mussels were placed on a wire platform raising them above the aquarium floor, so that they would not be smothered by accumulating sediment from the bottom. On all mussels (live and mortar-filled), five circular counting areas (20 $mm^2$) were marked on both shell halves. Inoculation with *F. vesiculosus* zygotes was carried out as described above. The aquaria were placed in a temperature regulated culture room at 15°C within a light–dark cycle of 12:12 h. Light intensity varied from 60 to 80 μmol photons $m^{-2}$ $s^{-1}$ and was provided by "Lumilux" tube lamps (L65 W/21 DS White) from Osram. Water was supplied by a flow-through system of unfiltered seawater which resembled the natural water supply to mussels as closely as possible (especially in terms of suspended matter). However, a built-in reservoir tank in the station's sea water system allows particles to settle before they leave the system which probably reduced the sediment load and thus limited the detectability of sediment related effects in this experiment. Five weeks after inoculation *F. vesiculosus* germlings were counted on the previously marked surface areas under a stereomicroscope (16 × magnification).

### *4.5. Statistical analyses*

Experiments were analysed by means of analysis of variance (ANOVA). In each case, data were tested for homoscedasticity using Cochran's test, and if necessary, transformations of dependent variables were performed to eliminate heterogeneity of variance. Details about the respective ANOVA model and transformations will be given in Section 5. Significance levels, *F*-statistics with degrees of freedom for effect and error ($F_{x,y}$) and mean square errors ($MS_{error}$) will be given for all results. In one case, non-parametric Mann–Whitney *U*-tests were performed (snail grazing experiment). For the randomized block designs, the statistical results are summarized as tables for all experimental factors. I always used a model in which the blocking factor was random (mixed-model ANOVA). Homogeneity of variances in these experiments (Cochran's test), was tested disregarding the blocking factor. In one case (the laboratory experiment on growth success of *F. vesiculosus* on mussel shells), a power analysis was performed a posteriori to demonstrate the effect of sample size and magnitude of effect ($\eta^2$) on the power of the experiment. Asterisks denote statistical significance in Tables and Figures as follows: *** $p<0.001$; ** $0.001<p<0.01$; * $0.01<p<0.05$. All computer analyses were carried out with the software package STATISTICA by Statsoft.

## 5. Results

### 5.1. Grazing of L. littorea on mussel beds

*L. littorea* was present on all mussel beds throughout the investigation period; however, abundance varied with site. In June 1995, simultaneous mapping of snail abundance and cover of ephemeral seaweeds showed that green ephemerals (*Enteromorpha* spp.) only grew on mussel beds with the lowest densities of *L. littorea* ($< 15$ ind. $m^{-2}$). When periwinkle densities were higher, the percent cover of *Enteromorpha* spp. was 0 (Fig. 5). No other ephemeral macroalgae were found.

In the experimental manipulations, periwinkles were reduced on mussel beds with and without *Fucus* cover at "Oddewatt". In the absence of *Fucus*, red algae (*Porphyra umbilicalis* and *P. leucosticta*) grew as the only ephemeral macroalgae on experimental plots with reduced snail densities (Fig. 6), often to complete surface cover. This effect was significant ($p = 0.009$, *U*-test). There was also a significant fence artifact with respect to *Porphyra* spp. biomass on *Fucus* uncovered plots ($p = 0.007$, *U*-test); however, compared to experimental factors its effect size was negligible (Fig. 6). Where *Fucus* was present, reduced grazing pressure of littorinids did not lead to growth of ephemeral seaweeds either on mussel surfaces or epiphytically on *Fucus*.

*L. littorea* reduction was effective in that snail abundances were significantly lower in all reduction treatments (Fig. 6 top, two-way ANOVA, $F_{1,16} = 83.135$, $p = 0.000$, $MS_{error} = 57.43$). This was true both in the presence and absence of *Fucus* cover;

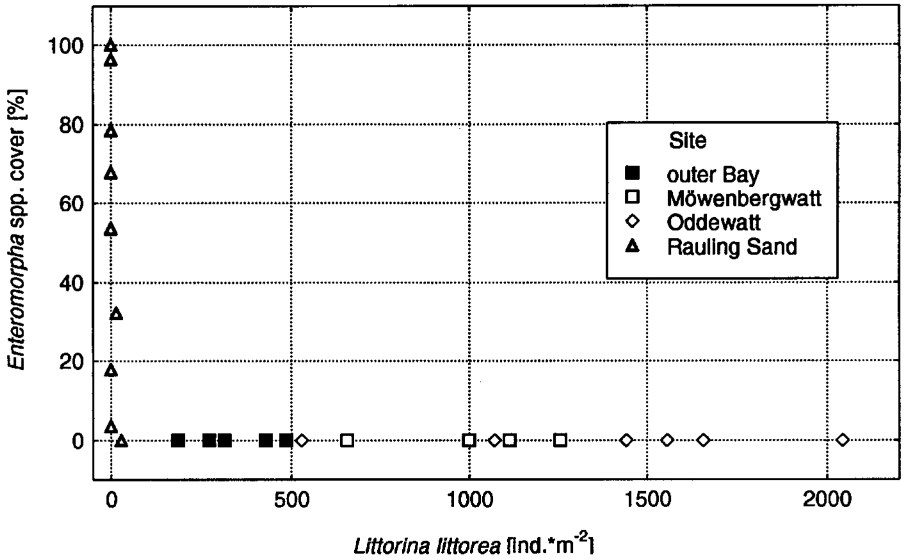


Fig. 5. Density of green algae (*Enteromorpha* spp.) and periwinkles (*L. littorea*) on mussel beds at different locations in and near Königshafen Bay. June 1995.

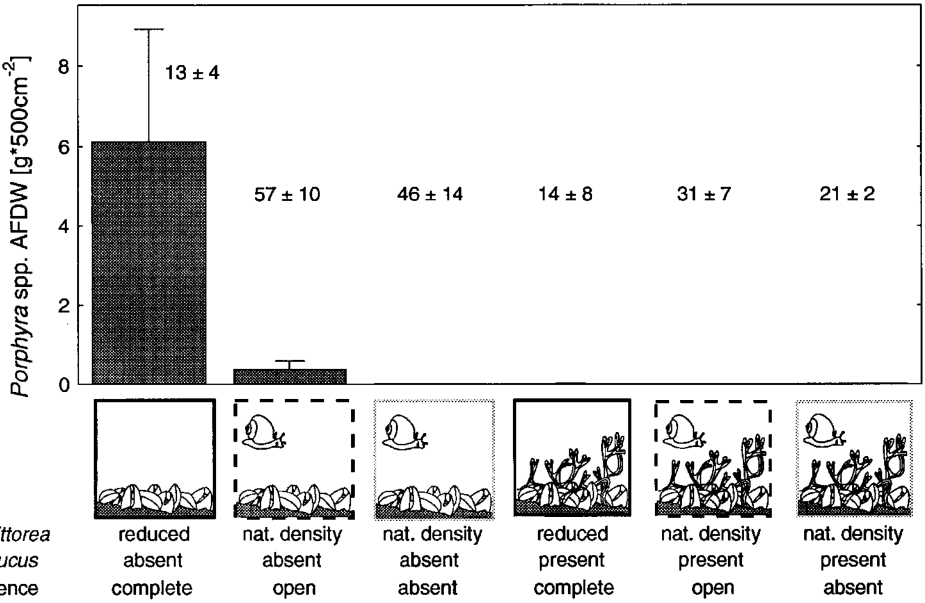


Fig. 6. Effects of snail grazing (*L. littorea*) on abundance of ephemeral red algae (*Porphyra* spp.) on mussel beds with and without *Fucus* cover. Means ($n = 5$) + 1 standard deviation. Densities of *L. littorea* at the time of data collection as numbers above bars (means, $n = 5 \pm 1$ standard deviation). July 1993.

however, overall snail densities were higher in the absence of *Fucus*, which reflects the natural variation of periwinkle density with *Fucus* cover on mussel beds (Albrecht and Reise, 1994).

### 5.2. Dispersal and sexual recruitment of *F. vesiculosus* propagules

Within the experimental period of approximately seven months, *F. vesiculosus* had colonized all of the settlement poles. The maximum length of plants at that time was 9 cm. Colonization density was generally highest on the flat pole tops where the wood had been washed out forming circular grooves. To disregard this artifact, *F. vesiculosus* was only counted on the pole circumference.

Highest *F. vesiculosus* abundances (41±26 ind. pole$^{-1}$) were reported from poles at 10 m distance when snails were excluded (Fig. 7). Ungrazed poles had significantly higher *F. vesiculosus* densities than grazed ones (two-way ANOVA, $F_{1,11} = 10.16$, $p = 0.009$, $MS_{error} = 244.42$, one pole was lost). In contrast, the distance of settlement substrata to the fertile population – within the investigated range of 5 to 25 m – had no effect on *F. vesiculosus* recruitment on poles (two-way ANOVA, $F_{2,11} = 0.65$, $p = 0.54$, $MS_{error} = 244.42$). Thus, sexual recruits of *F. vesiculosus* from fertile populations in the Wadden Sea have the potential to colonize suitable substrata within 25 m, and probably beyond this distance.

Regular observations of the settlement substrata showed an early colonization of poles

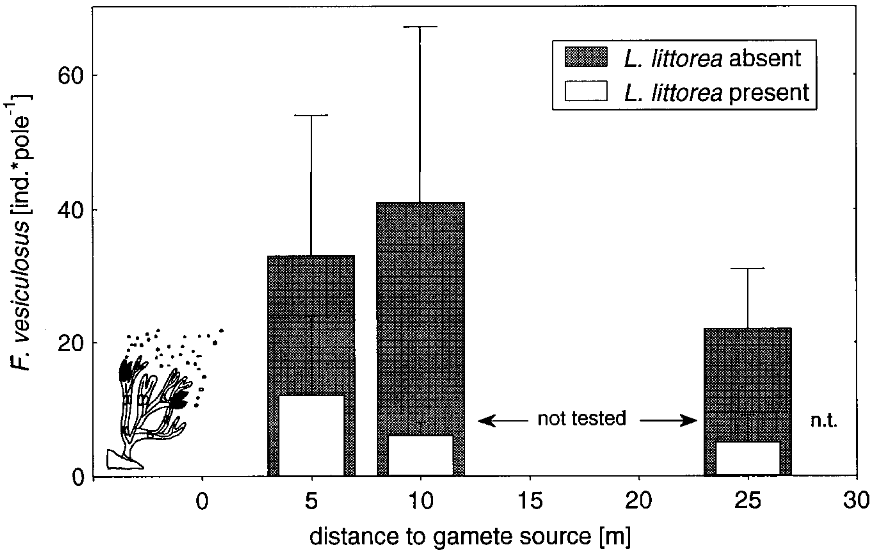


Fig. 7. Dispersal and recruitment potential of *F. vesiculosus* zygotes: number of *F. vesiculosus* individuals on artificial settlement substrata (wooden poles) with increasing distance from fertile population on rock. Means ($n = 3$) + 1 standard deviation. n.t. = Not tested. 1994.

with barnacle cyprids (within one week after installation). This led to a 100% barnacle cover of the poles and might have facilitated *F. vesiculosus* recruitment subsequently.

### *5.3. Post-settlement mortality of F. vesiculosus sexual recruits on mussel beds*

*F. vesiculosus* zygotes developed into adults on mf-shells under reduced grazing pressure by *Littorina littorea* (Fig. 8). This was more pronounced (but not significantly different) in the presence of a barnacle cover on mussel surfaces. Few *F. vesiculosus* individuals escaped grazing at natural snail densities in the presence of a barnacle cover on mussel surfaces. On live mussels there was generally no *Fucus* growth, even under reduced *L. littorea* grazing pressure. Densities of *F. vesiculosus* juveniles did not change between the two dates of data collection, July 12 and August 16, 1994. In August, plants had reached a maximum length of 3.5 cm. There were no fence artifacts. One year later the site was revisited, and the fucoids had grown to full maturity and fertility.

The abundance of *L. littorea* varied considerably among and within groups over the experimental period from April to October 1994 (Fig. 9). However, the graphical demonstration as well as the statistical analysis show a significant reduction of snail abundance in removal treatments compared to natural density plots until July 12, 1994, i.e., the time of first data collection for *F. vesiculosus* juveniles (Fig. 9 Table 1). The mean abundance of snails in reduction plots on July 12, 1994 (23±25 ind. $m^{-2}$, $n = 8$) was 9% of the average natural density (244±135 ind. $m^{-2}$, $n = 8$; fenced plots only). In August, snail abundance was much higher, namely 146±142 ind. $m^{-2}$ under removal conditions, as opposed to 378±139 ind. $m^{-2}$ in natural density treatments

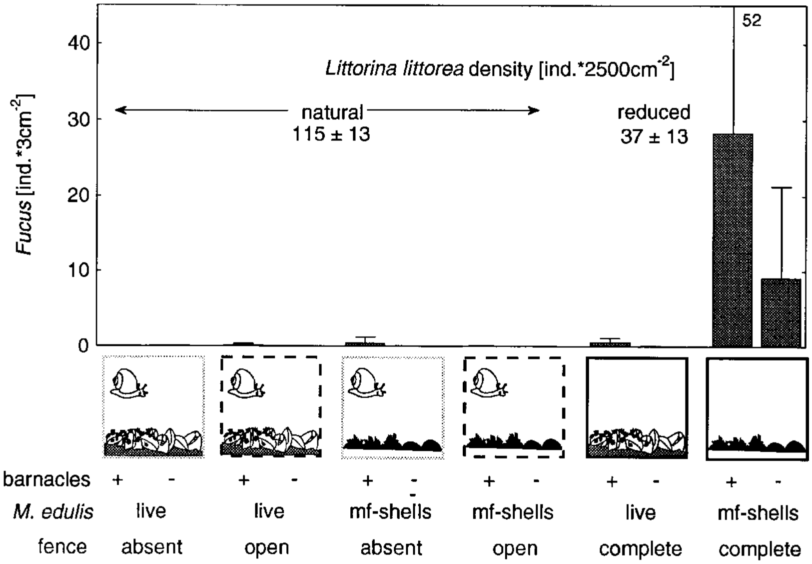


Fig. 8. Growth success of *F. vesiculosus* on mussel beds: density of juvenile individuals on previously inoculated mussel substrata within experimental plots. The experimental factors were snail density (*L. littorea*), mussel substratum ("mf-shells" = mortar-filled shells) and barnacle cover as experimental factors. Means ($n = 4$) + 1 standard deviation. August 1994.

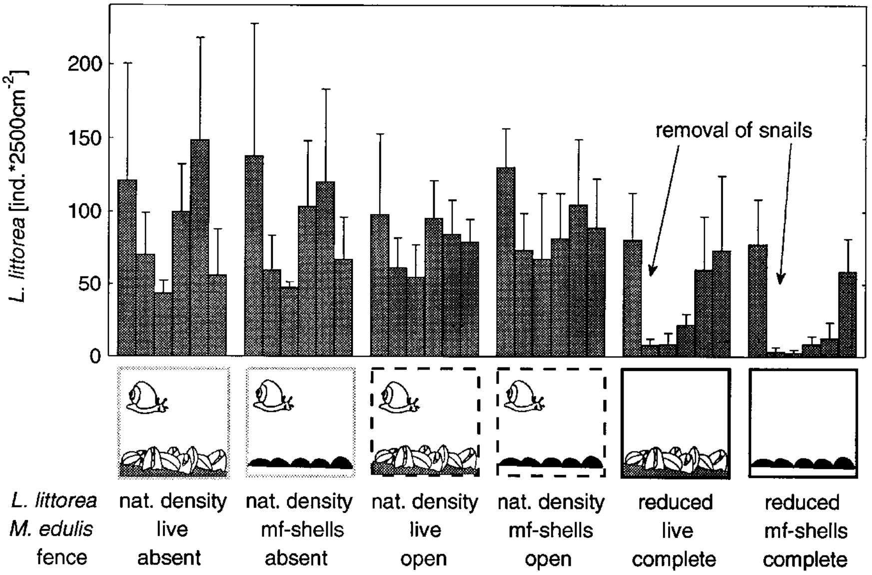


Fig. 9. Density of *L. littorea* on experimental plots within mussel beds. Means ($n = 4$) + 1 standard deviation for each of six sampling dates (left to right: April 4, July 6, July 12, August 5, August 8 and October 10, 1994). "mf-Shells" = mortar-filled shells.

Table 1
ANOVA results for reduction efficiency of *L. littorea* in the field experiment as recorded on August 16, 1994 (fenced treatments only)

| Independent variables:<br>Dependent variable: | | *Littorina* (*f*,2)<br>*L. littorea* density; transf. $\ln(x+1)$ | Substratum (*f*,2) | Block (*r*,4) |
|---|---|---|---|---|
| Effect | df | MS | *F* | *p* |
| *Littorina* | 1 | 23.730 | 42.515 | 0.000 |
| Substratum | 1 | 0.583 | 0.870 | 0.382 |
| Block | 3 | 0.417 | | |
| Lit. × Sub. | 1 | 0.924 | 1.651 | 0.230 |
| Residual | 9 | 0.558 | | |

The model was mixed (two fixed factors, *f*, block factor random, *r*).

(means±standard deviation). Overall, the reduction of *L. littorea* was successful despite high recruitment which had been observed in April and which led to a gradual growth of juvenile snails into larger size classes which were the target of the manipulations.

Percent cover of ephemeral green and red algae (*Enteromorpha* spp., *Ulva lactuca* and *Porphyra* spp.) was recorded on experimental plots on July 12, 1994 when these species were at the peak of their development. Whereas greens grew exclusively on artificial mussel substratum with reduced *L. littorea* densities, *Porphyra* spp. was found also on live mussels but with lower percent cover (Table 2). In the presence of natural grazing pressure of snails, neither of the ephemeral species grew on either substratum. Thus, cover of ephemeral macroalgae in this experiment also depended primarily on periwinkle abundance, (compare Tables 2 and 3 for *Porphyra* spp.), as in the previous grazing experiment (see above).

### *5.4. Impact of sedimentation on growth success of F. vesiculosus recruits on mussels*

Since growth of *F. vesiculosus* zygotes was unsuccessful on live *M. edulis* in the field even under highly reduced snail grazing pressure, differences between mf-shell surfaces and live mussels as substratum for *F. vesiculosus* zygotes in this environment were investigated further.

Five weeks after inoculation zygotes had grown to an average length of 300 to 500 μm, and were thus large enough to be quantified. For each mussel the shell carrying most of the *F. vesiculosus* individuals (because of its upward position during inocula-

Table 2
Results for % cover of *Porphyra* spp. on experimental plots (fenced treatments only) (means and standard deviations)

| Treatment | | % Cover of *Porphyra* spp. | | |
|---|---|---|---|---|
| *Littorina* | Substratum | Mean | S.D. | *n* |
| Natural | Live mussels | 0.25 | 0.50 | 4 |
| Natural | mf-shells | 5.00 | 10.00 | 4 |
| Reduced | Live mussels | 21.25 | 13.15 | 4 |
| Reduced | mf-shells | 56.25 | 40.29 | 4 |

Table 3
Results for % cover of *Porphyra* spp. on experimental plots (fenced treatments only* ANOVA)

| Independent variables: | | *Littorina* (*f*,2) | Substratum (*f*,2) | Block (*r*,4) |
|---|---|---|---|---|
| Dependent variable: | | % Cover of *Porphyra* spp.; transf. $\ln(x+1)$ | | |
| Effect | df | MS | *F* | *p* |
| *Littorina* | 1 | 34.243 | 38.021 | 0.000 |
| Substratum | 1 | 1.987 | 2.207 | 0.172 |
| Block | 3 | 0.779 | | |
| Lit. × Sub. | 1 | 0.055 | 0.061 | 0.811 |
| Residual | 9 | 0.901 | | |

The model was mixed (two fixed factors, *f*, block random factor, *r*)

tion) was identified and used in the analyses. Germling densities measured in five previously marked areas on each shell were then pooled for each mussel. Within each aquarium, values for five randomly selected live mussels and five mf-shells were averaged to provide two mean densities for juveniles per aquarium – one for live mussels, the other one for mf-shells.

In all three groups more *F. vesiculosus* recruits grew on mf-shells than on live mussels (Fig. 10a), which reflects the results from the field experiment (Fig. 8). Additionally, germling abundance was lowest on live and mortar-filled substrata in aquaria with the highest proportion of live mussels but this difference was not statistically significant. The power of the experiment was low under the given conditions (19% and 41% for germling density on live mussels and mf-shells, respectively). With replication of three per treatment, the magnitude of effect (i.e., the percentage of variation attributable to treatment effects) would need to be 65% in order to achieve a desirable power of 80% in the experiment (Table 4). Alternatively, doubling the number of replicates would have increased the power of the experiment to 84% for mf-shells and to 44% for live mussels with the magnitudes of effect remaining at 42% and 22% for the respective dependant variables (Table 4).

When recruit densities on live mussels and mf-substrata were pooled for all 30 mussels within one aquarium, the negative effect of live *M. edulis* on the success of *F. vesiculosus* development became more pronounced (Fig. 10b, one-way-ANOVA, $F_{2,6}=7.939$, $p=0.021$, $\mathrm{MS}_{\mathrm{error}}=0.06$). Qualitatively, the sediment on live mussels appeared stickier and more resistant to removal by mechanical action than particles on mf-shell surfaces.

## 6. Discussion

### *6.1. Absence of ephemeral seaweeds from mussel beds*

In the Wadden Sea primary hard substratum is practically non-existent. Single sand grains may qualify for hard substrata on a very small scale and are utilized by green algal spores for initial attachment. However, they lack stability over more than several

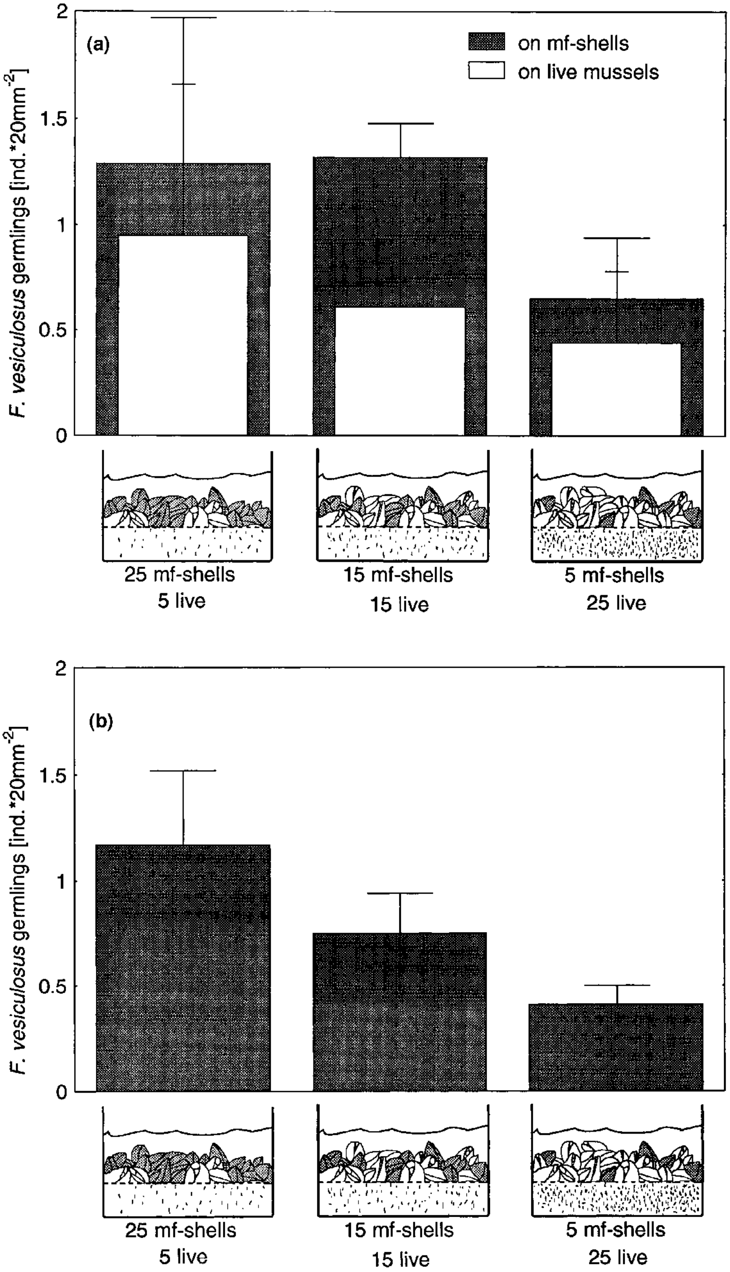


Fig. 10. Laboratory experiment to test the effect of live mussels on *F. vesiculosus* recruitment: (a) density of *F. vesiculosus* germlings on previously inoculated substrata [live mussels, mortar-filled (mf) shells] in different experimental treatments. Within aquaria, values were pooled from five randomly selected mussels of each type. (b) Overall density of *F. vesiculosus* germlings on mussel substrata in different experimental treatments. Within aquaria, values from all 30 mussels were pooled. Means ($n = 3$ aquaria) + 1 standard deviation. October 1994.

Table 4
Power analysis for laboratory experiment

| $N_{tot}$ | Magnitude of effect ($\eta^2$) | | | | | |
|---|---|---|---|---|---|---|
| | **mf-shells** | | **Live mussels** | | | |
| | **0.22** | 0.30 | **0.42** | 0.50 | 0.60 | 0.70 |
| **9** | **0.19** | 0.26 | **0.41** | 0.53 | 0.71 | 0.89 |
| 12 | 0.27 | 0.39 | 0.60 | 0.75 | 0.90 | 0.98 |
| 15 | 0.36 | 0.51 | 0.75 | 0.87 | 0.97 | 1.00 |
| 18 | 0.44 | 0.62 | 0.84 | 0.94 | 0.99 | 1.00 |
| 21 | 0.51 | 0.70 | 0.91 | 0.97 | 1.00 | 1.00 |

The power ($1-\beta$) under given magnitudes of effect ($\eta^2$ as the percentage of variation attributable to treatment effects) and sample size are in bold for both dependent variables. Power is then calculated for increased magnitudes of effect as well as for increased sample sizes.

days, which inhibits germination and further development of green algal settlers on them (Schories, 1995).

The attributes of intertidal mussel beds seemingly qualify them as alternative biogenic attachment substrata for both epibionts and seaweeds in a sea of sediment around them: they reach sizes of several hectares (Verwey, 1954), and they provide long term habitats because they may persist for decades (Nehls and Thiel, 1993). Nevertheless, the distribution of macroalgae on mussel beds does not reflect this apparent suitability as settlement surfaces: large areas of mussel beds are colonized by sessile macrofauna but remain free of seaweeds, and other parts carry a monospecific cover of *Fucus* which is not attached to the surface by a holdfast. It is unlikely that surface properties of the mussels preclude the colonization of shells by macroalgae, because (a) seaweeds readily grow on *M. edulis* shells in rocky shore habitats (e.g., *F. vesiculosus* grows on blue mussels at the island of Helgoland (Janke, 1990) and (b) the occurrence of sessile macrofauna on mussel shells (e.g., barnacles and sea anemones) is just as common in the Wadden Sea as on rocky coasts (pers. obs.).

I tested grazing by periwinkles, *L. littorea*, as a biological factor limiting the distribution of macroalgae on mussel beds, because densities of littorines in the Wadden Sea are especially high on such hard substrata. They may reach several thousand ind. $m^{-2}$ (Albrecht and Reise, 1994), but average abundances are usually in the range of several hundred ind. $m^{-2}$ and thus similar as on rocky shores (Lubchenco, 1978; Lein, 1980; Bertness, 1984; Janke, 1990; Wilhelmsen and Reise, 1994). Although the snail densities are subject to variation in space and time, the low abundance of *L. littorea* at "Rauling Sand" represents an exception on Wadden Sea mussel beds (compare to Wohlenberg, 1937; Albrecht, 1995; Wilhelmsen and Reise, 1994).

Under these low herbivory conditions ($<12$ *L. littorea* $m^{-2}$), *Enteromorpha* spp. formed complete covers on mussel beds. There was, however, no linear relationship between snail densities and percent cover of ephemeral macroalgae among the mussel beds investigated. Instead, the relationship between both variables reflected a threshold response of algal growth to low grazing pressure.

Similarly, the field experiments confirmed that *Fucus*-free mussel beds were colonized by ephemeral red algae (*Porphyra* spp., 1993) and/or greens (*Enteromorpha* spp., *Ulva* *lactuca* and *Porphyra* spp., 1994) if periwinkles were reduced to at least one-third of natural densities. At moderate and high densities ($>260$ ind. $\text{m}^{-2}$ at "Oddewatt"), *L. littorea* grazing removed newly settled propagules of ephemeral macroalgae from mussel surfaces, preventing their development into adult plants. In situations with low herbivory from periwinkles, different species assemblages of ephemerals grew on the mussels (*Porphyra* spp. at "Oddewatt" 1993, *Enteromorpha* spp., *Ulva lactuca* and *Porphyra* spp. at "Oddewatt" 1994 and *Enteromorpha* spp. at "Rauling Sand" 1995), most likely reflecting differential supply of propagules in the water column which is highly variable between sites and years (Schories, 1995). It also indicates the similarities in growth response of all of these ephemeral species when grazing pressure is temporarily or spatially reduced on mussel beds.

In the presence of *Fucus*, no ephemeral green or red algae developed on mussel shells under reduced grazing pressure. I attribute this result to (a) the direct interference of adult *Fucus* with settlement and germination of green and red algal propagules through shading and whiplashing of the thalli (Schonbeck and Norton, 1980; Cousens, 1985; Lüning, 1990) and (b) the reduced settlement surface on mussel shells underneath a *Fucus* canopy. *Fucus* thalli decrease flow-rates and thus increase sedimentation within the mussel–*Fucus* matrix. This leads initially to more mussel individuals being largely buried in sediment and eventually to a much reduced mussel density compared with mussel patches without *Fucus* cover (Albrecht and Reise, 1994). Whereas mussels often form hummocks in the absence of *Fucus* (increasing the total attachment surface within a patch), the sediment-free shell surface underneath a *Fucus* canopy, i.e., attachment substratum for epibionts, is highly restricted.

### 6.2. Why are no sexual recruits of F. vesiculosus found on mussel beds?

On Wadden Sea mussel beds *Fucus* reproduces only vegetatively. Furthermore, there is no colonization of mussel beds with sexual recruits from fertile *F. vesiculosus* populations elsewhere. During the dispersal of *F. vesiculosus* zygotes from such hard substratum populations, there are various sources of mortality which potentially prevent the successful establishment on mussel beds. (Fig. 11): (a) after release from the parent plant (and assuming successful fertilization – see Serrao et al., 1996 for *F. vesiculosus* in the Baltic), zygotes will be removed by predators in the plankton or will fall onto unsuitable settlement substratum (pre-settlement mortality). (b) Propagules which reach mussel beds will be decimated during settlement by filtration and digestion of *M. edulis* (Dayton, 1973; Foster, 1975; Santelices and Martinez, 1988). This effect is likely to gain importance with increasing aggregation density (Wahl et al., 1998). (c) Zygotes surviving this stage and successfully settling on mussel surfaces will be subject to post-settlement mortality, e.g., grazing by *L. littorea* (see below).

In this study the different mortality factors before and during settlement were not quantified. However, I tested whether the distance from fertile *F. vesiculosus* populations to the nearest mussel bed was within the range of dispersal of *F. vesiculosus* recruits under the existing environmental conditions. The maximum distance tested was 25 m, because within this range smaller mussel aggregations allow the stepwise colonization of larger beds. In other habitats dispersal distances for fucoid propagules

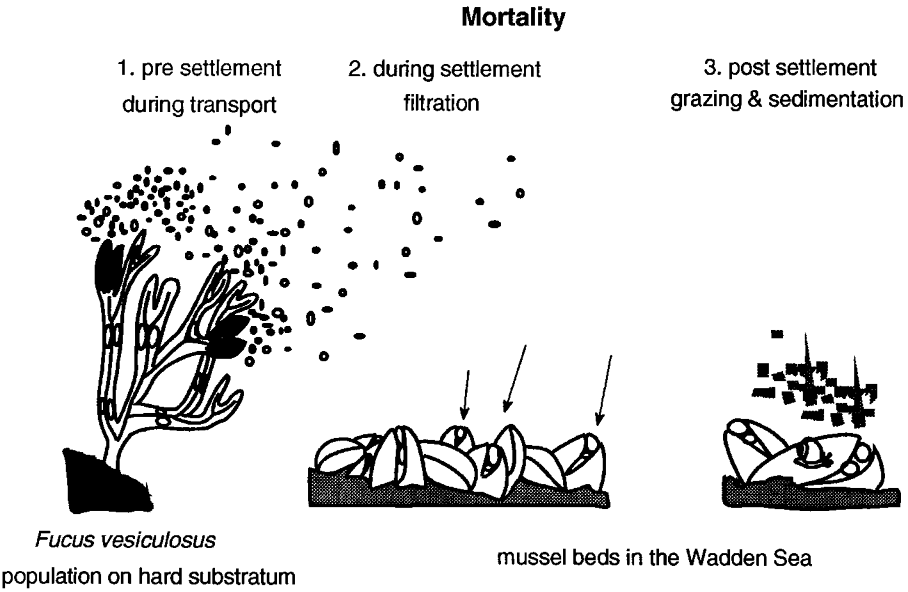


Fig. 11. Sources of mortality of *F. vesiculosus* propagules after release from a fertile hard substratum population: prior to settlement (1) through losses during transport in the water column, during settlement (2) on intertidal mussel beds through filtration by mussels and after settlement (3) due to grazing and sedimentation processes.

are only several metres (Santelices, 1990; Vadas et al., 1992). This is usually related to high sinking rates in water of low or intermediate current speeds. On tidal flats of the Wadden Sea tidal currents are often strong (up to 60 cm $s^{-1}$, hydrodynamic model, Backhaus and Hartke, University of Hamburg, unpubl.) and thus facilitate wide dispersal of propagules. The number of juvenile *F. vesiculosus* which settled successfully on collecting substrata within 5 to 25 m from the source population was approximately two orders of magnitude higher than in a similar study of *Sargassum muticum* germlings by Deysher and Norton (1982). In both investigations, and despite higher sinking rates of the larger *Sargassum* germlings (Norton and Fetter, 1981), the recruitment shadows of both species were similar between 5 and 25 m, i.e., there was no decline in the number of successfully settled zygotes. This may indicate that *F. vesiculosus* – as *Sargassum* – also has the sharpest decline of successful settlers within the first 5 m from the source population. Whatever the case may be, *F. vesiculosus* recruitment to suitable settlement substrata was successful across at least 25 m from the fertile population in this high flow environment. Anecdotal evidence for the colonization of isolated hard substrata which were kilometres away from any fertile *F. vesiculosus* population (pers. obs.) confirm the potential for a wide dispersal range of this species in the Wadden Sea.

Grazing by *L. littorea* can be an important source of post-settlement mortality factors for experimentally introduced *F. vesiculosus* zygotes on mussel beds. When grazing pressure of periwinkles was reduced, zygotes grew into fertile adults on mf-mussel substratum. This effect was even stronger in the presence of barnacles on the substratum, because in the crevices between barnacle individuals grazing efficiency was further diminished. In this respect the results are concordant with effects of grazing on ephemeral algae (both in this study and in rocky shore investigations, e.g., Lubchenco, 1983). They also reflect the fact that juveniles of fucoids are much more susceptible to grazing than adults which are often mechanically and chemically defended against herbivory (Steneck and Watling, 1982; Denton et al., 1990). In contrast, *F. vesiculosus* zygotes did not grow successfully on live mussels in the experiment, despite the fact that mussels are often utilized as secondary substratum by fucoids on rocky shores (Janke, 1990) as well as at the rocky breakwater site in this study.

What then distinguishes live mussels from mf-shell substratum after settlement of *F. vesiculosus zygotes* in this environment? Theisen (1972) showed that mussels use their foot to clean their own shell surface. This is effective in juvenile *M. edulis* because the relation of foot size to shell surface is larger than in adults and allows substantial flexibility. Consequently, juvenile mussels are rarely overgrown by epibionts. For adults the efficiency of the cleaning process decreases (Wahl, unpubl. data) and larger *M. edulis* on both rocky and soft sediment shores are often heavily fouled. Alternatively, a mechanism preventing growth of *F. vesiculosus* zygotes on live mussels in the Wadden Sea is the accumulation of biodeposits through filtration. Mussels produce faeces and pseudofaeces which are deposited on the shell surface. The higher the concentration of inorganic particles is in the water column the more pseudofaeces are produced and accumulated by mussels (Bayne et al., 1993). For *F. vesiculosus* zygotes 100–200 μm in length this may lead to severe shading or complete burial by sediment particles on the shell. In comparison to ephemeral macroalgae, fucoids have low growth rates (Littler and Arnold, 1982; Hales and Fletcher, 1989) and are unable to escape sedimentation through fast development. Similarly, the survival rate of kelp spores (*Macrocystis pyrifera*) can drop to 10% under a sediment cover of 450 μm (Devinny and Volse, 1978).

Results from the laboratory experiment which intended to separate these two factors of mortality for *F. vesiculosus* zygotes (shell cleaning vs. biodeposition) indicated that biodeposition was more critical: germling survival was lowest on both types of substratum in aquaria with the highest proportions of live mussels. Despite the lack of statistical significance of these results, the power analysis supports the interpretation because under the given experimental conditions there was a 60 to 80% chance of not detecting true differences between treatment means (Table 4). Doubling the replication of the experiment would have substantially increased the power, even if the magnitudes of effect remained identical (42 and 22%). Thus, with such adjustments to the experimental design, I would likely have found the trends revealed in Fig. 10 reflected as statistically significant results.

In the Wadden Sea with extremely high particle concentrations in the water column the negative effect of biodeposition by mussels on attached zygotes of *F. vesiculosus* is much more pronounced than in usually less productive rocky shore habitats. Dittmann (1987) compared biodeposition on mussel beds in Königshafen Bay to several rocky shore habitats and found twenty-fold higher rates in the Wadden Sea (25 g $m^{-2}$ $yr^{-1}$ compared to 11.91 g $m^{-2}$ $yr^{-1}$, rocky eulittoral in Japan, Tsuchiya, 1980 and 1.09 g $m^{-2}$ $yr^{-1}$, rocky sublitoral in the Baltic, Kautsky and Evans, 1987). Biodeposition is crucial for seaweeds with slow growth rates, whereas ephemeral species such as *Enteromorpha* spp., *Ulva* spp. and *Porphyra* spp. escape sediment burial on mussel surfaces by fast growth. The abundance of ephemerals on mussel beds in the Wadden Sea is regulated largely by grazing, which is similar as on rocky shores. Sexual recruits of *Fucus* are subject to the overriding environmental factor in the Wadden Sea – sedimentation – and its interaction with the macrofauna, i.e., filtration by mussels. The life history of *F. vesiculosus* forma *mytili*, which omits all juvenile stages susceptible to grazing and biodeposition and, instead, relies only on the vegetative reproduction of adults, has a clearly adaptive value under these conditions.

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