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Factors structuring the *Mytilus*- and *Zostera*-community in the western Baltic: an experimental approach

Strukturbestimmende Faktoren für die *Mytilus*- und *Zostera*-Gemeinschaft in der westlichen Ostsee: ein experimenteller Ansatz

von
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GLOSSARY

α	chance of erroneously rejecting the null-hypothesis when in fact it is true (type I error)
ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
Bonferroni-adjustment	the experimentwise error rate is kept at α=0.05 by dividing the significance level by the number of comparisons performed
Cochran's test	test for homogeneity of variances among groups with equal number of elements (i.e. balanced design)
df	degrees of freedom
(experimental) factor	independent variable with presumed effect on one or more response variables
factorial design	experimental design in which each level of one factor is combined with each level of a second (or more) factor
homoscedasticity	homogeneity of variances among groups in an ANOVA
interaction	the effect of a factor A depends on the level of another factor B
main effect	in a factorial experiment the effect of a single factor without interaction
MAN(C)OVA	Multivariate Analysis of (Co)Variance
MS	mean squares = sums of squares divided by degrees of freedom
multi-homoscedasticity	n-dimensional homogeneity of variances among n dependent variables in a multivariate analysis of variance
n	total number of replicates

N	number of samples if they contain subsamples
nested analysis	a random experimental factor is hierarchically arranged (=nested) within another factor
response variable	dependent variable, parameter under investigation
treatment	a certain combination of experimental factors
type I error	the null-hypothesis is rejected although it is true
type II error	the null-hypothesis is not rejected although it is false
2x3 ANOVA	factorial ANOVA with 2 levels of experimental factor A combined with 3 levels of factor B
ω^2	proportion of variance explainable by an experimental factor (relative effect size)
*	significant at the $p<0.05$ level
**	significant at the $p<0.01$ level
***	significant at the $p<0.001$ level

ABSTRACT

The principal objectives of this dissertation were (1) to explain the ecological-scale distribution of blue mussels (*Mytilus edulis*) in Kiel Fjord (2) to examine why, in shallow water (1-3 m), mussels occur more often in association with eelgrass (*Zostera marina*) than as pure stands and (3) to examine whether mussels have an effect on *Zostera* growth, shoot density and vegetative propagation. Field observations and experiments were conducted in Friedrichsort (FO) and Moeltenort (MOE) by means of SCUBA diving.

Triplicate passive mussel spat collectors were deployed during the main settlement period to assess the contribution of spatial variations in settlement to mussel distribution. They revealed that on a scale of decimeters to meters spatial variation was generally low and that spat densities were not significantly different in the two water depths studied (2 and 6 m). The densities of juvenile mussels were compared among the principal substrata found in shallow water (mussel bed, *Zostera* meadow, *Zostera/Mytilus* mixed stands and bare sand) over a period of 15 mo. On pure mussel beds, recruit abundances were only 50% of those found on both substrata with a *Zostera* canopy. I also regularly sampled density and feeding performance of seastars (*Asterias rubens*) and shore crabs (*Carcinus maenas*) on these substratum types. Whereas *Carcinus* densities were always low compared to those of seastars, and crabs were totally absent during winter months, *Asterias* individuals were present throughout the year with densities between 5 and 35 ind/0.25 m^2. They strongly preferred juvenile mussels (<1 yr old) over adult individuals. The predation impact of *Asterias* on juvenile mussels was found to be similar among the 3 substratum types: adult mussel bed (a) with and (b) without eelgrass, and (c) pure eelgrass. Length/frequency distributions of mussel recruits also suggest that juveniles suffered a similar and high predation mortality on these substrata. Therefore I suggest that the modification of the hydrodynamic regime inside the *Zostera* canopy (with and without mussel understory) led to a higher recruitment via secondary settlement compared to pure mussel beds. According to the frequency distributions settlement continued from August 1993 until January 1994. On substratum type pure sand, recruit densities were always markedly lower compared to the other substrata except for autumn 1992 when densities

comparable to those in *Zostera* stands were attained. According to the spat collector data, this occurred after an approximately 6-fold higher settlement intensity than in 1993. However, a predator exclusion experiment running for 3 mo in autumn 1992 revealed that none of the juveniles survived on bare sand due to heavy *Asterias* predation.

I found that drifting mussel clumps represent an important means of mussel dispersal in Kiel Fjord. A drift collector fence of 12 m length which was installed parallel to the shoreline in 4 m depth caught 21 kg (FW) of mussels during one year, corresponding to approximately 50 mussel clumps which were torn loose and transported downslope. Since, in mussel beds in 6 m depth, recruitment was to be only 25% of the average density found on beds in 2 m, these drifting clumps probably represent a major source of mussels for these depths.

In a *Mytilus* transplantation experiment, the effects of presence or absence of stable primary substratum, presence or absence of predators, and of two water depths (2 and 6 m) on growth and dispersal of mussel clumps were tested in a factorial design with 7 out of 8 possible treatment combinations.

All transplanted clumps survived the observational period of 10 mo. However, areal changes were very different among treatments. Juvenile mussels (0 to 1-yr age class) contributed mainly to the 6.3-fold increase in clump area without predators in 2 m depth. With predators, clumps changed their area only little. In 6 m depth, exclusion of predators had a much lower, but also significant positive effect. Statistical analysis (ANCOVA) confirmed that water depth and presence or absence of predators had both a highly significant effect on clump growth. Calculated as relative effect size ω^2, the two chosen water depths accounted for 16% and presence or absence of predators for 52% of the total variance in clump area. No cage artefacts were evident in a control experiment in which roof cages were compared to completely uncaged plots.

A comparison between the proportions of recently eaten mussels being crushed (= eaten by crabs) vs. opened without shell damage (= eaten by seastars) revealed that during its highest abundance in summer, *Carcinus* was responsible for at most 15% of the predation caused mortality in mussels (>10 mm length).

Stable substratum type had no effect on growth but a strong effect on drift distance and dispersal of mussel clumps. Twenty-two drift events ranging from 20 cm to 12 m were recorded in 8 replicate shallow clumps transplanted onto sand. In contrast, none of the mussel patches attached to stable substratum drifted during the 10 mo of observation.

In Kiel Fjord, in 1-3 m depth, a higher percentage of mussel beds occurs in mixed stands with eelgrass than in pure stands (68% and 84% at FO and MOE, respectively). In a canopy removal experiment on permanent plots I tested the effects of presence or absence of *Zostera* on the susceptibility of mussel beds to storm disturbance. The experiment revealed that eelgrass significantly reduced the loss of mussel cover during two storm periods at both sites. Furthermore, moving mussel clumps showed a strong tendency to settle inside *Zostera* meadows. No effect of *Zostera* was found on the density of *Asterias* on adult mussel beds nor on the proportion of seastar individuals feeding on juvenile mussels. On pure mussel beds, there was a tendency that a higher proportion of *Asterias* individuals fed on adult (>30 mm) mussels compared to beds with *Zostera*. I attribute that to the lower density of mussel recruits which were available for seastars on this substratum type.

In a density manipulation experiment, mussels were either added to *Zostera* patches or removed from existing *Zostera/Mytilus*-associations in order to test the effects of mussels on density, vegetative propagation and growth of eelgrass. I found no effect of these experimental manipulations on the shoot density of *Zostera* from April to October 1993. Likewise, observations on a series of permanent plots over one growth period showed that adjacent mussel patches did not impede the vegetative propagation of eelgrass patches. Instead of damaging eelgrass by interference competition, mussels enhanced eelgrass growth. At the end of August, plants in the *Mytilus*-addition treatment had a 36% higher leaf area than the controls, whereas mussel removal led to an area decrease of 16% compared to the controls. Since at the same time, the sediment porewater concentrations of ammonium and phosphate doubled in presence of *Mytilus*, I infer that *Zostera* is nutrient-limited in the sandy, organically poor sediments of the shallow subtidal zone. *Mytilus* facilitates *Zostera* by the biodeposition of organic material via faeces and pseudofaeces. A correlation between porewater ammonium concentration and plant size

supports the contention that nitrogen is growth limiting. In contrast, no relationship was found between porewater phosphate concentration and plant size.

ZUSAMMENFASSUNG

Folgende Fragestellungen sollten in der vorliegenden Dissertation beantwortet werden: (1) Welches sind die verbreitungsbestimmenden Faktoren für die Miesmuschel (*Mytilus edulis*) in der Kieler Förde ? (2) Warum kommen im Flachwasser (1-3 m Wassertiefe) Muschelbänke häufiger in Assoziation mit Seegras (*Zostera marina*) als in Reinbeständen vor ? (3) Beeinflußt die Anwesenheit von Miesmuscheln in *Zostera/Mytilus*-Mischbeständen Wachstum, Sproßdichte oder vegetative Verbreitung des Seegrases ? Die Untersuchungen wurden im Rahmen taucherischer Beobachtungen und durch Freilandexperimente in der Kieler Förde an den Stationen Friedrichsort (FO) und Möltenort (MOE) durchgeführt.

Passive Muschel-Larvenfänger (3 Parallelen) wurden während der Haupt-Larvenfallsaison aufgestellt, um den Beitrag der räumlichen Variation des Larvenfalls an der Muschelverbreitung zu untersuchen. Auf einer Skala von dm bis m war die räumliche Variation gering und die Siedlungsdichten der juvenilen Muscheln waren zwischen den zwei beprobten Tiefen, 2 und 6 m, nicht signifikant voneinander verschieden. Die Dichten von Muschelrekruten wurden über eine Periode von 15 Monaten zwischen den wichtigsten im Flachwasser anzutreffenden Substraten verglichen (Muschelbank, *Zostera*-Wiese, *Zostera/Mytilus*-Assoziation und Sand). Auf reinen Muschelbänken erreichten die Rekruten-Abundanzen nur etwa 50% der Dichten, die auf beiden Substraten mit Seegras vorgefunden wurden. Ich beprobte außerdem die Dichte und Freßaktivität der beiden wichtigsten epibenthischen Muschel-Predatoren, dem Seestern (*Asterias rubens*) und der Strandkrabbe (*Carcinus maenas*), auf diesen Substrattypen. Während *Carcinus* im Vergleich zu *Asterias* selten war und während der Wintermonate ganz fehlte, waren Seesterne das ganze Jahr über mit Dichten zwischen 5 und 35 Ind/0.25 m^2 vorhanden. Sie

bevorzugten juvenile Muscheln (<1 Jahr) deutlich gegenüber adulten. Der Wegfraß von juvenilen Muscheln durch Seesterne war auf den Substraten Muschelbank (mit und ohne Seegras) sowie reiner Seegraswiese gleich hoch. Auch Längen-Häufigkeitsverteilungen deuteten darauf hin, daß Jungmuscheln auf allen 3 Substrattypen einem gleichen und intensiven Fraßdruck unterliegen. Es ist daher zu vermuten, daß die erhöhte Rekrutierung innerhalb der *Zostera*-Wiese gegenüber reinen Muschelbänken auf einer Veränderung des Strömungsregimes durch das Seegras beruht, die zu einer erhöhten Zufuhr von Jungmuscheln aus der sekundären Larvenphase führt. Die Häufigkeitsverteilungen der Juvenilen zeigten, daß eine Besiedlung von August 1993 bis Januar 1994 anhielt. Auf Sand waren die Jungmuschel-Abundanzen deutlich niedriger als auf den übrigen Substraten. Nur im Herbst 1992 wurden ähnliche Dichten wie auf den *Zostera*-Substraten vorgefunden. Dies ereignete sich nach einem Larvenfall, der nach den Larvenfängerdaten 6mal so intensiv war wie im darauffolgenden Jahr 1993. Ein im Herbst 1992 durchgeführtes Räuberausschlußexperiment ergab, daß Jungmuscheln auf reinem Sand wegen des starken Fraßdrucks durch Seesterne nicht überlebten.

Verdriftende Muschelklumpen stellen in der Kieler Förde eine wichtige Form der Muschelverbreitung dar. In einem 12 m langen Fangzaun, der parallel zur Strandlinie in 4 m Wassertiefe aufgestellt wurde, wurden im Laufe eines Jahres 21 kg (FG) Muscheln vorgefunden. Dies entspricht etwa 50 Muschelklumpen, die von Stürmen losgerissen und hangabwärts transportiert wurden. Da die Rekrutierung auf Muschelbänken in 6 m Tiefe nur etwa 25% der Werte auf flachen Bänken erreicht, stellen diese driftenden Klumpen eine wichtige Zufuhr von Miesmuscheln in diese Tiefen dar.

In einem Miesmuschel-Verpflanzungsexperiment wurden die Effekte der An/Abwesenheit stabilen Substrates, der An/Abwesenheit von Predatoren und von zwei Wassertiefen auf das Wachstum und die Verdriftung von Muschelklumpen untersucht. In einem faktorielle Experimentaufbau wurden 7 von 8 möglichen Faktorenkombinationen realisiert.

Alle transplantierten Klumpen überlebten den 10-monatigen Beobachtungszeitraum. Die Flächenentwicklung der Klumpen waren jedoch unter den verschiedenen Versuchsbedingungen sehr unterschiedlich. Juvenile Muscheln stellten einen wesentlichen Anteil der bei Ausschluß von Predatoren um den

Faktor 6,3 gewachsenen Muschelfläche in 2 m Tiefe. Dagegen erhöhten Muschelklumpen in 2 m Tiefe in Anwesenheit von Predatoren ihre Ausdehnung nur wenig. In 6 m Tiefe hatte der Ausschluß von Predatoren ebenfalls einen signifikanten, wenn auch schwächeren positiven Effekt auf das Klumpenwachstum. Die statistische Auswertung (ANCOVA) bestätigte, daß sowohl die beiden gewählten Wassertiefen als auch An/Abwesenheit von Predatoren einen hochsignifikanten Einfluß auf die Klumpenausdehnung hatte. Eine Berechnung der relativen Effektgröße ω^2 ergab, daß die Wassertiefe 16% und die An/Abwesenheit von Predatoren 52% der Variation der Klumpengröße erklären konnte.

Ein Vergleich der Anteile gefressener Miesmuscheln, deren Schalen zerbrochen (= von Strandkrabben gefressen) oder unbeschädigt geöffnet waren (= von Seesternen gefressen), zeigte, daß *Carcinus* während seiner höchsten Abundanz während der Sommermonate für höchstens 15% der Muschel-Mortalität verantwortlich war.

Stabiles Substrat hatte keinerlei Einfluß auf das Flächenwachstum der Muschelklumpen, jedoch einen starken Effekt auf deren Verdriftung. Insgesamt drifteten 8 auf sandige Bereiche verpflanzte Klumpen 22mal und legten dabei Entfernungen zwischen 20 cm und 12 m zurück. Im Gegensatz dazu verdriftete keiner der auf stabilem Substrat befindlichen Muschelklumpen während der 10 Monate.

Im Flachwasser der Kieler Förde zwischen 1 und 3 m ist der Anteil der mit Seegras vergesellschafteten Muschelbänke höher als der von Reinbeständen (68% in FO und 84% in MOE). Der Einfluß des Seegras-Blätterdaches auf die Anfälligkeit von Muschelbänken gegenüber Sturmzerstörung wurde in einem Experiment untersucht, in dem Flächen nach Entfernung der Seegrassprosse mit unbehandelten Flächen verglichen wurden. Die Anwesenheit von Seegras reduzierte die Sturmverluste von Muschelbänken hochsignifikant während zweier Sturmperioden an beiden Standorten. Außerdem blieben driftende Muschelklumpen bevorzugt im Seegras liegen. Die Anwesenheit von Seegras hat keinen Einfluß auf die Abundanz von Seesternen auf Muschelbänken. Auch der Anteil von *Asterias*-Individuen, die juvenile Muscheln fraßen, war auf Muschelbänken mit und ohne Seegras gleich hoch. Nur für adulte *Mytilus* (>30 mm) bestand auf reinen Muschelbänken die Tendenz, daß sie von *Asterias* zu

einem höheren Anteil gefressen werden. Dies kann auf die niedrigeren Rekrutendichten auf reinen Muschelbänken gegenüber *Zostera/Mytilus*-Mischbeständen zurückgeführt werden.
In einem weiteren Experiment wurde die Dichte von Muscheln im Seegras verändert, um ihren Einfluß auf Dichte, Wachstum und vegetative Verbreitung von *Zostera* zu untersuchen. *Mytilus* hatte keinen Effekt auf die Dichte der *Zostera*-Sprosse von April bis Ende Oktober 1993. Auch zeigten Beobachtungen an Dauerquadraten, daß angrenzende Muschelbänke die vegetative Ausbreitung des Seegrases nicht verlangsamten. Anstatt *Zostera* zu stören, wird dessen Blattwachstum von Miesmuscheln gefördert. Ende August hatten Pflanzen, denen Muscheln hinzugepflanzt wurden, eine um 36% erhöhte Blattfläche, während eine Wegnahme von Miesmuscheln zu einer Erniedrigung der Blattfläche um 16% im Vergleich zu den Kontrollflächen führte. Da sich zur gleichen Zeit die Nährstoffkonzentrationen des Sediment-Porenwassers in der Anwesenheit von *Mytilus* verdoppelten, erscheint eine Nährstofflimitation des Seegraswachstums auf den sandigen, organisch armen Sedimenten des sehr flachen (1-3 m) Sublitorals wahrscheinlich. *Mytilus* erhöht die Sediment-Nährstoffkonzentrationen über die Biodeposition von Faeces und Pseudofaeces. Eine Korrelation zwischen Ammonium und Blattlänge läßt vermuten, daß Stickstoff das limitierende Nährstoffelement ist. Im Gegensatz dazu waren die Phosphat-Konzentration im Porenwasser nicht mit den Blattlängen korreliert.

PHOTOGRAPHS

Photo 1. Mussel bed of approximately 1 m^2 in area in 2 m depth at FO. Photo was taken in October 1993.

Photo 2. In 6 m depth *Mytilus* beds consist mainly of large mussels (>5 cm in length). Photo was taken in December 1992 at FO.

Photo 3. View into drift collector fence towards deeper water. Fence was 1 m in height and installed in 4 m depth at Friedrichsort.

Photo 4. Mussel clump transplantation experiment: Incomplete (roof) cage with vexar mesh as substratum type in 2 m depth after 8 mo of exposure. Stainless steel meshes were regularly cleaned with a wire brush.

Photo 5. *Mytilus* transplantation experiment: complete cage with opened roof in 2 m depth. One-year old mussels contributed considerably to the 6.3-fold area increase during the 10 mo experimental period.

Photo 6. Photograph of a *Zostera/Mytilus* patch with an adjacent strip of pure mussels at MOE in 1.8 m depth in September 1993. Note the margin of the mussel patch extending onto the bare sand and the marking stake in the center of the picture.

Photo 7. Detail of a dense *Mytilus* understory bending a *Zostera* shoot aside. Photograph was taken in March 1993 at the experimental site FO in 2 m depth.

Photo 8. Tagged mussel clump of *Mytilus* transplantation experiment in front of marking stake in 2 m depth at FO.

Chapter 1
General introduction

Ecology is the study of interactions which determine distribution and abundance of species in space and time. According to this definition by Krebs (1985), among major goals of benthic community ecology have been to provide explanations of (1) large scale zonation of species on rocky shores across the tidal gradient (2) small scale patchiness (= mosaic structure) within one depth range (3) succession, i.e. the sequence of species composition during colonisation of new space.

Major lines of progress in the field of community ecology have been obtained from work done in the rocky intertidal. From these studies several general ecological hypotheses or concepts have been formulated such as the "keystone predator hypothesis" (Paine 1971, Paine 1974) or the "intermediate disturbance hypothesis" (Connell 1978). However, as it will be shown later, most of the mechanisms regulating benthic communities are general and can be equally applied to soft-bottom environments (Dayton 1984).

In a synthetic overview, Pickett & McDonnell (1989) divided the community regulating factors into 3 groups: (1) community site availability (2) species availability and (3) species performance. Within all 3 groups, environmental vectors interact with biological factors. Physical disturbance (for example wave shock) creates free space made available for arriving seaweed propagules or planktonic larvae of sessile animal species. Which species will actually colonise the bare area depends on the composition of arriving larvae or propagules. It has been shown for barnacle cyprids that their spatial distribution is determined mainly by the transport of the water masses (Gaines & Bertness 1992). On a finer spatial scale, nearshore current patterns are also involved. For example Denny & Shibata (1989) demonstrated that a seaweed propagule will encounter the seafloor within the narrow range of 3 m off the parent plant in white water surf-zones. This readily explains the limited dispersal range macroalgae may have in these environments. Larval availability and recruitment is more important for the structure of benthic

communities the higher the consumer pressure and the lower the absolute densities of recruits are (Menge 1991).

After the provision of space and its subsequent colonisation, species "performances" comprises the most complex array of factors. They include interactions of the organisms with the physical environment such as ecophysiological traits and resource availability, and species interactions such as competition, predation and allelopathy.

Resource availability in the environment in conjunction with the ecophysiological characters of species were the first factors to which distribution patterns were related. The large scale zonation of macroalgae and sessile species across the tidal gradient of rocky shores early attracted attention of marine biologists (Lewis 1964, and references therein). The upper and lower distribution boundaries have been attributed mainly to the tidal gradients of environmental stress, that is increasing exposure time to air with increasing tidal elevation. Species were supposed to be ordered in zones running parallel to the shoreline because they possess different tolerance to desiccation. This is part of the critical tide level concept.

However, one of the principal results which has emerged from community ecology is that, although the ecophysiological properties determine the survival range of organisms, the fundamental niche is never realised in nature but is restricted by species interactions (realised niche). Chapman & Lindley (1980) constructed a light budget for the kelp *Laminaria solidungula* and demonstrated that this kelp species had its lower distribution range in a depth where the incoming radiation was 10-fold higher than the calculated minimal light demands for this species. Clearly, it is not ecophysiology alone but its interaction with competitive processes and predation which structures benthic communities.

Connell (1961a, 1961b) was one of the first workers to demonstrate that species interactions may play an important role in regulating zonation patterns. He worked with two barnacle species occurring in distinct zones with little overlap in the estuary of River Clyde, Scotland. *Balanus* (=*Semibalanus*) *balanoides* occurred from the low intertidal up to 1.50 m tidal elevation whereas *Chthamalus stellatus* was found above. With transplantation experiments, he demonstrated that *Chthamalus* only survived lower on the

shore when *Balanus* was removed. However, in contrast to *Chthamalus*, *Balanus* was not able to survive higher on the shore within the *Chthamalus* zone. Here, only the latter species is able to withstand the elevated desiccation stress and finds a refuge from being outcompeted by *Balanus*. Hence, whereas the higher distribution limit is set by ecophysiological constraints, the lower is maintained by competitive interactions.

How both interactions, competition and predation themselves, interact was shown in another early and most influential study done by Robert Paine (1974) on the Pacific east coast of North America. In excluding a predatory seastar (*Pisaster ochraceus*) from a plateau of bedrock he demonstrated that mussels (*Mytilus californianus*) would monopolise the lower intertidal after a few years. He coined the "keystone predator concept" which essentially states that one single species may determine the community structure in that it allows the co-existence of competitively inferior species (here macroalgae) by removing competitively dominant species.

For the Atlantic NW coast, one of the most integrative qualitative models of community organisation was developed mainly by Bruce Menge and Jane Lubchenco. At protected and moderately exposed sites, the mid-intertidal is dominated by a lush canopy of rockweeds (*Fucus* spp.), although *Fucus* species were shown to rank low in the competitive hierarchy. Barnacles as well as ephemeral algae were both shown to be higher in competitive rank and to displace fucoids. A series of field experiments revealed that consumer species so diminish competitive superior species that *Fucus* spp. may flourish. Ephemeral algae are grazed by periwinkles (*Littorina* spp.) (Lubchenco 1980, Lubchenco 1983) whereas barnacles and mussels are controlled by whelks (*Thais* (=*Nucella*) *lapillus*, Menge 1976, 1978). Menge (1983) emphasised that, although many other species are present, the community structure is actually maintained by a single species, i.e. dogwhelks. Thus, the keystone predator concept being developed on Pacific coastlines was successfully transferred to the Atlantic.

A second major goal of community ecology is to explain small scale spatial patterns of distribution which occur within one zone with relatively uniform environmental conditions. It is the so-called patchiness which contributes largely to the species richness in littoral communities. In several brilliant experiments, Dayton (1971) showed that it is the interplay between the provision of new space by physical disturbance and the species interactions which maintain patchiness in rocky shore communities of the Pacific coast of North America. Sousa (1979) showed that in intertidal boulder fields, species diversity and patchiness is maintained by the infrequent overturning of the cobbles due to storms and formulated the model of patchiness being a "mosaic of successional stages of a different age" (Sousa 1984, Sousa 1985).
Inherent to all these examples is that community organisation is not at equilibrium but rather that small scale disturbances continuously remove resident species, start a new sucessional sequences and move the community away from a stable point. Connell (1978) proposed that species diversity is maintained at best under a moderate disturbance regime and formulated the "intermediate disturbance hypothesis" which integrates the models of patchiness as a "mosaic of successional stages" and the keystone predator concept. Based on his experiments made on rocky shores, he attributed species diversity of such very different communities such as rain forests and coral reefs to a moderate disturbance regime which prevents competitively superior species to become dominant.
This is in striking contrast to earlier hypothesis on species diversity which claimed environmental stability over a longer time as precondition for species-rich communities (Sanders 1968).

Although modern benthic experimental community ecology started mainly with work done on hard substrata, the approach has been successfully applied to soft substrata. The reason for the imbalance in numbers of studies among hard and soft substrata arises partly from the practical difficulties in manipulating infaunal animals because they are generally small and delicate and an experimenter runs a great risk of introducing procedural artefacts (Dayton 1984).

Whereas a hard bottom can be approximated as a two-dimensional surface which provides mainly a place to settle on, soft substrata differ in one important feature from rocky shores in that soft-bottom species have a much more intimate relation to their substratum. Most of them live inside the sediment and they build their tubes out of sediment particles. Deposit feeders eat the sediment while suction feeders "vacuum" the sediment surface. Another difference from hard substrata is that, based on arguments proposed by Peterson (1977, 1979), space is seldom a limiting resource within the 3-dimensional space of soft substrata. Thus, spatial competition probably does not play the crucial role it exerts on rocky shores (Roughgarden 1986). However, pre-emption of space by dense stands of adults or trophic ammensalism have been discussed as competitive mechanisms occurring between resident communities and arriving larvae by Woodin (1976). She proposed that settlement of larvae is either prevented by sediment movement by burrowing deposit-feeding species. Or arriving juveniles are eaten by adult suspension feeders. In the latter case, however, the distinction between competition and predation becomes difficult.

Since the sediment properties exert a strong influence on the resident infauna, several biological interactions which have been demonstrated on soft substrata involve the alteration of the sediment's properties by the activity of a certain species. For example, Woodin (1978) demonstrated that tube-building polychaetes (*Diopatra* sp.) stabilise the sediment and thus mitigate the disturbance effects of burrowing crustaceans for co-occurring infaunal species. A series of field experiments carried out in the sheltered tidal flat of Königshafen (Wadden Sea) also revealed several significant biotic interactions. For example, predation was found to have a marked impact on several infaunal species (Reise 1977). Mats of green ephemeral algae (*Enteromorpha* spp.) had a strong negative impact on the macrozoobenthos living in the sediment underneath (Schories & Reise 1993). Recruitment of these mat-forming species depends on the presence of snails (*Hydrobia* spp.) which represent the only suitable attachment site for germlings in this soft-bottom environment. The growing plants become anchored to the mobile substratum by activities of lugworms (Reise 1983).

By 1970, Johnson (1970) proposed that patchiness in soft-bottom communities is maintained by small-scale disturbance events which initiate new colonisation

events. Actually this is an early formulation of the "intermediate disturbance hypothesis" explained above. In a series of field experiments VanBlaricom (1982) demonstrated that disturbances created by digging sting rays are responsible for infaunal patchiness in a subtidal sandy sediment off California. For recolonisation of these disturbed patches, immigration of adult species was found to be most important.

The community studied in this dissertation differs from "true" endobenthic soft-bottom situations in that both, seagrasses and mussels, are partly epibenthic and modify the sediment they are rooted in or live on.

Besides mangroves seagrasses are the only root-possessing group of marine angiosperms and include approximately 50 species. They form the structuring element of a group of unique ecosystems found in shallow soft-bottom sediments from boreal to tropical latitudes (den Hartog 1977, for an overview). Inside the seagrass meadow the physical environment is markedly altered compared to adjacent sand flats. Current velocities are lower due to canopy friction (Fonseca et al. 1982, Fonseca & Fisher 1986) and turbulences increase especially at the meadow edge. As a consequence, suspended particles settle out and the sediment becomes finer and richer in organic matter. Together with the root/rhizome system, the seagrass canopy markedly decreases sediment mobility and erosion. In a canopy removal experiment, Orth (1977) demonstrated experimentally that infaunal species diversity and abundance increases through the presence of a seagrass meadow because erosion and burial, which are major mortality source on soft-bottoms, are prevented. Among many other taxa, bivalve species were found to recruit better inside seagrass meadows than outside. This is partly due to an intensified settlement inside seagrass meadows due to hydrodynamic alterations by the canopy (Eckman 1987). Also, post-settlement mortality caused by predation is strongly reduced (Peterson et al. 1984, Peterson 1986). Attached to seagrass blades during their early life stages, bay scallops (*Argopecten irradians*) have a higher chance to survive in face of epibenthic predators (Pohle et al. 1991, Ambrose et al. 1992). The root/rhizome system of seagrasses was also shown to offer protection to infaunal organisms in that it impedes burrowing of predatory blue crabs (*Callinectes sapidus*, Blundon & Kennedy 1982).

Occurring on soft-substrata, mussel beds posses a marked inertia (that is stability in the face of challenge or perturbation, Dayton et al. 1984). Dankers (1993) reported the extraordinary persistence of mussel beds in the highly fluctuating environment of the Wadden Sea for periods of over 30 yr. Although the turnover of mussel individuals is high the mussel matrix is maintained over several generations. Again, as with *Zostera* or other seagrass species, it is the modification of the physical environment, here the provision of secondary hard substratum to conspecifics, which ensures the relative persistence of these species with their associated fauna in a fluctuating environment. Both, seagrass and mussel beds, are structurally dominant species which provide shelter and substratum for a rich assemblage of other plant and animal species (*Zostera*: Orth 1977, 1992. *Mytilus*: Asmus 1987). Their presence or absence is therefore essential for the whole community of associated species. In that respect, this study deals not only with the factors controlling the populations of eelgrass or mussels, but with the whole community.

Community ecology vs. ecosystem models. Community ecology does not deal with the "currency" of energy flow as it is done in ecosystem compartmental models. These two approaches represent a divergence in ecology present since the 1950s (Chapman & Johnson 1990, Lawton & Jones 1993) and, probably, do not simply represent one side of the same coin. Community structure (i.e. species abundance and distribution) can hardly be predicted from a knowledge of fluxes since important classes of species interactions such as facilitation or competition for resources other than food (e.g. space) cannot be expressed in terms of energy units. Dayton et al. (1974) provided an illustrative example why species which seem to be unimportant for the community in terms of biomasses may in fact structure the system. In an Antarctic sponge community a relatively rare sponge (*Mycale acerata*) is the competitive dominant. However, its rare status is maintained by the feeding activity of another relatively rare species, the seastar *Perknaster fuscus*.
The already mentioned keystone role of *Pisaster* on the rocky shores of the NE Pacific elucidated by Paine (1974) provides another example: Although this seastar definitely structures the system, it is not common and contributes little to the total energy flowing through the benthic food web.

Additionally, serious practical difficulties emerge in determining the size and magnitude of fluxes of the numerous compartments even the simplest systems posses. A complete ecosystem analysis needs enormous resources of manpower. For example, to construct the Baltic *Fucus* ecosystem model, a team of 20 scientists worked together to develop an energy circuit model for single summer days (Jansson et al. 1982).
Furthermore, confidence limits of the ecosystem compartments or of the transferred energy proportions between them have seldom been given for macrophyte dominated systems. It has already been shown by Miller et al. (1971) that variances accumulate after each step in the flux calculations. As a consequence most parameter estimates are not significantly different from zero after a few calculation steps.
However, although their predictive value is probably low, ecosystem compartmental models may provide a description of the main energy pathways within a food web. Furthermore, knowledge on the magnitude of primary production sets limits for estimates of secondary (consumer) production.

Methodology and logics of community ecology. To this point, in community ecology descriptive, correlative and experimental approaches have been applied. The International Biological Programme or phytosociological studies of the Braun-Blanquet school provide some examples to the purely descriptive collection of data on different communities. The hope of these studies which lack a priori formulated ostensible hypotheses is that, later, some useful insight can be extracted from the data.
In correlative approaches a falsifiable hypothesis may be formulated, i.e. that a biological variable does not correlate with an abiotic parameter. However, there are severe pitfalls in using only observational data. A significant correlation between two variables, e.g. tidal height (independent variable) and the abundance of a certain species (dependent variable) must not be confounded with a causal relationship among both variables. In fact, variations in the dependent variable may be caused by a third, unknown covarying factor. For example, in the classical studies by Paine (1974), the lower distribution limit of mussels (*Mytilus californianus*) was certainly perfectly correlated with tidal height. However, Paine's experiments demonstrated that not tidal height alone

determined the vertical distribution of mussels but that it was ultimately predation by the seastar *Pisaster* which prevented mussel from colonising the lower intertidal. *Pisaster* in turn was impeded from long feeding excursions to the upper intertidal by physiological constraints (desiccation stress).

The third and to date most appropriate approach to deal with explanations of species distribution and abundance is strong inference ecology (Underwood & Denley 1984). In terms of science theory this is a hypothetical-deductive approach which involves the construction of a model from previous observations and/or results. The important difference to descriptive approaches lies in the second step in which a testable, that is falsifiable, null-hypotheses is derived (Underwood 1990). This is based on the arguments of Popper (1959) who elucidated that it is logically impossible to prove a positive hypothesis. Instead, we are only able to gain information on the world outside by disproving alternative null hypotheses. In a last step, acceptance or rejection of the null hypothesis refines the previous model.

In practice, the interactions among species and between organisms and their physical environment are treated directly by means of field experiments. Often, the densities of one or more selected species are changed. For example, predators are excluded, the density of competing species is increased, or dominant species which are supposed to competitively suppress co-occurring species are removed (Hairston Sr. 1989). Manipulations should involve all possible combinations of single factors, i.e. the design should be orthogonal. Only then it is possible to disentangle the main and interactive effects of all potential factors involved (Underwood 1981).

The experimental standard of field experimentation has made major progresses in the last 10 yr. In the already cited study by Paine (1974), the experimental design was clearly pseudo-replicated (Hurlbert 1984), that is the rocky platform from which seastars were removed was not replicated but only the mensurative units (i. e. the bolts which indicated the lower border of the *Mytilus californianus* bed). However, a wrong experimental design does not necessarily render the biological result false but it greatly increases the chances to draw incorrect conclusions from the results.

Basic information on experimental design is given by Green (1979) and Hurlbert (1984). In brief, a good experimental layout involves replication of

the experimental units, a random allocation of the sites and procedural controls to assure that manipulations occurred due to the manipulated factor and not to artefacts introduced by the manipulation. For example, in predator exclusion experiments on soft-bottom environments, hydrodynamic effects introduced by the cage, but not the exclusion of predators, often altered the faunal composition (Arntz 1977, Hulberg & Oliver 1980). Therefore, incomplete cages which allow access to predators but are supposed to produce the same hydrodynamic alterations must be installed in a control experiment and compared to completely uncaged plots (Virnstein 1978 , Hulberg & Oliver 1980).

The subsequent statistical analysis of experimental data involves most often parametrical statistics (analysis of variance, ANOVA). Since biological data almost never meet the ANOVA assumptions of being normally distributed, they should be transformed to a log-scale (in the case of proportion data angular transformed, Sokal & Rohlf 1981). As a second important effect, this assures that interactions between 2 or more independent variables are additive (Hurlbert & White 1993). If furthermore, data are balanced, i.e. if all groups of dependent variables possess the same number of replicates, simulations showed that violations of the assumption of homogeneous variances among groups do not bias the outcome of the analysis (Underwood 1981). If the transformed variances are homogeneous there remain no restrictions against performing parametric ANOVA on biological data.

On the other hand, the advantages of parametric against non-parametric statistical inference are striking. Only ANOVA designs enable the experimenter to construct models in which not only simple effects (effects involving only one independent variable) but also interactions between factors can be examined (Underwood 1981). The non-parametric analogues of ANOVAs (e.g. Kruskal-Wallis test) only enables testing for the effect of one factor (which may, however, have several levels). Also, when a larger number of groups is present, the chances of making a type I error (rejecting the null-hypothesis when it is true) during multiple comparison procedures is increased in non-parametric statistic compared to ANOVA.

In this dissertation, both correlative investigations and experiments will be used. In both approaches, falsifiable hypothesis will always be formulated. However, emphasis of this study was to perform field experiments with a cor-

rect design, with the aim to disprove a priori formulated null-hypotheses using inferential statistics.

Ecological background. In the western Baltic, a depth zonation of epibenthic communities as well as their mosaic arrangement in space has long been recognised (Schwenke 1964, Schwenke 1969a, Schwenke 1969b). However, most work undertaken to date has been purely descriptive (Breuer & Schramm 1986, Vogt & Schramm 1991) or did relate distribution patterns entirely to ecophysiological characters of the macroalgae (Schramm et al. 1989). In attempting to explain macrozoobenthos abundance, field experiments on the role of predation were unsuccessful (Arntz 1977) or predation by epibenthic fishes (Gobiidae) showed little effects on community structure (Berge & Hesthagen 1981). However, in a correlative analysis using multivariate methods, environmental vectors such as water depth and light have been successfully related to the structure and composition of phytobenthic communities (Kautsky & van der Maarel 1990).

Eelgrass (*Zostera marina* L.) meadows are widespread at sheltered to moderately exposed sites in the whole of Kiel Bight. Extensive mussel beds (*Mytilus edulis* L.) can be found in sheltered bays and Fjords as well as on exposed undersea sills (Meißner 1992).

In Kiel Fjord, mussel beds are patchily distributed. They are often found associated with *Zostera*. Pure *Zostera* meadows, pure stands of mussels and *Zostera/Mytilus*-associations form a mosaic of patches which are interrupted by sand. Only very limited information exists on possible interactions between *Zostera* and *Mytilus* (Gründel 1980). In the face of ongoing eutrophication of the Baltic (Larsson et al. 1985) knowledge on the nature of this plant-animal interaction is especially interesting, because eutrophication processes have been shown to weaken seagrass stands and restrict their distribution in many regions of the world (Giesen et al. 1990, Walker & McComb 1992). On the other hand, increased primary production resulted in higher food supply for filter feeders such as *Mytilus*. As a consequence in the Baltic, mussels have increased their biomass above the halocline (Cederwall & Elmgren 1980, Brey 1986). Deleterious interference of mussels with eelgrass have been reported

from the Wadden Sea (Ruth 1991) but also in Kiel Bight (Gründel 1980). Therefore, knowledge on the nature of the *Mytilus/Zostera* interaction is greatly needed.

The study sites. The Western Baltic to which Kiel Fjord belongs, is a transition area between the fully marine environment of the adjacent North Sea and the brackish central parts of the Baltic Sea (the Baltic Proper). In the surface waters, salinity varies from 10 to 18‰ S depending on the flow conditions at the nearby openings to the adjacent Kattegat and Skagerrak. In the Baltic proper, salinities range only from 4 to 7‰ (Siedler & Hatje 1974). Sandy to muddy substrata are predominant in Kiel Bight. Primary hard substrata are only present in form of boulder fields (lag sediments) covering approximately 30% of the sea bottom between 0 and 6 m in open Kiel Bight (Babenerd & Gerlach 1987). In sheltered bights such as Kiel Fjord, these lag sediments are almost absent.

Observations and experiments were mainly done at two sites in Kiel Fjord, Friedrichsort (hereafter FO) and Möltenort (hereafter MOE) (Fig. 1). Both sites are sheltered with a maximal wind fetch of 7 km and 6 km from southerly directions for FO and south-westerlies for MOE, respectively. MOE may receive swells from severe northern storms against which FO is completely protected. The prominent wind direction in this region of Europe is south-westerly, therefore both sites are regularly exposed to waves of 0.3 to 0.5 m height. The sediment of both sites, FO and MOE consists of well sorted, medium grained silicate sand with 50-60% of the dry weight belonging to the 250-500 µm fraction. It is poor in organic content (0.42±0.06% SD loss of ignition on bare sand, n=5). In 6 m depth, the sediment is muddy sand with 4-6 % organic content.

Salinities ranged from 13 to 20‰ in the surface water and temperatures from 1.7 °C to 19 °C during the study period. Although lunar tides are negligible in the Baltic Sea, irregular wind driven sea level changes often have an amplitude of ±50 cm around mean water level (MWL) and a decline of 1 m below MWL was attained during strong south-westerly gales several times in winter 1992/93.

Objectives. The major goal of this dissertation is to explain the factors which control the distribution patterns in a shallow soft-bottom site which is dominated by *Zostera marina* and *Mytilus edulis*. Specifically the principal objectives are (a) to explain the ecological-scale distribution of blue mussels (*Mytilus edulis*) in Kiel Fjord (b) to examine why in shallow water (1-3 m) mussels occur more often in association with eelgrass (*Zostera marina*) than as pure stands and (c) to examine whether in *Zostera/Mytilus* mixed stands, mussels have an effect on growth, shoot density and vegetative propagation of eelgrass.

Contents of the thesis. Beside the introductionary chapter, this dissertation is divided into 5 sections. Chapter 2 examines the influence of recruitment on the distribution of *Mytilus*. In chapter 3, the factors controlling growth and dispersal of adult mussel patches are examined. Chapters 4 and 5 are on the association between *Zostera* and *Mytilus*. Chapter 4 deals with the processes which may cause the preferential occurrence of *Mytilus* in association with *Zostera* in the shallow subtidal of Kiel Fjord. Chapter 5 is on the effects mussels may have on growth and vegetative propagation of eelgrass. Each chapter has its own IMRAD structure. In chapter 6, general conclusions on the results of the foregoing 4 sections will be presented.

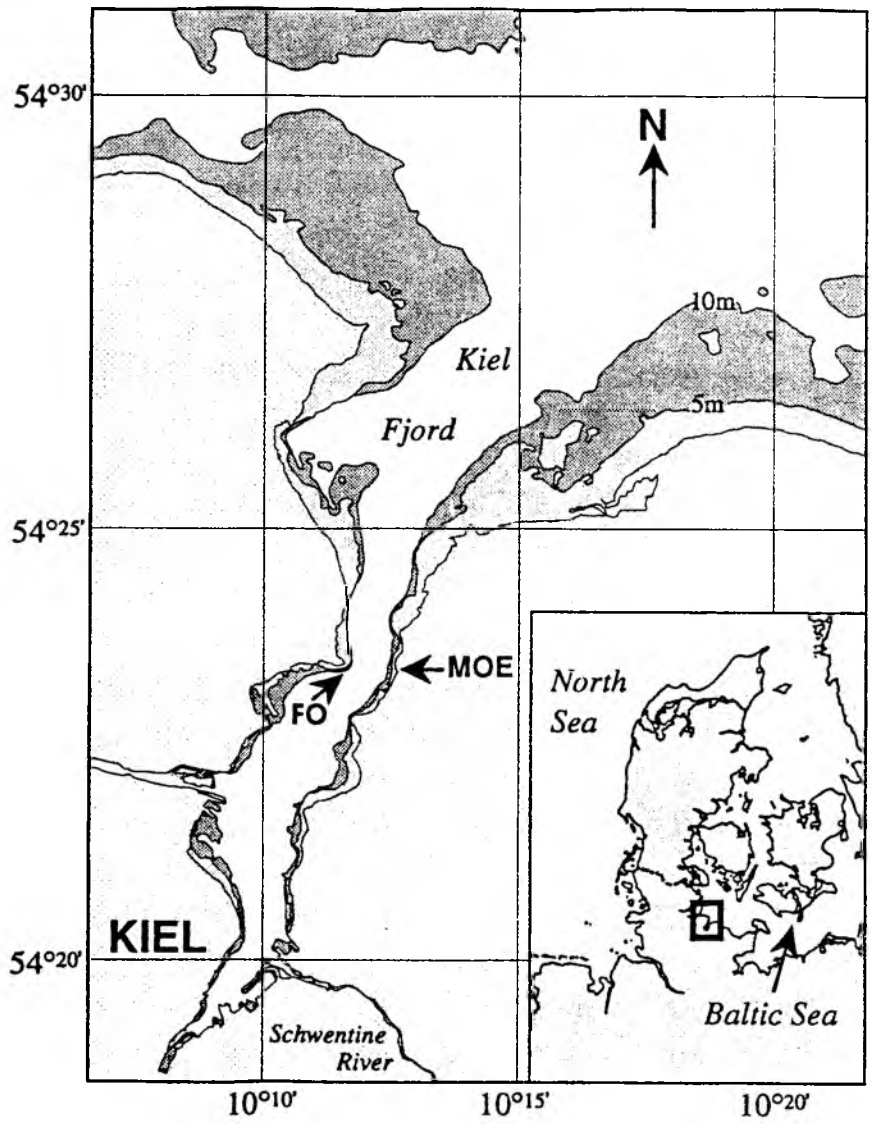


Fig. 1. Map of the study sites located in Kiel Fjord, Western Baltic. Most experiments were done in a military restricted area at Friedrichsort (FO). Additional observational data were obtained at Möltenort (MOE). Experiments on effects of *Zostera* canopy on mussel beds were also conducted at MOE.

Chapter 2
Effects of variation in settlement, substratum type and predation on recruitment of *Mytilus*

2.1 INTRODUCTION

Recruitment often plays a critical role in controlling the distribution of marine invertebrate species (Connell 1985, Butman 1987). Also in regulating the distribution of mussels (*Mytilus* spp.) it has been identified as a major factor (Dayton 1971, Robles 1987, Petraitis 1991). Recruitment involves at least three arrays of sub-factors (Connell 1985): (1) pre-settlement processes, i.e. abundance and dispersal of competent larvae (2) settlement and (3) post-settlement mortality. Whereas dispersal of planktonic stages is largely a function of hydrodynamic transport processes (e.g. Eckman 1987, Gaines & Bertness 1992), settlement denotes a responsive behaviour by the individual (Keough & Downes 1982). In practice, recruitment is defined as the abundance of juveniles which survived for a certain period of time (Connell 1985).

In *Mytilus edulis*, defining settlement is complicated since young *Mytilus* often exhibit two settlement phases (deBlok & Geelen 1958). Having grown to about 1-3 mm in length they may leave the primary settlement site by actively cutting their byssus moorings (Board 1983). Settlement subsequent to this second pelagic phase was referred to as secondary settlement by Bayne (1964). During primary settlement, mussel plantigrades have strong preferences for settling on filamentous substrata such as filamentous algae or hydroids (deBlok & Geelen 1958, Eyster & Pechenik 1987, Pulfrich & Ruth 1993). On rocky shores, barnacles are often the preferred attachment site (Petraitis 1991). A migration onto beds of adult conspecifics takes place mainly during secondary settlement (deBlok & Geelen 1958, Bayne 1964, Suchanek 1978, Ruth 1991), but direct, primary settlement onto mussel beds has also been reported (McGrorty et al. 1990)

Although some information exists on the temporal settlement variability of *Mytilus* from studies on fouling communities in the Western Baltic (Kersting 1981), little is known on spatial variation in *Mytilus* settlement which could

contribute to adult mussel distribution. Rumohr (1980) observed that mussel spat preferred buoyant soft-substrata deployed in 15 m depth rather than at greater depths. Likewise, Richter (1975) found a settlement preference for artificial substrata in 11 m depth compared to 15 and 19 m. In the Baltic proper, Kautsky (1982b) reported a preference of *Mytilus* for settlement ropes in 3 m depth compared to greater depths. Throughout the whole study period, young mussels were never prominent on natural substrata in depths >5 m at the experimental site FO. Large mussel individuals (>5 cm) were common, however, in deep water (Fig. 3.6, Photo 2). Therefore, one objective is to examine whether spatial variation in mussel settlement contributes to the distribution patterns in adult mussel beds.

The third array of factors contributing to overall recruitment, post-settlement mortality, is most complex and involves various mortality sources. Substratum type plays a crucial role in determining survival of settled spat (Rumohr 1980, McGrorty et al. 1990, McGrorty & Goss-Custard 1991). Richter (1975) reported that survival and subsequent monopolisation of artificially deployed soft substrata occurred only on cobble, but not on sandy or muddy substrata. Whereas on soft substrata, sedimentation and subsequent suffocation of spat may play a critical role (Rumohr 1980), on physically suitable substrata, predation is the single most important source of post-settlement mortality in juvenile mussels (Seed 1976, Robles 1987, Robles & Robb 1993). Important mussel predators such as seastars and crabs often prefer smaller mussel size classes against adult individuals (Seed 1993, and references therein). In Kiel Bight, Anger et al. (1977) and Gründel (1980) observed heavy predation of seastars (*Asterias rubens*) on mussel spatfall.

Often, different types of substrata mediate the predation caused post-settlement mortality. It is well known that young mussels find shelter against predation in the interstices of their large conspecifics (Seed 1969, Suchanek 1978, Petersen 1984, Bertness & Grossholz 1985, McGrorty et al. 1990). Within seagrass meadows, a higher post-settlement survival of bivalve recruits has also been attributed to a lower predation pressure (Peterson 1986, Orth 1992). The spatial structure of plant shoots may interfere with the foraging activity of epibenthic predators such as crabs (Revelas 1982). Seagrass blades provide an above-bottom spatial refuge for juvenile bay scallops (*Argopecten irradians*)

which were found to suffer much less predation mortality when attached to *Zostera* leaves during their early live stages (Pohle et al. 1991, Ambrose et al. 1992).
Additionally, the presence of a seagrass canopy may enhance bivalve settlement due to its modification of the hydrodynamic environment (Eckman 1987). Hoven et al. (1991) hypothesised that higher densities of *Mytilus* on the apical parts of eelgrass leaves is due to a greater chance of encountering the moving blades. In Kiel Bight, Gründel (1980) observed very high densities of mussel spat on *Zostera* leaves. Short et al. (1991) recognised that primary settlement in adjacent eelgrass meadows enhanced mussel recruitment onto nearby mussel beds via secondary settlement.
The second objective of this study was to estimate the substratum specific recruitment of *Mytilus*. Specifically I tested whether recruitment is affected by presence or absence of *Zostera* and presence or absence of adult *Mytilus*, and if so, whether this can be attributed to a lower predation impact. Since in the shallow subtidal of Kiel Fjord *Zostera* and *Mytilus* both occur as pure stands, as well as in association, the effects of presence or absence of both species on mussel recruitment was tested in all combinations.

2.2 MATERIAL AND METHODS

Mussel spat collectors. Passive spat collectors were deployed during the summer month of 1992 and 1993 to gain information on the settlement potential of *Mytilus*. In 1992, settlement was sampled without replication with one passive larval collector deployed in 2 m and 6 m depth, respectively. A rectangle (15x15 cm) made of nylon gauze fabric (mesh size 4x4 mm) mimicked filamentous substrata which are preferred attachment sites for mussel spat. It was held upright in the water column by a wooden frame. Settlement densities were determined at 4 dates during the main settlement period only (May 28, June 6, July 18 and August 1, 1992).
In 1993, *Mytilus* recruitment was assessed in two depth (2 and 6 m) with triplicate passive larval collectors of a different construction, which were developed by Pulfrich & Ruth (1993) for monitoring mussel spatfall in the Wadden Sea. A cylindrical frame carried the same type of nylon gauze fabric used in 1992 (Fig. 2.1).

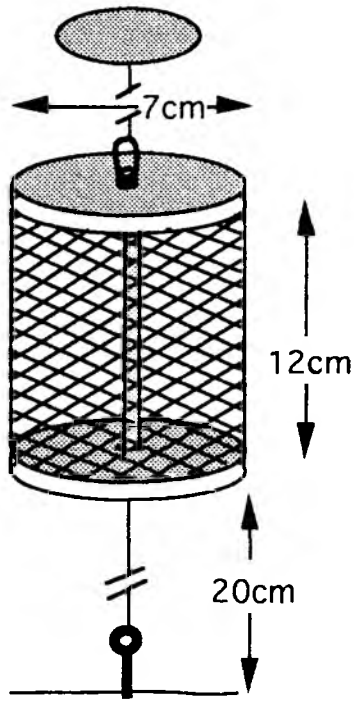


Fig. 2.1. Passive settlement collector used to sample *Mytilus* spat. Collector surface was made of petticoat nylon gauze. This device was developed by Pulfrich & Ruth (1993).

These collectors were held upright by a buoy and deployed haphazardly approximately 2 m apart from each other in the two selected water depths of 2 and 6 m. In July 1993 in 2 m depth, 3 additional replicates were set up inside a *Zostera* meadow. Each collector was at least 2 m distant from the meadow edge. For sampling, the collectors were immediately put into 2 l plastic bottles in the field since mussel spats will detach rapidly from the substratum when disturbed. For storage, only the nylon gauzes were deep frozen. Samples were shaken with sea water after thawing until the spat had detached quantitatively. After sieving through 125 µm mesh screen and staining with Bengal rose, spats were counted under a dissection microscope. Because of massive recruitment, the samples taken on July 8 and 19, 1993 were sub sampled using a plankton sample divisor. Three tenth of the original sample volume was counted.

In both years, the time interval of exposure was always between 2 and 3 weeks. Thus, I did not determine settlement alone but also early post-settlement mortality. This was however minimised since both collector types

were situated 20 cm above bottom and this prevented access to epibenthic predators.
For the 1993 data only, spat numbers were statistically analysed. Two 2-way ANOVAs were performed: one (4x2)-ANOVA with sampling date and water depth as independent factors (data for collectors outside *Zostera* meadow). The first 3 sampling dates were omitted from analysis because the very low settlement numbers on these dates contributed very little to the total spat abundance during summer and led to severe heterogeneity of variances. A second ANOVA with the factor "presence or absence of *Zostera*" was performed on the last 3 sampling dates when collectors were deployed inside and outside the meadow. Additionally, the spat densities obtained on July 8 and 19, 1993 which had to be sub sampled, were analysed in a nested ANOVA design, with water depth as factor and collector nested in water depth.
Spat numbers were log-transformed and checked for homoscedasticity by Cochran's test

Substratum specific recruitment. *Mytilus* recruitment on natural substrata was sampled every 3 mo with cores of 36 cm^2 (6.8 cm in diameter) on the principal substratum types found in 2 m depth (bare sand, *Zostera*, *Zostera/Mytilus* mixed patches and pure *Mytilus* beds) on 5 dates between February 1993 and January 1994. Additionally, on mussel beds in 6 m depth, abundances of young mussels were determined on 3 dates (January, April, August 1993). After the patch of a given substratum type had been selected, the position of the core was haphazardly allocated by tossing it from 1 m height onto the sea bottom.
In the laboratory, the upper 2 cm of the sediment core was sieved through a 500 µm mesh screen and deep frozen for storage. No smaller mesh screen was used because more than 50% of the substratum consisted of sand grains >250 µm. After thawing, samples were stained with Bengal rose and recruits were counted under a dissection microscope. On August and October 1993, and January 1994, length of young mussels was measured to the nearest 1 mm. Length-frequency distributions were plotted for the substratum types *Zostera*, *Zostera/Mytilus* and *Mytilus* for the last 3 sampling dates. Mussels younger than one year were distinguished from older but growth suppressed individuals found inside mussel aggregates by their lighter shell colouration.

On September 22, 1992 only, samples with a core size of 14 cm in diameter (154 cm^2) were taken triplicate. These samples were interpreted only graphically and not included into a statistical analysis since the sample variance is a function of the sample area.
Recruit densities on natural substrata were analysed with a 2-way (3x5)-ANOVA with substratum type and sampling date as experimental factors. Originally I planned to separate substratum effects into components of presence/absence of adult *Mytilus* and presence/absence of *Zostera* using a 3-way ANOVA with all 4 combinations of presence or absence of both species. However, recruit densities on sand (i.e. adult *Mytilus* and *Zostera* absent) were very low compared to the other 3 treatment combinations and often zero for several replicates. Therefore, no statistical comparison was performed among sand and the other substratum types. Recruit densities on *Mytilus* beds in 6 m depth were compared to beds in 2 m depth a two-way (3x2) ANOVA with sampling date and depth as factors.

Applying inferential statistics requires that the error terms are randomly distributed among replicates (Mendenhall 1967, Green 1979). This, in turn, is only assured if samples are taken at random, i.e. if the chance to be chosen is equal for all sites in a selected stratum. True randomisation by using random number tables or grids is often difficult to realise in the field. In this study, allocation of cores and quadrates was done haphazardly by tossing the sample devices from 1 m height onto the bottom. Although this method is not truly random, I could think of no mechanism by which I would have introduced a subjective bias except that central parts of the patches were sampled with a greater chance.

Abundance of mussel predators. Predators were censused to examine whether differences in their abundance could account for differences in predation caused mortality of *Mytilus* among substratum types. At the experimental site FO as well as in the whole Kiel Fjord, the seastar *Asterias rubens* and the shore crab *Carcinus maenas* were identified as most prominent predators. However, crabs were present only from May to October and always occurred in densities below 1 ind/0.25 m^2. Therefore, their feeding impact was ignored.

Seastars were counted and their feeding performance recorded in quadrates of 50x50 cm on the following substrata: (1) bare sand (2) pure *Zostera* (3) pure *Mytilus* patch, (4) *Zostera/Mytilus* mixed patch. Six independent patches were selected within a strip of 50 m parallel to the shoreline. Within the pre-selected patch, the sample area was allocated haphazardly by tossing a frame from 1 m height onto the sea-bottom. The individuals were turned upside down, their prey item recorded and the seastar diameter was measured. Four size classes of mussels were distinguished: (1) 2 mm<*Mytilus*≤10 mm (2) 10 mm<*Mytilus*≤30mm (3) 30mm<*Mytilus*≤50mm (4) *Mytilus*>50mm. I did not consider *Asterias* biomasses since the linear correlation between density and biomasses in 50 plots composed of all substratum types was strong ($p<0.0001$, $r^2=0.77$).

The density of *Asterias* on the different substratum types was analysed as follows: in a 2-way (3x6) ANOVA *Asterias* abundances were compared among the substrata pure *Zostera*, pure *Mytilus* and *Zostera/Mytilus* mixed patches on 6 sampling dates. Since on most sampling dates, *Asterias* densities on sand were below 1 ind/0.25 m^2 and often zero in several plots, a parametric statistical comparison between sand and the other substrata was done only on September 22 and October 21, 1992 (2-way ANOVA).

Estimating substratum type dependent predation impact. The effect of substratum type on the feeding performance of seastars was analysed using two different statistical approaches. Differences in the proportion of seastars feeding on mussels of different size classes were tested among substratum types using contingency tables (χ^2-tests). To do this, the feeding performance data were treated as category variables and pooled over all sampling dates. The null hypothesis was always that substratum type had no influence on the proportion of *Asterias* individuals feeding on mussels of a given size class.

In a second set of statistical analyses, the specific seastar abundances of individuals feeding on juvenile *Mytilus* (i.e. the size class 2-30 mm) were treated as continuous density variables and compared among substrata. In a 2-way (3x6)-ANOVA I compared the 3 substrata *Zostera* and *Zostera/Mytilus* and *Mytilus* on 6 dates. However, this analysis was unbalanced since feeding performance was sampled on only 4 dates on *Zostera*. A second, balanced (2x6) ANOVA compared only substrata *Mytilus* and *Zostera/Mytilus* on 6 dates. Subsequent to the ANOVAs linear contrasts were performed to identify

group means which were responsible for significant date*substratum type interactions. Their significance levels were Bonferroni-adjusted. Seastar numbers were (log+1)-transformed and checked for homoscedasticity by Cochran's test.

Predator exclusion experiment. In July 1992 an attempt was made to exclude predators from *Zostera* patches. Since I assumed that caging above the *Zostera* canopy would produce strong cage artefacts I installed exclusion fences. Four *Zostera* patches were encircled by a wire mesh fence of 1x1 m in area, 30 cm height and 6x6 mm mesh size. The upper edge was bent perpendicular to the outside. However, exclusion of predators, namely of *Asterias* failed completely since they immigrated into the fenced areas within days after the removal.
Therefore, a caging experiment was initiated on September 20, 1993, excluding all larger epibenthic predators from the juvenile mussel beds covering sandy areas at that time. Four complete and 4 incomplete (2-sided) cages of 50x50 cm area an 20 cm height were haphazardly dispersed in 2 large sandy patches. The choice which plots received a treatment was done at random. The wire mesh had an opening of 6x6 mm. Complete uncaged plots were also set up to control for potential cage artefacts. Sampling was done at initiation and termination (on December 18, 1992) of the experiment with a underwater camera with flash and close up lens in the central part of the plot. The photographs sampled an area of 17x22 cm (=374 cm^2). Response variable was the cover of young *Mytilus* which was determined with a random point method using the digitised image of the colour slide and an image analysis program running on a NeXT workstation (Huckriede 1992). The cage experiment was not analysed statistically since young mussel cover was virtually zero on December 18, 1992 in both cageless and incomplete caged plots.

2.3 RESULTS

Spat collectors. The abundances of recruits which settled onto the spat collectors are shown in Fig. 2.2. In 1992, the peak settlement period was approximately 6 wk earlier compared to 1993. Since different types of spat

collectors were used in 1992 and 1993, only a non-statistical comparison is possible between years. Under the assumption that the shape of the collecting surface had only minor influence on settlement density, 1992 spat abundances were standardised to the surface area of the collector types deployed in 1993 (i.e. 131 cm^2). Based on these data, the cumulative abundances of mussel spat collected on 4 dates during the main settlement period was nearly 6-fold higher in 1992 compared to 1993 (*Mytilus* individuals x 10^3 /131 cm^2: 199 and 142 in 1992, 36 and 28 in 1993, in 2 m and 6 m water depth, respectively).

In both years, the number of newly settled mussel recruits in 6 m depth was approximately 70% of the density found in 2 m. Only the replicated sampling in 1993 allowed a statistical analysis of these differences. A 2-way (2x4) ANOVA with water depth and sampling date as factors revealed that water depth had only a non-significant effect (2-way ANOVA, $F_{(1,16)}=3.67$, $p=0.0734$, ns). A nested analysis performed only on the 2 sub sampled data sets of July 8 and 19, 1993 gave the same results (2-way nested ANOVA, $F_{(1,8)}=0.4489$ $p=0.522$).

The effect of presence or absence of *Zostera* on spat density in 2 m depth was tested on 3 sampling dates only. Within the *Zostera* meadow, recruitment onto the spat collectors was significantly lower compared with those set up on bare sand (2-way ANOVA, $F_{(1,12)}=19.69$, $p=0.0008$, Bonferroni-adjusted significance **). Interactions between sampling date and presence/absence of *Zostera* were not significant.

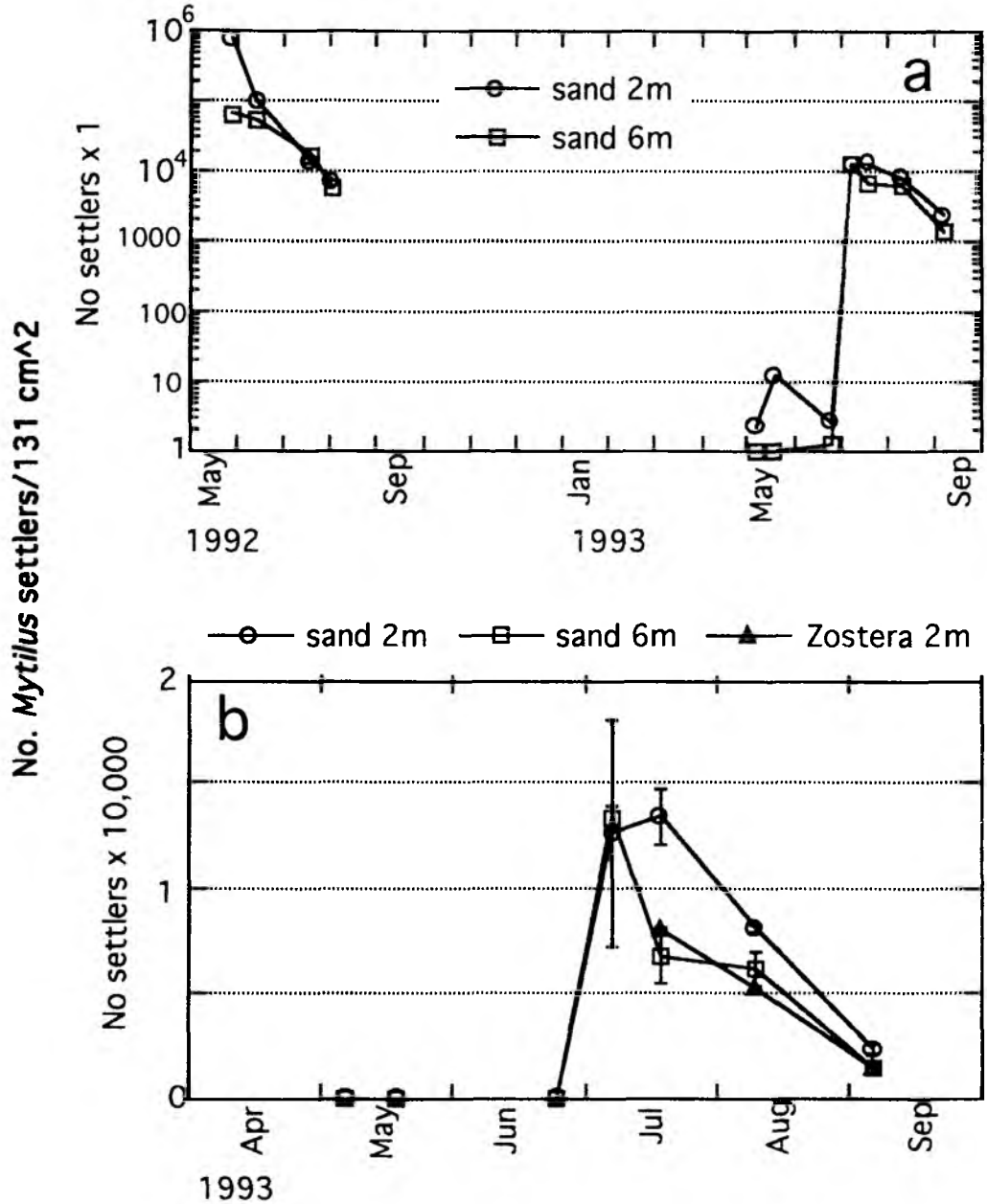


Fig. 2.2. Number of *Mytilus* recruits sampled by passive settlement collectors. Panel (a) shows settlement densities in two depths during the summers 1992 (which were non-replicated) and 1993 on a logarithmic scale. Panel (b) shows the triplicate 1993 data on a linear scale ±1 SE.

Recruitment on natural substrata. Substratum type had a marked effect on the density of juvenile mussels (Fig. 2.3). Recruit abundances on both substratum types with a *Zostera* canopy increased in response to the settlement

of spat in summer 1992 and 1993. On adult *Mytilus* beds, recruit densities varied less in time compared to *Zostera* and *Zostera/Mytilus* patches. This is even more striking if I include the data taken in September 1992 after the settlement event which was probably 6 times more intense than in 1993. The statistical analysis revealed that substratum type and the interaction between substratum and date were highly significant. Although the 5 sampling dates span over one main settlement event (July/August 1993), the main effect of date was not significant (Tab. 2.1). That is that only the proportion of mussel recruits found on the different substrata but not their overall density changed with time.

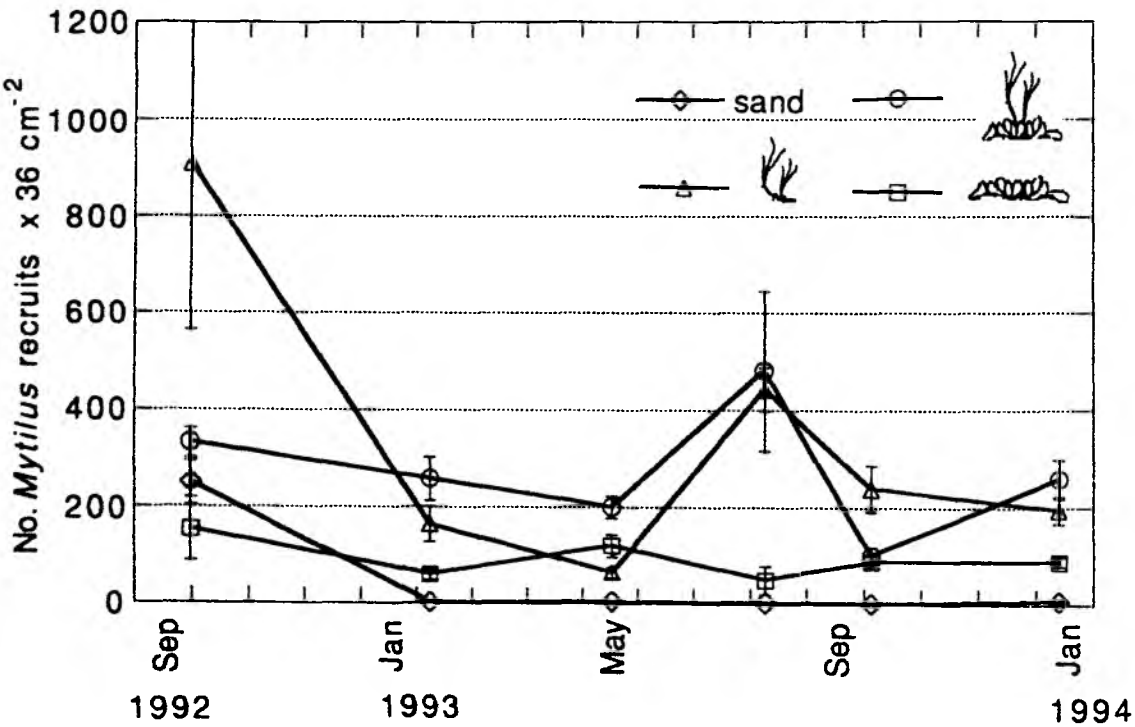


Fig. 2.3. Abundance of *Mytilus* recruits on natural substrata. Six replicate cores of 36 cm^2 in size were sampled approximately 3-monthly. Error bar is ±1 SE. In September 1992 only, sample size was 159 cm^2 and replicate number n=3. Therefore, these data are standardised for the smaller cores sizes and were analysed only graphically. For statistical analysis see Tab. 2.1.

A set of planned comparisons was performed to identify sample means which were responsible for significant date*substratum type interactions. All subsequent comparisons given below are Bonferroni-adjusted for the numbers of comparisons. Recall that the abundances sampled in September 1992 (due to a different sample size) as well as densities on sand are not included into statistical analysis.

Recruit densities on both substrata having *Zostera* (pure *Zostera* and *Zostera/Mytilus*) were not significantly different, yet significant interactions between date and substratum type were found. This was mainly due to the density drop on *Zostera/Mytilus* patches in October 1993 to values significantly lower than on pure *Zostera*.

Comparing both substrata, *Zostera* and *Zostera/Mytilus* association, with pure *Mytilus* in two separate ANOVAs revealed that both had significantly higher recruit density compared to pure *Mytilus*, as it was indicated by significant main effects of substratum type. Again, significant interactions between date of sampling and substratum type were found since recruit densities showed marked fluctuations in time on both substrata with eelgrass. Densities on substratum *Zostera* were lower compared to both other substrata in May and non-significantly different from substratum pure *Mytilus* in October 1993.

On substratum *Zostera/Mytilus* mixed stands, recruit density were significantly higher on 4 out of 5 dates compared to pure *Mytilus* beds except in October 1993 when they were statistically similar.

Tab. 2.1. Two-way (3x5)-ANOVA: Comparison of *Mytilus* recruitment densities sampled 3-monthly on 5 dates from January 1993 to January 1994 among the substrata *Zostera*, *Zostera/Mytilus* and *Mytilus*. Number of replicates n=6, core size was 36 cm^2. Data were log-transformed and homoscedasticity was checked by Cochran's test. For significance of means comparisons see text.

Source of variation	df	MS	F	p	conclusion
substratum type	2	1.8134	22.316	<.0001	***
date	4	.0594	0.7311	0.5736	ns
date*subsuratum type	8	.6518	8.0218	<.0001	***
Error	74	.0813			

During the 3-monthly intervals on both substrata having *Zostera*, recruit densities decreased while they increased complementary on mussel beds devoid of *Zostera*. Only the development in spat densities on *Zostera/Mytilus* (but not

on *Zostera*) between August and October 1993 were exceptional in that they decreased as did pure *Mytilus* beds.
In autumn 1992 only, mussel recruits covered almost all sandy patches found at the experimental site. However, few of the spat survived until February 1993 and from that time on their density was always markedly lower compared to the other 3 substrata. This is also true for abundances sampled August 1993, although at that time settlement showed a peak in intensity according to the larval collectors.
In 6 m depth, recruitment onto the beds formed of large adult mussels was only 25% of the densities found on beds in 2 m depth. Mean densities of recruits±1SE on 3 sampling dates (May, August and October 1993) were 86±14 ind/36 cm^2 in 2 m depth compared to only 21±10 ind/36 cm^2 in 6 m depth (2-way ANOVA on (log+1)-transformed densities: effect water depth, $F_{(1,30)}=40.6$, $p<0.0001$). The interaction between sampling date and water depth was non-significant ($p>0.05$).

The length/frequency distributions were not expressed as proportions of the total juvenile mussels because for recruitment, the absolute densities which attain a critical size are most important (Fig. 2.4). They revealed that in August 1993 on both, pure *Zostera* meadow and *Zostera/Mytilus* mixed patches, more individuals belonging to size classes <5 mm were found compared to pure mussel beds. However, 3 mo later adult mussel patches revealed a similar size distribution than the other 2 substrata. This suggests that later in the year, *Mytilus* recruits migrate from *Zostera* onto adjacent mussel beds. On all 3 substrata the majority of recruits was smaller than 5 mm. This suggests that settlement continued until January 1994. The steep decrease in abundances of mussels >5 mm indicates that the newly settled spat suffered from an almost complete mortality. Few of these recruits attained a size >10 mm although growth rates of 20 mm during one post-settlement season are reported in Kiel Fjord (Boje 1965).

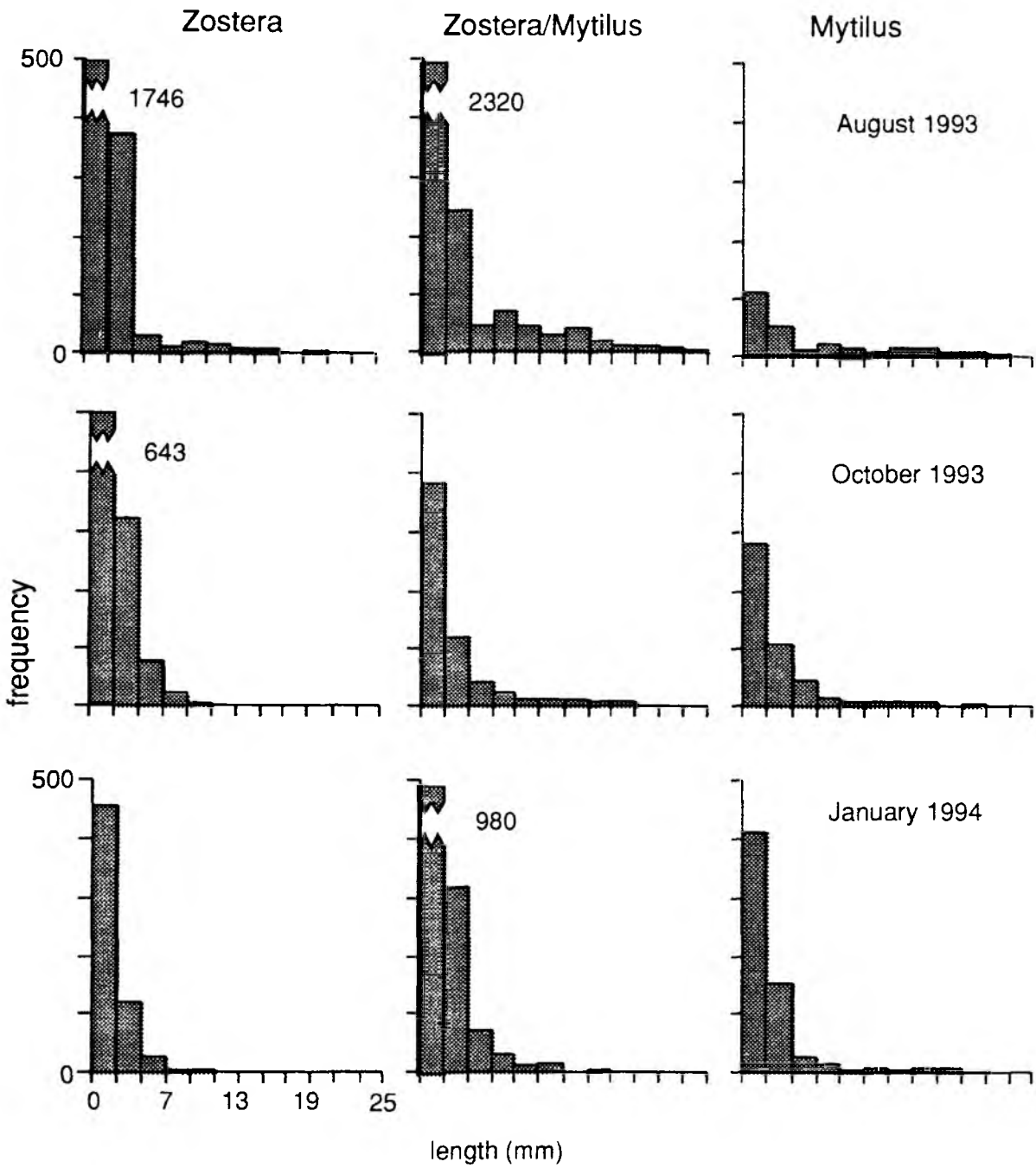


Fig. 2.4. Length/frequency distribution of *Mytilus* recruits on natural substrata on 3 dates. All young mussels (<1 yr) in 6 replicate core samples of 36 cm^2 were measured. Data represent the last 3 sampling dates of which abundances are shown in Fig. 2.3. Note that juvenile mussels <1 mm in length were omitted from the data.

Predator exclusion experiment. The outcome of this experiment was unambiguous. The cover of juvenile *Mytilus* decreased from 65±12% on September 22 to zero cover on December 18, 1993 on both treatments with predators (2-sided and no cage). Juvenile beds did only survived under the protection of cages (55±14% cover). Therefore, no statistical test was applied to confirm the experimental results or to check for possible cage artefacts.
In preying on the juvenile mussel beds, *Asterias* played a major role. In autumn 1992, its density on bare sand was between 11 and 13 ind/0.25 m^2 which is 10 times the density found on bare sand on 4 subsequent sampling dates during the year 1993. All *Asterias* dwelling on the sand flat were feeding on young mussels during that time, swallowing several individuals at once.
On January 29, 1993 the cages were revisited after three severe storms during January 1993. Although they had remained in place, young mussels within the closed cages were partly killed by burial or washed away by waves.

Abundance of predators. Fig. 2.5. shows densities of *Asterias* on all 4 sampled substrata in 2 m depth. A statistical comparison of *Asterias* densities including substratum type sand was done only on 2 sampling dates (September 22, and October 21, 1992). A (3x2)-ANOVA with substratum type and sampling date as factors revealed a highly significant effect of substratum ($F_{(2,30)}$=13.6, $p<0.0001$) but not of date or the interaction term ($p=0.62$ and 0.79, respectively). In post-hoc means comparisons it appeared that densities on sand were higher compared to adult *Mytilus* beds (with and without *Zostera*) on both dates ($p<0.0001$, ***). In autumn 1992 , seastar abundance within pure *Zostera* stands was estimated only once (on September 22). A one-way ANOVA revealed that abundances on sand were not significantly different from those in *Zostera* meadow, but both were higher than on adult mussel beds (α Bonferroni-adjusted as $\alpha/3$, $p=0.0004$, **). High *Asterias* densities on sand and within *Zostera* coincided with an intense settlement of young *Mytilus* during that time of the year (see Fig. 2.3).

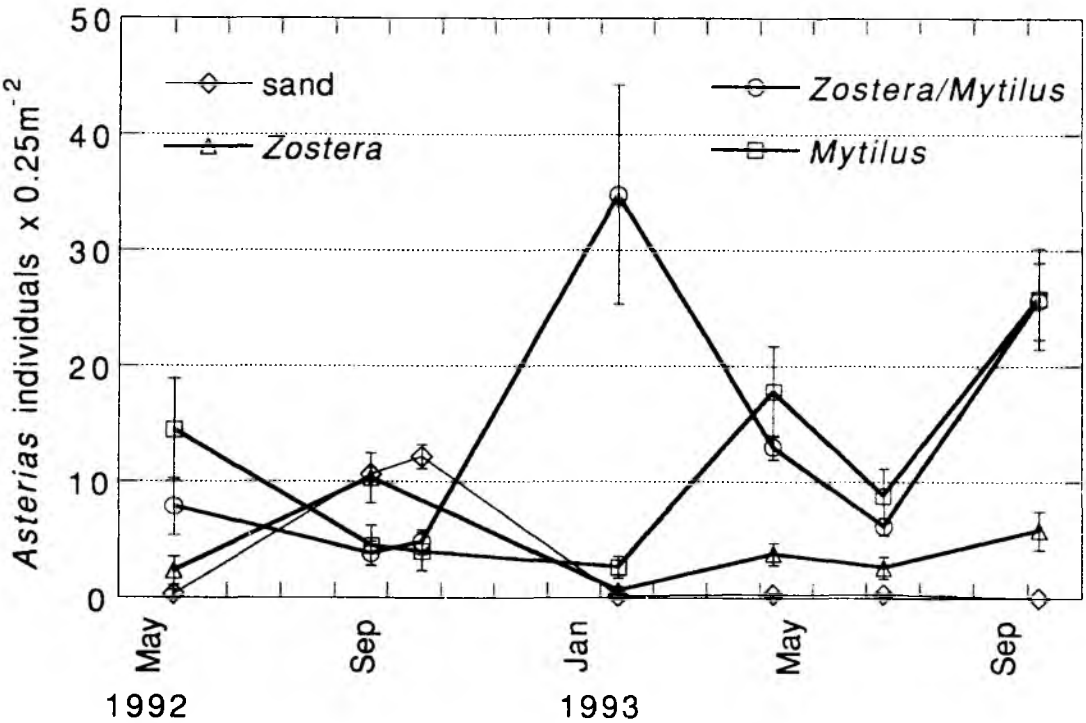


Fig. 2.5. Abundance of *Asterias* on natural substrata in 2 m depth. Individuals were censused in 6 replicate quadrates of 0.25 m^2. Error bars represent ±1 SE. See Tab. 2.2 for statistical analysis.

Tab. 2.2. Two-way (3x6) ANOVA: effects of substratum type (exclusive sand) and sampling date on *Asterias* abundance on 6 sampling dates (Oct 20 1992 not included). Six replicate samples were taken in quadrates of 0.25 m^2. Counts were logarithmic (log+1)-transformed and checked for homoscedasticity by Cochran's test. For significance of post-hoc means comparisons see text.

Source of variation	df	MS	F	p	conclusion
substratum type	2	3.4863	47.079	<.0001	***
date	4	.7817	10.556	<.0001	***
date*substratum type	8	.3527	4.7629	<.0001	***
Error	75	.0741			

A (3x6)-ANOVA on *Asterias* abundances on substrata *Zostera*, *Zostera/Mytilus* and *Mytilus* revealed that the main factors "substratum type" and "sampling date" as well as their interaction were highly significant (Tab. 2.2) Post-hoc means comparisons by linear contrasts on selected hypotheses gave the following results (all significance levels Bonferroni-adjusted): the

abundance of *Asterias* was always lower on *Zostera* compared to both adult mussel bed substratum types ($p<0.0001$, ***) except for September 22, 1992, when it was higher compared to both other substrata ($p=0.0057$, **). This significant difference and the densities of *Asterias* on February 8, 1993 which were markedly higher on adult mussel beds with *Zostera* compared to both other substrata ($p<0.0001$, ***) led to the significant "date*substratum type" interaction. *Asterias* abundances on the substrata *Zostera/Mytilus* and *Mytilus* will be compared including 3 more sampling dates in chapter 4. It will be shown that except for densities in January 1993, no difference exists among these 2 substrata.

Substratum specific predation impact. Besides the abundances of predators, a major question of interest was whether on any of the three substrata (*Zostera*, *Mytilus* and *Zostera/Mytilus*) a higher proportion of *Asterias* was feeding on juvenile mussels (Fig. 2.6). Since only 1.7% (6 out of 334) of total prey items in 2 m depth were species other than *Mytilus*, the proportion of feeding *Asterias* corresponded almost perfectly to those individuals feeding on *Mytilus* and the selection of other prey will be neglected in further discussion. A 3x3 contingency table revealed a highly significant difference among all 3 substrata ($\chi^2=134$, df=4, $p<0.0001$). Therefore, the 3x3 table was split into pairwise comparisons (under consideration of Bonferroni-adjustment which was $\alpha_{adj}=\alpha/7$) to detect which substrata were different from each other. Whereas the proportions of *Asterias* individuals feeding on both juvenile mussel size classes compared to all other individuals present were similar among substrata *Zostera/Mytilus* and *Mytilus* ($p=0.217$), different proportions were found in *Zostera* compared to both other substrata (*Zostera* vs. *Zostera/Mytilus* $\chi^2=48.8$, $p<0.0001$,***; *Zostera* vs. *Mytilus* $\chi^2=35.8$, $p<0.0001$, ***). Finally I tested which size classes differed in the proportion of *Asterias* feeding on them. Inside a *Zostera* meadow, a higher proportion of seastars fed on mussels between 2 and 10 mm compared to both other substrata ($p<0.0001$, ***). In contrast, fewer seastars fed on 10 to 30 mm large mussels on *Zostera* compared to both other substrata (trend for *Zostera* vs. *Zostera/Mytilus* $p=0.0072$; *Zostera* vs. *Mytilus* $p=0.0007$, **). However, this was probably due to the lower abundance of mussels of this size class on substratum type pure *Zostera*.

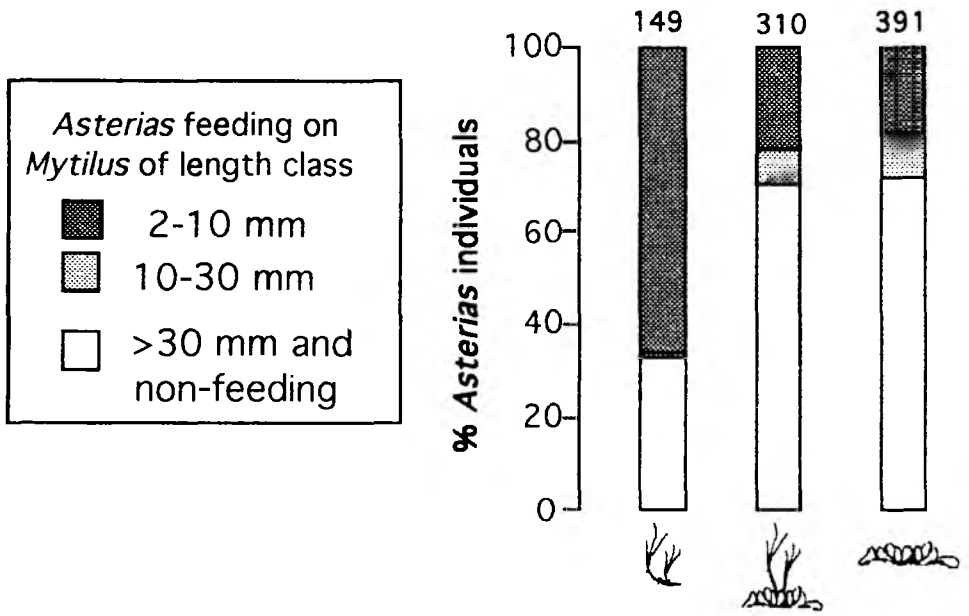


Fig. 2.6. Pooled proportions of *Asterias* individuals feeding on different size classes of mussels on 3 different substrata on 6 dates (*Zostera/Mytilus* and *Mytilus*) and 4 dates (*Zostera*). Significance of differences among substrata were tested by contingency tables and are given in the text. Numbers on top of the bars represent the total number of censused seastars.

Integrating feeding performance and abundance. Differences in *Asterias* food item specific abundances were analysed after pooling individuals feeding on both juvenile size classes (2 to 10 mm and 10 to 30 mm). This was necessary to apply parametric ANOVA because variance heterogeneity occurred when both abundances were treated separately due to several zero densities. A 2-way (3x6) ANOVA revealed that substratum type had no effect on the abundance of *Asterias* individuals feeding on juvenile mussels, yet the interaction "date*substratum type" was significant (Tab. 2.3). Linear contrasts revealed that this was entirely due to *Asterias* abundances on pure *Zostera*. They were significantly lower in April 1993 compared to both other substrata ($F_{(1,82)}=7.92$, $p=0.0064$, Bonferroni-adjusted significance *). Higher abundances in *Zostera* meadow in September 1992 coincided with an intense settlement of young *Mytilus* during that time of the year 1992 (see Fig. 2.3).

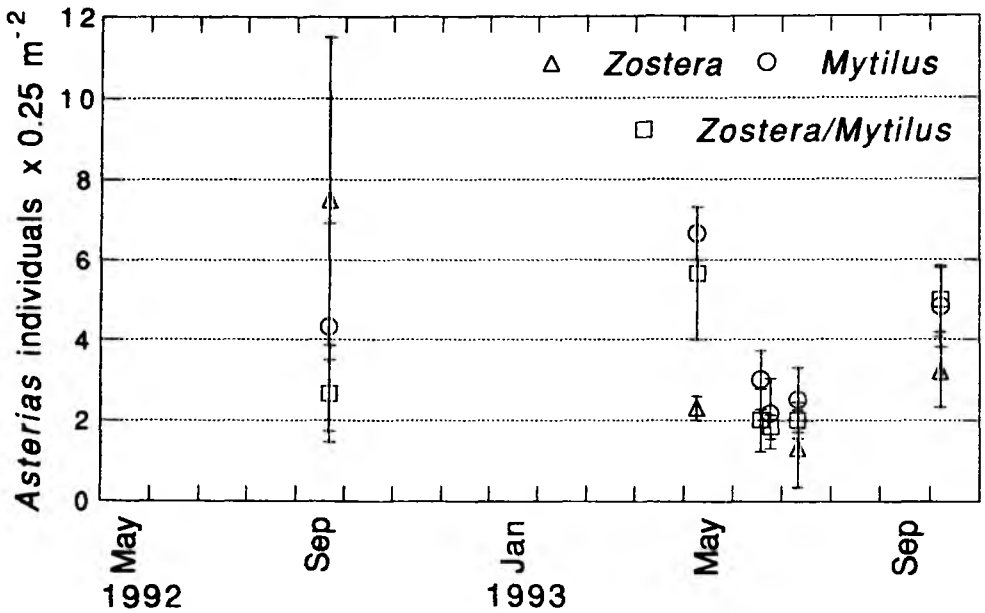


Fig. 2.7. Abundance of *Asterias* individuals feeding on juvenile mussels (2 to 30 mm in length) on 6 replicate quadrats of 0.25 m^2 on the substrata *Zostera*, *Zostera/Mytilus* and *Mytilus*. See Tab. 2.3 and 2.4 for statistical analysis. Error bars represent ±1 SE.

Another 2-way ANOVA was performed with balanced data (n=6) collected on 4 sampling dates comparing the substrata *Zostera/Mytilus* and *Mytilus* only (Tab. 2.4). It revealed that the presence of *Zostera* had no significant effect on the abundance of *Asterias* feeding on juvenile mussels (2 to 30 mm in length). The interaction between sampling date and substratum type was also non-significant.

Tab. 2.3. Two-way (3x6) ANOVA: comparison of densities of *Asterias* individuals feeding on juvenile mussels (2 to 30 mm) among 3 substrata (*Zostera*, *Zostera/Mytilus* and *Mytilus*) in quadrats of 0.25 m^2 on 6 sampling dates from September 22, 1992 to October 22, 1993. Note that the design is unbalanced. The sample size is n=6 except for September 1992 and April 1993, when only 3 replicates were obtained on *Zostera/Mytilus* and *Mytilus*. On *Zostera*, feeding performance was sampled on 4 dates only (see Fig. 2.7) Therefore, no test for homoscedasticity was performed.

Source of variation	df	MS	F	p	conclusion
substratum type	2	.0745	1.4565	.2402	ns
date	5	.3073	6.0085	.0001	**
date*substratum type	8	.1231	2.4060	.0238	*
Error	68	.0512			

Tab. 2.4. Comparison of *Asterias* abundances of individuals feeding on juvenile mussels (2 to 30 mm length) among substrata pure *Mytilus* and *Zostera/Mytilus* by a 2-way ANOVA on 4 sampling dates (June 18, June 23, August 10, October 22, 1993). Design is balanced with a sample size of n=6. Homoscedasticity of (log+1)-transformed data was checked with Cochran's test. Significance levels were Bonferroni-adjusted since data are parts of a larger ANOVA (see Tab. 2.3) ($\alpha_{adj} = \alpha/2$, ns$\geq$0.025, * 0.025>$\alpha\geq$0.005, ** 0.005>$\alpha\geq$0.0005, *** α<0.0005).

Source of variation	df	MS	F	p	conclusion
date	3	.2512	5.5471	.0028	**
Zostera present/absent	1	.0227	.5012	.4831	ns
date**Zostera* present/absent	3	.0262	.5791	.6322	ns
Error	40	.0453			

In summary, *Mytilus* recruits were more abundant on the whole year average on substratum types *Zostera* and *Zostera/Mytilus* compared to pure *Mytilus* beds. However, interactions between substratum type and sampling date were also found to be significant since abundances on substrata with *Zostera* canopy fluctuated stronger in response to settlement than did densities on pure *Mytilus* beds. *Asterias* densities were higher on adult mussel beds, irrespective of presence or absence of *Zostera*, compared to pure *Zostera*. Only after an intense settlement event in autumn 1992, seastar abundances were higher on pure *Zostera* than on adult mussel beds. Only at that time, abundances on sand were higher than those found on mussel beds and similar to those on pure *Zostera*. Within pure *Zostera* stands, the proportion of *Asterias* feeding on juvenile mussels (2 to 10 mm) was significantly higher compared to pure mussel beds and *Zostera/Mytilus*. However, since the total abundance of

Asterias within pure *Zostera* was always lower in comparison to both other substrata possessing adult mussels, the abundance of seastar individuals which were found feeding on juvenile *Mytilus* was similar among all 3 substrata.

2.4 DISCUSSION

The first objective of this study was to estimate spatial variation in settlement intensity of *Mytilus* recruits onto standardised substrata. The observed variation in numbers of larvae arriving at one of the triplicate spat collectors varied remarkably little within treatments on several dates as indicated by small standard errors. When larger variations occurred (on sand 6 m depth: July 8, 19, August 10. On sand 2 m depth: July 19), I was able to attribute them in 2 out of 4 cases to methodological flaws. On July 8, fouling of the nylon gauze with filamentous algae was markedly different among collectors in 2 m depth on sand. Hence, the surface available for settling larvae and consequently, their abundance differed among collectors. On July 19, a seastar had climbed onto one of the spat collectors deployed in 6 m depth and fed on the newly settled recruits.
In the Western Baltic, peak settlement rates are reported to occur during late May and June (Schütz 1964, Boje 1965). During this study in 1992, the peak settlement occurred during the same time period, but in 1993, it was approximately 4 wk later. Absolute settlement intensity varied considerably among both years. Cumulative settlement densities were approximately 6-fold higher in 1992 compared to 1993. On artificial settlement ropes Kautsky (1982b) found cumulative settlement densities of $2*10^6$ ind$*m^{-2}$. For 1993, these densities are in the same order of magnitude than those found in the present study. However, in 1992, spat densities at FO were approximately 10-fold higher (12 to $14*10^6$ ind$*m^{-2}$).

Collectors deployed inside *Zostera* patches always had lower settlement densities. At a first glance this may contradict work of Eckman (1987) and Peterson (1986). They found increased settlement rates of bivalves inside seagrass meadows and attributed that to a significant current reduction and

increase in turbulence within the meadow which facilitates settlement. However, my results do not necessarily contradict their work since the observed effect in this study may be a settlement shadow sensu Roughgarden et al. (1988). They suggest that with increasing distance from meadow edge settlement decreases since arriving larvae readily settle onto the first blades they encounter. Yet, my spat collectors were not deployed near the meadow edge, but at least 2 m away from the margin of the sand flat. However, these conclusion are highly speculative because I have no information on the recruitment density from the meadow margin inwards.
I conclude that variation in dispersal and distribution of competent larvae in the water column on a scale of meters to 10s of meters can be neglected in explaining the distribution of mussels at the experimental site. Rather, processes affecting settlement such as substratum preferences of spat and differences in post-settlement mortality, namely predation, contribute mainly to the observed patchiness as well as to depth distribution.

While I have no information on active settlement choice of mussel recruits, field observations as well as the predator exclusion experiment indicate that in fact, large differences exist in mortality rates young mussels suffer on the different substrata. I followed the density of *Mytilus* recruits over 15 months on all 4 principle substratum types in shallow water. These data integrate settlement and various sources of post-settlement survival. Since only 5 quantitative samples were taken during this period, an interpretation of the effect of season using the factor "date of sampling" is not permissible. Based on the arguments proposed by Morrisey et al. (1992) separating effects of season from temporal variations occurring at all other time scales is only possible if sampling dates are randomly dispersed in an a priori selected time intervals (i.e. seasons in this case). However, my hypothesis was not to detect seasonal differences in recruitment densities, but substratum effects over a longer time interval. Therefore, my regular sampling design may well provide an estimation of how different types of substrata affect recruitment throughout a period of 15 months.
Recruitment of *Mytilus* was best on both substratum types having a *Zostera* canopy. The substrata *Zostera/Mytilus* associations and pure *Zostera* showed significantly higher recruitment densities than adult mussel beds. This result was unexpected since the presence of both adult mussels and seagrass canopies

are reported to increase bivalve recruitment. Yet in this study, the effects of both species were not additive when occurring in mixed stands.

The frequency distributions suggest that young mussels first settle onto substrata with *Zostera*. Later, they are migrate onto adjacent mussel beds. This is in complete concordance with studies by Short et al. (1991) who found that for mussel beds, adjacent *Zostera* meadows were important sources for *Mytilus* recruits. Although it has been shown that *Mytilus edulis* spawns during one distinct period, which may be different dependent on the region (Seed 1976, and references therein), secondary settlement has often been reported to be continuous (Robles 1987, McGrorty et al. 1990, Robles & Robb 1993). My data further support the contention that the supply of *Mytilus* recruits via migration following primary settlement is very important and may continue throughout the year.

Whereas in 1992, dense settlement occurred onto bare sand in 2 m depth, mussel recruits were almost absent on that substratum type in 1993. I attribute that to the approximately 6-fold higher spat abundance in 1992 compared to 1993. Young (1983) reported that if no other suitable substrata are present, young mussels will settle even on sand. Since then young conspecifics are preferred as attachment sites over sand grains this requires a density which is high enough to ensure that the majority of spat individuals will encounter a neighbour to attach to. In this way lines or nets of young mussels are formed on sandy substrata. Results of this study are in concordance with observations made in the Wadden Sea (North Sea) where settlement of *Mytilus* onto bare sand is also observed only in years with extraordinarily high settlement densities (Dankers 1993).

Regardless of whether settlement occurs on bare sand at all, experimental evidence shows that young mussels can rarely survive on this substratum type. They are very rapidly eaten by seastars which engulf several small mussels at a time. Year to year variation in settlement intensity may therefore have little effect on mussel distribution since the mortality on unsuitable substrata such as bare sand is very high.

Asterias increased its abundance in response to the occurrence of young mussels which represent their preferred prey. Therefore, *Asterias* densities on pure *Zostera* were always much higher compared to bare sand since the abundance of *Mytilus* recruits in the meadow was markedly higher compared to sand (except for September/October 1992). If young *Mytilus* as preferred

prey are superabundant on bare sand, as in autumn 1992, the density of *Asterias* as well as the proportion of feeding individuals increases markedly from nearly zero to densities up to 16 ind/0.25 m^2. These abundances are as high as those found within *Zostera* or on adult mussel beds.

A significantly higher proportion of *Asterias* were found feeding on juvenile mussels in pure *Zostera* stands compared to both substratum types with adult beds (χ^2-test). However, absolute abundances of *Asterias* individuals feeding on juveniles were found to be similar among all 3 substrata (pure *Zostera*, *Zostera/Mytilus* and pure *Mytilus*) because *Asterias* was less abundant in pure *Zostera* patches. Probably seastars were generally more abundant on pure *Mytilus* and *Zostera/Mytilus* patches because they prefer substratum types which offer a secondary hard substratum, i.e. adult mussels. I suggest that the mortality young mussels suffer through *Asterias* predation is just as high within the spatial complexity of stands of *Zostera* as it is within the interstices of adult mussel conspecifics and that the above bottom architecture of the eelgrass meadow probably does not interfere with the foraging activity of seastars. This contention is further supported by the length/frequency distributions. They demonstrate that on all 3 substratum types very few of the individuals of the juvenile cohort which settled in August 1993 survived the strong predation pressure. The results of the predator exclusion experiment performed on bare sand indicates that, in contrast to all other 3 substratum types, foraging of *Asterias* is more effective than the supply with secondary settlers onto this substratum type.

In this context it is important to notice that the observed frequencies of seastars feeding on a given *Mytilus* size class do not represent their true diet (Peterson & Bradley 1978). The time *Asterias* needs to prey upon an adult (i.e. >30 mm) mussel is much longer compared to the time needed to engulf a young *Mytilus* individual. Laboratory observations revealed that the feeding time of an average sized seastar on mussels of 40 mm length ranged between 2 and 24 h. In contrast, several mussel recruits of 2-10 mm length were engulfed as whole within one hour (personal observations). Fairweather & Underwood (1983) pointed out that these differences in prey handling time may lead to biases up to the factor of 100 in estimating the true diet of a predator. However, I did not consider prey handling times since I was only interested in relative differences of feeding impact among substrata. Therefore it is perfectly justifiable to compare among feeding performance specific

Asterias densities or frequencies in order to estimate differences in the actual feeding impact among substrata. On the other hand, the observed preference of *Asterias* for small mussel size classes over adults is probably much stronger than only the frequencies of seastar individuals might suggest.

On pure mussel beds, post-settlement mortality seems to act in a density dependent manner because neither the 6-fold variation in settlement intensity between the years 1992 and 1993 nor the seasonal variation is very much reflected by the recruit abundances. This buffering of variations in density of juvenile mussels is remarkable because other studies report a much higher variation in mussels of the 0-year age group on mussel beds (McGrorty et al. 1990).

Although I have no experimental data on the effects of physical disturbance on mussel recruitment, qualitative observations showed that, within *Zostera* stands, young *Mytilus* survived winter storms of 1992/93 and 1993/94. Furthermore, core samples taken within pure *Zostera* in February 1993 revealed that mussel recruits survived inside the meadow whereas they were completely absent from bare sand. Whereas adult *Mytilus* individuals seldom attach to eelgrass shoots, young mussels do, and form little aggregations around the non-growing leaf sheath of *Zostera* right above the sediment surface. Here, their risk of being buried and/or dislodged is much reduced. When they occur in association with the matrix of a mussel clump or bed, young mussels are only affected by physical disturbance if the whole patch is dislodged by storms.

Although I did no experimental tests, I assume that leaves of *Zostera* provided a refuge from predation only for the very young individuals (<3 mm) for a narrow time span soon after settlement. In 1992 and 1993 from September onwards, the majority of recruits were found directly on the sediment and the *Zostera* leaves were completely free of mussel spat. This observation further supports the contention that the recruitment continuing until January 1994 consisted mainly of secondary settlers.

Very weak recruitment was found on mussel beds in 6 m depth. Since I have no information on how many young mussels actually settled on this substratum type, poor recruitment may be either due to lack of settlement or poor post-settlement survival. Whatever the exact reason, siltation plays probably a

major role at the site. *Mytilus* spat either avoided the muddy sand in 6 m depth or they were suffocated soon after settlement. The critical depth where siltation and sedimentation become too high to allow survival of *Mytilus* settlers is a function of the exposure of the site. This depth will therefore be higher at more exposed sites or at sites which receive in and outflowing currents from wind-induced sea level changes. Additionally, the amount of suspended material received may differ strongly between sites. In this respect, the experimental site at FO is probably an extreme and not representative since suspended material transported by northern storms into Kiel Fjord comes to rest and sedimentates in the shelter of the small peninsula north of FO. I estimate that at FO, sediment conditions and exposure found in 6 m depth correspond roughly to those in 15-20 m depth in open Kiel Bight. Therefore, my results are in concordance with two other studies from the Kiel Bight which found poor settlement intensity and no survival of spat on soft substrata in depths below 15 m (Richter 1975, Rumohr 1980).

In summary, recruitment processes play an important role in determining the observed distribution patterns of *Mytilus* on a local scale. There is observational evidence that the presence of *Zostera* exerts a strong influence on the recruitment density of *Mytilus*. This effect is independent of the presence of adult mussels. Since observations on the most abundant predator found at the site, *Asterias rubens*, revealed no difference in the feeding impact on juvenile mussels among the 3 substrata (pure *Zostera*, *Zostera/Mytilus* and pure *Mytilus*) I suggest that hydrodynamic factors play a major role in producing the observed pattern. The large blade area of the eelgrass canopy together with a current reduction and an increase in turbulence all may act together and increase the chance for primary and secondary settlers to settle inside the meadow. Thus, the occurrence of a high proportion of *Mytilus* beds associated with *Zostera* can be at least partly explained by the increased recruitment onto substrata with a *Zostera* canopy. The depth distribution seems to be partly controlled by weak recruitment in depths >5 m which attained only 25% of the recruitment in beds in 2 m depth. Since young mussels preferentially survived on adult *Mytilus* beds with and without *Zostera*, existing patches are renewed and patchiness is maintained.

Chapter 3

Effects of substratum type, water depth and predation on growth, dispersal and survival of *Mytilus* patches

3.1 INTRODUCTION

Mytilid mussels are often dominant components on intertidal shores of the northern hemisphere temperate zone (Seed & Suchanek 1992). Although being well adapted to a hard bottom existence they are also able to colonise soft-bottom substrata. Aggregations of conspecifics which are not attached with their byssus threads to primary substratum but to each other may form extensive beds (Seed 1976). In the Wadden Sea (North Sea) these aggregations may attain 100s of meters in diameter (Ruth 1991, Nehls & Thiel 1993). Beds of blue mussels are an important benthic component in the Western Baltic as well (Kellermann 1981, Brey 1984). Extensive subtidal beds are important food resources for overwintering ducks in the open Kiel Bight (Kirchhoff 1979, Meißner 1992). Mussel beds are also abundant on the soft-bottoms of sheltered sites such as Kiel Fjord (Schütz 1964, Schwenke 1969a, personal observations).

Most experimental work on the factors controlling mussel abundance and distribution was done in the intertidal zone of rocky shores. Classical work of Paine (1971, 1974) demonstrated that predation by seastars controls the lower distribution limit of the mussels *Mytilus californianus* and *Perna canaliculus*. Seastars cannot forage on mussels in the higher intertidal because of physiological constraints during low tide. There is anecdotal evidence that subtidal mussel beds on the sandy bottoms of the Wadden Sea suffer more from predation by seastars, fishes and crabs than intertidal beds (Dankers 1993). As a consequence, only few of these beds become older than one year.

Under most circumstances mussels must find a refuge from predation to occur subtidally (Seed, 1993). On rocky shores, this refuge may be a spatial in form of crevices in rocks or within multiple kelp holdfasts (Suchanek 1978) or on top of seamounts where seastars are rare (Seed & Suchanek 1992). As an alternative mussel individuals might attain a refuge from predation by growing beyond a critical size (Kitching et al. 1959, Paine 1976).

Additionally, in the intertidal wave exposure has been demonstrated to mediate

predation pressure. Since at exposed sites, predators cannot forage effectively due to wave shock (Menge 1976, Menge 1978) or their density is low due to the risk of dislodgement by waves (Christie 1983) mussels occur in the lower intertidal or upper subtidal zone.

In the semi-enclosed Baltic Sea, lunar tides are absent and except for those beds situated near the mean water level, *Mytilus* occurs almost entirely in the subtidal. In the central parts of the Baltic (Baltic proper), blue mussels may monopolise the shallow subtidal to a depth of 30 m. Kautsky (1981) suggests that this is due to the absence of important epibenthic predators such as the shore crab (*Carcinus maenas*) and the seastar (*Asterias rubens*) which might control *Mytilus* abundance. Both predators do not tolerate the low salinity levels of central parts of the Baltic Sea (5-7‰ S).

Kiel Bight and its adjacent bights such as the study site Kiel Fjord belong to a transition zone which is situated between the fully marine environment of the Atlantic and the lower salinity Baltic proper. Here, surface salinities range between 12‰ and 18‰ S and never drop below 10‰ S (Siedler & Hatje 1974). As a consequence, in Kiel Bight both crabs and seastars are present (Kowalski 1955, Nauen 1978). Preliminary observations showed that *Asterias* especially is very abundant ranging in density from 20 to 120 ind*m^{-2} (unpublished observation) in Kiel Fjord.

On rocky shores, besides factors affecting mussel recruitment (for discussion see chapter 2), patchiness of mussel distribution has been shown to be a consequence of disturbances which create free space and initiate a new successional sequence. These disturbances may be of physical origin like wave shock or log battering (Dayton 1971, Paine & Levin 1981, Sousa 1985, Denny 1987) or involve biological agents such as heavy predation (Dayton 1971, Suchanek 1978). If storms are the source of disturbance, dislodged mussel clumps are often washed onto the shore and die (Witman & Suchanek 1984, Witman 1987). In soft-bottom environments however, dislodgement of mussels does not necessarily mean patch mortality. Rather, a moderate disturbance regime may fractionate existing beds and disperse the resulting clumps over the area (Kautsky 1982b). Mussel clumps can either be transported along shore or to deeper water where they may come to rest and establish a mussel patch. For a sheltered area of the Wadden Sea (Sylt, Königshafen) drifting mussel clumps were shown to be an important source of patch formation (Thiel & Reise 1993).

The objective of this study is to identify the factors which control the abundance and distribution of *Mytilus* in the shallow subtidal of Kiel Fjord. Specifically I will test the influence of stable substratum type, of two water depths and of predators on growth and survival of mussel clumps and on their dispersal.

3.2 MATERIAL AND METHODS

Size distribution and abundance of *Mytilus*. The depth distribution of mussel beds was censused in spring 1993 using 1x1 m quadrates. Ten to 16 sample areas were randomly allocated within the selected depth horizon. The bed area was drawn onto a pre-formatted writing board. In the laboratory, the encircled patch area was measured and calculated. Mussel size distribution on natural mussel beds in 2 m and 6 m depths was sampled twice with cores (N=3 to 6) of 14 cm diameter (=154 cm^2).

Distribution and activity of predators on natural mussel beds. At the experimental site (FO), predators were censused to gain information whether their abundance and feeding activity is correlated with the depth distribution of *Mytilus*. On natural mussel beds in 2 m and 6 m depth, *Asterias* was censused on plots of 50x50 cm and their food items were recorded as described in chapter 2. Individuals of *Carcinus* was not included since their densities on pure mussel beds were always low compared to those of *Asterias*. Two nocturnal dives gave additional qualitative information on the activity of crabs as well as on foraging activity of fishes on mussels.
Asterias densities on natural mussel beds were compared on 4 sampling dates (January, April, July, October 1993) with a one-way ANOVA with "water depth" as factor.
The proportions of *Asterias* feeding on different size classes of mussels were pooled for all 4 sampling dates and the following hypotheses were tested using contingency tables (χ^2-square tests): (1) on mussel beds in 2 m depth, the proportion of *Asterias* feeding on mussels between 30 and 50 mm is higher compared to large mussel adults (>50 mm) (2) the proportion of *Asterias* individuals feeding on all adult (>30 mm) mussels is lower on mussel beds in 6 m compared to 2 m depth.

Laboratory feeding experiment. This experiment was designed to test whether large (>50 mm) mussel individuals found below 5 m depth attained a refuge from predation by size (Photo 2). Mussels of two different size classes were offered to *Asterias* held in plastic containers of 40x60x35 cm which were continuously flushed with seawater from Kiel Fjord. In spring 1993, 3 sub-experiments were performed with different *Asterias* individuals ranging from 90-120 mm in diameter. This corresponds to the upper size range of *Asterias* found at the site. In the first sub-experiment (2 wk duration), approximately equal fresh weight of mussels of each size class was given to the seastars, corresponding to 10 large sized mussels (>50 mm) and 50 mussels between 30 and 40 mm. During the second experimental period (1 wk) two independent experiments were performed presenting either equal wet weight or equal numbers of mussels of both size classes to *Asterias*.
In both experiments H_0 was that *Asterias* did not prefer any of both size classes. This was statistically tested with contingency tables (χ^2-tests).

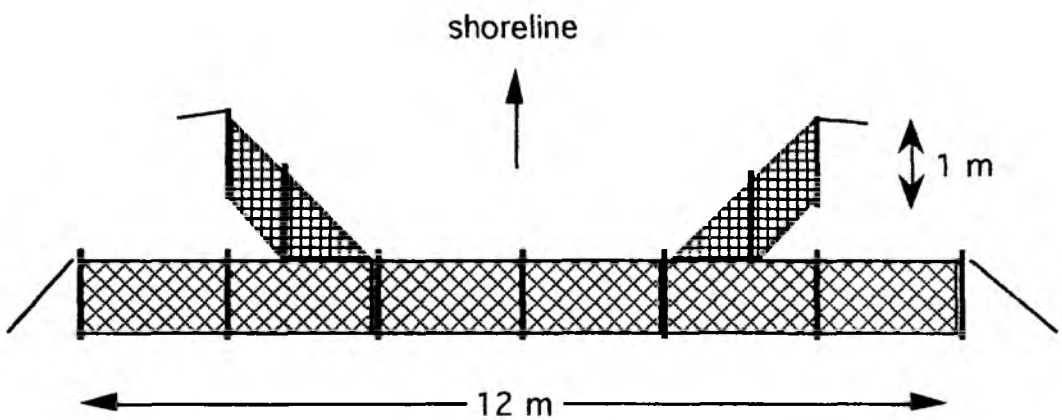


Fig. 3.1. Diagrammatic view of the drift collector fence which was set up at Friedrichsort (FÖ) from December 1992 to December 1993. Mesh size of the vexar material was 4x4 cm.

Abundance of drifting clumps. Based on preliminary field observations I hypothesised that drifting mussel clumps are an important mode of mussel dispersal in Kiel Fjord. To estimate the abundance of mussel clumps transported along shore and to deeper water, a collector fence made of vexar meshes with 4x4 cm openings and 1 m height was designed (Fig. 3.1, Photo 3). It was installed in 4.5 m depth in December 1992. In monthly intervals, all mussel clumps and drift algae caught in the fence were sampled. The mussel

patches were counted and their wet weight was determined in the laboratory.

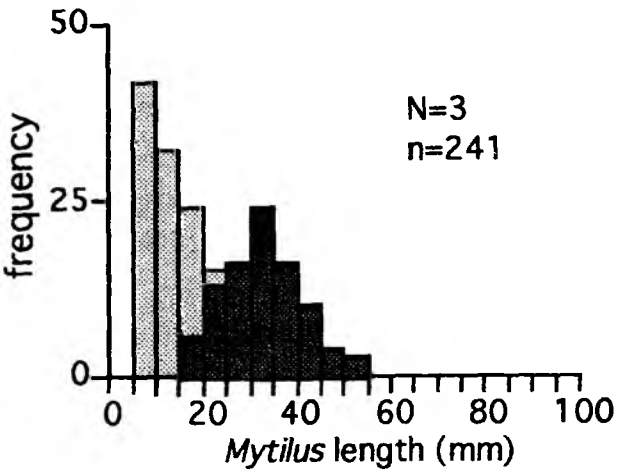


Fig. 3.2. *Mytilus* length distribution of the source patch for the transplantation experiment. Light shaded bars represent young (<1 y old) individuals. Individuals <5 mm are not included.

Mytilus-transplantation experiment

Experimental factors. In an experimental approach, survival and growth of mussel clumps was followed under various conditions over a period of 10 month. In February 1993, mussel clumps originating from one big patch in 2.5 m depth a few meters distant from the shallow experimental units were transplanted onto haphazardly selected experimental plots within two stripes (in 2 and 6 m depth) of 30 m parallel to the shoreline. Their size distribution is shown in Fig. 3.2. Clumps had an average initial area of 355±20 cm^2 SE (n=18) which corresponds approximately to the average size of naturally occurring clumps found in a field survey on February 20, 1993 (253±59 cm^2 SE, n=13).

Three experimental factors were tested on 4 replicate clumps, each having two levels: water depth, predator presence or absence and substratum type. Two water depths were chosen: 2 m which corresponds to the depth of maximal mussel bed coverage (Fig. 3.5), hereafter referred to as "shallow", and 6 m depth, hereafter referred to as "deep".

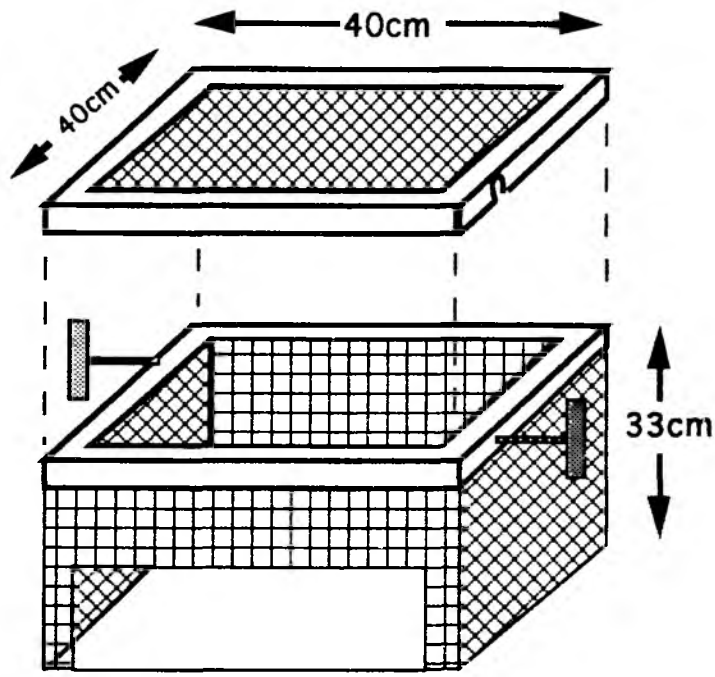


Fig. 3.3. Cage construction used to exclude epibenthic predators in the *Mytilus* transplantation experiment. Front side shows roof cage having an opening of 36x15 cm. The cage frame made of PVC-angles carried stainless steel wire mesh with 6x6 mm openings. The cage top can be removed using two screws. The cage sides were buried 5 cm into the substratum.

Predation was manipulated in two levels (presence/absence) by closed and incomplete (roof) cages. The cages (40x40 cm in area and 33 cm in height) were made out of 6 mm stainless steel mesh which was glued to a frame of grey PVC angle material. The upper side of the cage was fixed to the frame with two large screws and could be readily opened in the field (Fig. 3.3, Photo 4 and 5). Roof cages had openings of 36x15 cm in all four sides and allowed access to predators.

During the last 4 mo of the experimental period only, two of the original cages were replaced by bigger ones (50x50x30 cm, same stainless steel mesh material) in those plots where the mussel clumps had completely covered the ground area of the standard cage type (1600 cm^2). I assumed that potential cage artefacts were not significantly different between both cage sizes.

I chose vexar plastic meshes (mesh size 10x10 mm) to manipulate the factor "substratum type". They should mimic an optimal stable substratum which is a limiting resource in Kiel Fjord and Kiel Bight (Babenerd & Gerlach 1987). Furthermore, they were designed to provide a control group for the estimation of drift distances (see below). Laboratory tests showed that adult mussels will

attach their byssus threads to the material within days. Cages and meshes were fixed with iron stakes and cable ties at all 4 edges.
In Kiel Fjord in 2-4 m depth, mussels are often associated with eelgrass (*Zostera marina*). Although highly desirable, no caging was feasible above the seagrass canopy, since the plants attain 1 m in height during summer. Cages of that size would not survive even a moderate storm. Furthermore, since seagrass is restricted to water depth less than 4 m (Kobarg 1993), an inclusion of *Zostera* as experimental factor would have rendered a factorial design impossible.

Control experiment. A second sub-experiment was designed to test for potential cage artefacts. In both depth, completely uncaged plots were compared to roof cages. All treatments had vexar nets as substratum type, thus the total number of experimental plots was 16 (4 replicates times 2x2 treatment combinations, Fig 3.4 a). The control experiment was restricted to the artificial stable substratum because I feared that clumps were lost quickly before I would have been able to detect a potential cage artefact.

Experimental design. Given 4 replicates, the complete factorial design with 3 factors each having two levels will result in 2x2x2x4=32 experimental plots. Cleaning of 32 complete or roof cages from fouling algae (especially during spring) would have far exceeded the time constraints for working with SCUBA diving. Therefore, the treatment combination "shallow*predators absent*mesh" was completely omitted from the experimental design of the main experiment (Fig. 3.4 b). Hence, the factorial design became incomplete, with only 7 out of 8 possible treatment combinations. Additionally, the number of caged plots was reduced by replacing two treatment combinations by their completely uncaged counterparts under the assumption that no cage artefacts would be evident.

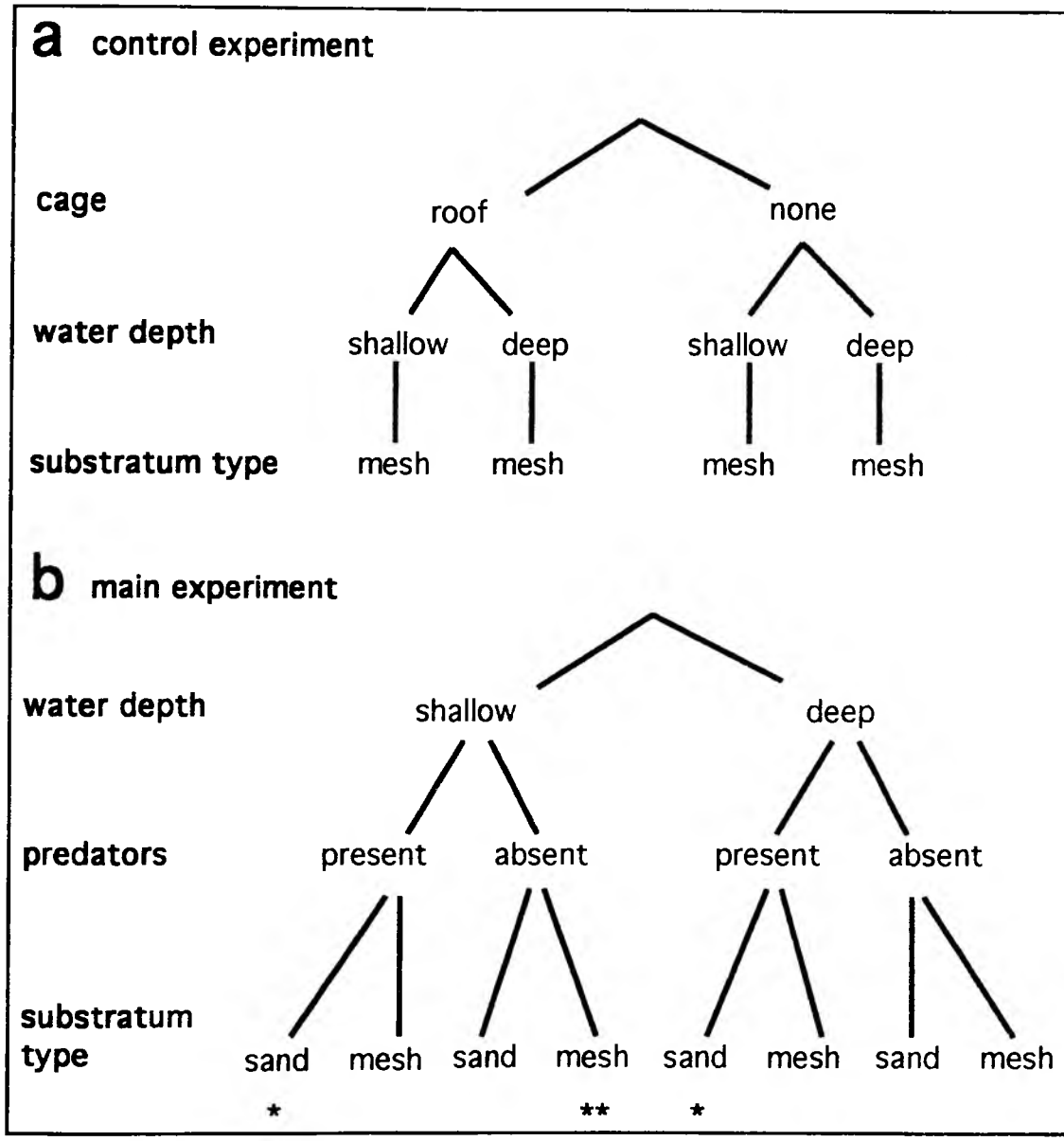


Fig. 3.4. *Mytilus*-transplantation experiment: design of control experiment for cage artefacts (a) and of main experiment (b). Treatments of the control experiment had always stable substratum type (i.e. vexar meshes). Each treatment combination had 4 replicates. In the main experiment (b) the treatment combination "shallow/predators absent/mesh" (**) was completely omitted. The two treatments marked with one asterisk (*) had no cage instead of a roof cage.

The incomplete factorial enables me to analyse all first order interactions involving two main factors but not the one second order interaction present (water depth * presence/absence of predators * substratum type).
Closed cages were inspected for presence of predators every 2 to 4 weeks. Exclusion of crabs and seastars >3 cm in diameter was perfect during the

experimental period. Only few small crabs (0.5-1 cm carapace width) entered both, the shallow and deep cages. Seastars smaller 3 cm in diameter were present in only deep cages throughout the study period. Both juvenile predators were removed whenever visiting the cages (at least 4-weekly). Meshes were cleaned with a wire brush monthly during winter and fortnightly during spring and summer months.

Response variables. Three response variables were measured: (1) area of the mussel clumps (2) abundance of predators (*Asterias* and *Carcinus*) in all uncaged and roof caged plots (3) drift distance of clumps. Clump area was determined photographically every 2 mo using a camera with flash attached to a frame. The clumps under complete or incomplete cages were photographed after having the roof unscrewed and removed. The colour slides were then processed into S-VHS video signals and further analysed on a NeXT-computer with an image analysis software developed in our department (Huckriede 1992). On the digitised image, the mussel clump was encircled and the area calculated.

On the mussel patches, *Asterias rubens* and *Carcinus maenas* were counted on 8 sampling dates in 4 to 6-weekly intervals. Only *Asterias* individuals >3 cm in diameter and *Carcinus* individuals >2 cm carapace width were included.

As a second response variable, the drift distances of uncaged clumps were recorded. To do this and to re-allocate dislodged clumps, all uncaged clumps were marked using a plastic label which was attached to the clump by wrapping a long cable tie through the center of the clump (Photo 8).

Clumps were replaced to their original position approximately every 4 weeks. Thus, for the response variable "drift distance", the experiment was restarted monthly. Since I feared the loss of clumps of the treatment combination sand/shallow/no cage due to dislodgement over a longer distance this treatment had 8 replicates.

Statistical analysis. Two sets of hypotheses were tested in both main and control experiments. Factorial MANOVAs were used to test whether experimental factors had an effect on mussel clump area during the whole experimental period of 10 month. Therefore, each 2-monthly sampling date was treated as an independent variable (Farrell 1989, Howell 1992). With an ANCOVA, the cumulative effects of experimental manipulation were tested on the last sampling date (December 13, 1993) only.

The multivariate analysis (MANOVA) has the advantages of having a greater power of detecting a real difference. At the same time, it minimises the risk of

committing a type I error and eliminates the problem of non-independence among consecutive sampling dates in the same plots (Johnson & Field 1993). For hypothesis testing, I chose the Pillai Trace-statistic and its F-approximation. It is recommended by Johnson & Field (1993) as being the most robust against violations of multi-normality and multi-homoscedasticity compared to other multivariate statistics (e.g. Hotelling's Trace, Wilk's Lambda).

Although the data sets of both experiments would allow an multivariate analysis of covariance (MANCOVA) using the initial clump size as covariate, this was not legitimate since there were significant covariate*factor interactions.

Before performing MANOVAs, the treatment combinations were tested by a one-way ANOVA to determine whether significant differences existed among treatments on the first sampling date. This was not the case for both main and control experiment (main experiment: $F_{(6,21)}=1.086$, $p=0.402$; control experiment: $F_{(3,12)}=0.157$, $p=0.678$). Therefore, I was justified in not taking account differences in initial mussel clump area.

Clump areas were log-transformed to achieve homogeneity of variances. In the univariate analysis, homoscedasticity was tested with the procedure of Cochran. In this and all subsequent multivariate analysis, multi-homoscedasticity and -normality was checked using a modified Hawkins-test (Johnson & Field 1993). The differences of the medians among the A_{ij} vectors of all groups never exceeded the critical value of 0.85.

With the results from the ANCOVA, the relative effect sizes of the experimental factors were calculated. The following formula (Howell 1992, p.407) was used:

$$\omega^2 = (SS_{treat} - (k-1)MS_{error}) / (SS_{total} + MS_{error})$$

where k = number of treatments, SS = sums of squares, MS = mean squares, and treat = treatment.

Predator abundances on all open plots of the main and control experiment were analysed for effects of water depth, substratum type and presence/absence of cage. The data set had to be split into two sets of MANOVAs since not all treatment combinations were realised on plots allowing access to predators (combinations "roof cage*sand" were omitted in both depths, see Fig. 3.4): (1) a 2-way MANOVA with depth and substratum type as factors (2) a 2-way

MANOVA with presence/absence of cage as factors. *Asterias*-numbers were (log+1)-transformed.
Counts of *Carcinus* could not be analysed with parametrical methods, since their abundance on experimental clumps was generally much lower compared to *Asterias*. As a consequence, transformation was not sufficient to reduce heterogeneity of variance. As an alternative, a Mann-Witney U-test was performed comparing the treatments with incomplete cages vs. uncaged plots on 4 sampling dates. The significance level on each sampling date was not Bonferroni-adjusted since each comparison was considered as an independent hypothesis.
No statistical analysis was applied on the drift distance data.

Proportion of predation by *Carcinus* vs. *Asterias*. The importance of predatory impact of crabs vs. seastars on mussels >10 mm in length was estimated using the proportion of crushed vs. undamaged opened mussels in the transplanted clumps. While seastars leave the shells of their bivalve prey intact, crabs crush the shells to feed on *Mytilus* (Menge 1979, Moody & Steneck 1993). On March 10 and June 26, 16 clumps (8 in each depth) and on August 20, 24 clumps (12 in each depth) were examined. Each clump was composed of 30 to 80 adult mussels.
The proportions of mussels opened by *Asterias* and *Carcinus* were compared among uncaged plots and plots having a roof cage with a χ^2-test using a 2x2 contingency table.

3.3 RESULTS

Coverage and size distribution of mussels. At the experimental site Friedrichsort (FO), *Mytilus* beds ranging from 0.25 to 5 m^2 in area are patchily distributed on a gently sloping (2-3°) sandy substratum (Photo 1). Coverage is highest within a stripe between 1.5 and 2.5 m water depth but never exceeds 18±5% SE cover (Fig. 3.5). In 1 to 3 m depth, mussels are often found associated with *Zostera*. The nature of this co-occurrence will be discussed in detail in chapters 4 and 5. Here, I will restrict discussion to all other factors affecting *Mytilus* distribution.

Below 5 m depth, 10±8% of the substratum is covered with aggregations of large individuals (>50 mm length, Photo 2). Their mean size is app. 20 mm higher compared to those in the shallow water (Fig. 3.6).

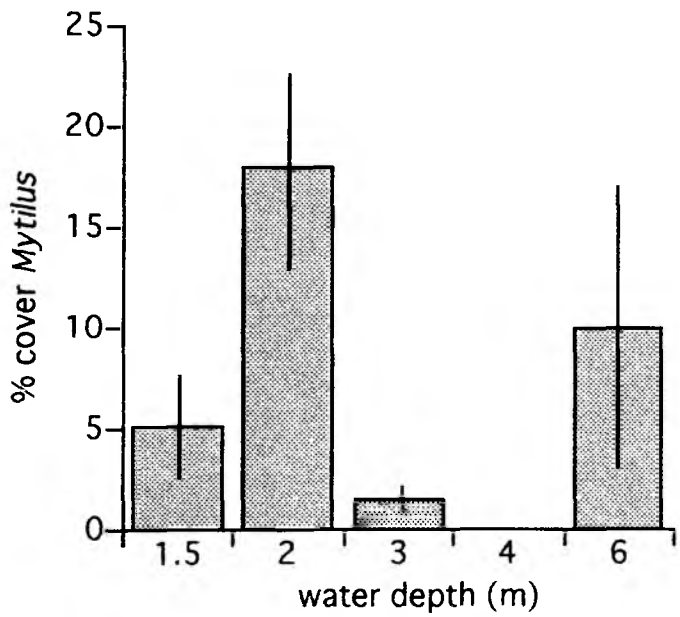


Fig. 3.5. Distribution of mussels at the experimental site FO (Friedrichsort). Sample size was 1 m^2, number of replicates n=16 in 2 m depth and n=10 in 1.5, 3 and 4 m and n=6 in 6 m water depth. Error bar ±1SE.

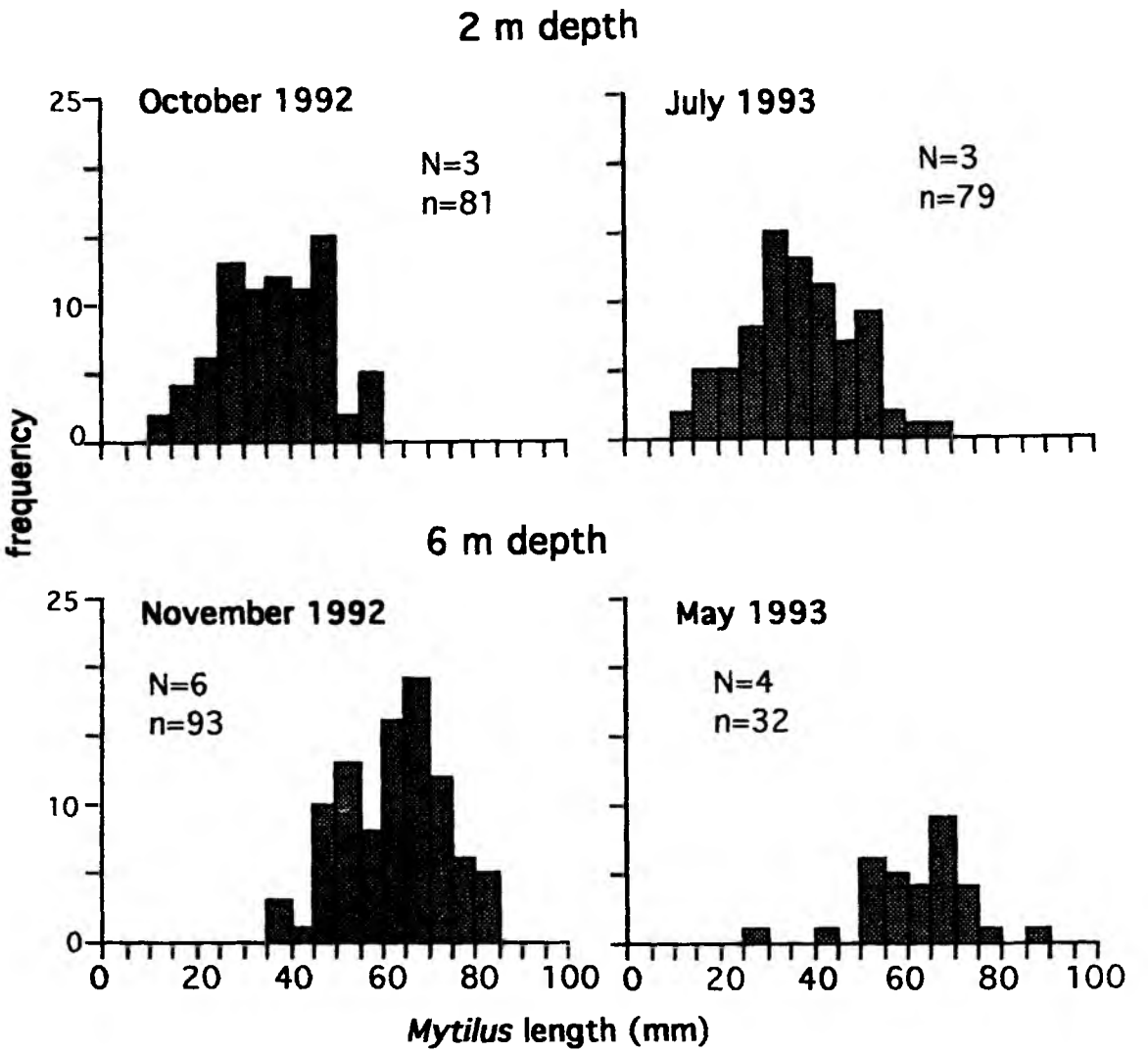


Fig. 3.6. Comparison of lengths distributions of *Mytilus* among 2 (above) and 6 m (below) depth on two dates at FO. One-year old individuals were not considered.

Distribution and activity of predators on natural mussel beds. A 1-way ANOVA revealed that *Asterias* was equally abundant on natural mussel beds in both water depths ($F_{1,46}$= 0.0542, p=0.0817).

Very few food items other than *Mytilus* were consumed during the study period. Of 556 seastars whose food items were recorded on mussel beds in both depths, 141 individuals were found feeding. Of the feeding individuals, only 4 (2.8%) fed on barnacles (*Semibalanus balanoides*), one individual (0.7%) fed on periwinkles (*Littorina littorea*) and one (0.7%) on a crab carcass (*Carcinus maenas*). In 2 m depth, 25 out of 391 (6.4%) *Asterias*

individuals were found feeding on adult mussels of size class 30-50 mm only, but never on those >50 mm although they were present on shallow beds (Fig. 3.6). The differences among proportions of individuals was highly significant (χ^2= 25, p<0.0001).

In 6 m depth, most of the seastars (94%) were not feeding. Of 165 investigated individuals, only 6 (3.6%) attacked mussels larger than 50 mm.

Differences among proportions of seastars feeding on both adult mussel size classes (30-50 mm plus >50 mm) were compared among depths. A trend was found for *Asterias* to feed in a significantly lower proportion on adult mussels (>30 mm) in 6 m depth compared to mussel beds in 2 m depth (χ^2=3.385, p=0.0658).

Laboratory feeding experiment. During all 3 sub-experiments, *Asterias* never fed on mussels >50 mm in size but preyed on individuals between 30 and 45 mm length (Tab. 3.1). For all 3 sub-experiments, the proportions of mussels fed of the smaller size class was significantly higher (experiment (1) χ^2=23, p<0.0001, exp. (2) χ^2=13, p=0.0005, exp. (3) χ^2=9, p=0.0042).

Most of the mussels found in 6 m depth are larger than 50 mm (Fig. 3.6).

Tab. 3.1. Results of a laboratory feeding experiment with *Asterias* as predator and *Mytilus* of different size classes as prey organisms. Three seastars measuring 90 to 120 mm in diameter were held in plastic containers of 40x60x35 cm which were continuously flushed with seawater from Kiel Fjord. Three sub-experiments were performed over two periods of 2 and 1 week, respectively, with different *Asterias* individuals. In the first two sub-experiments, approximately equal fresh weights of mussels of each size class were given, corresponding to 10 large sized mussels (>50 mm) and 50 mussels of 30 to 45 mm length. During the second experimental period, the same weight and the same numbers of mussels of both size classes were given to two groups of seastars.

		Temp	No. *Mytilus* offered (mm)		No. *Mytilus* eaten (mm)	
Repl.	period	℃	30-45	>50	30-45	>50
A	7.4.-				10	0
B	21.4.93	6-8	50	10	9	0
C					4	0
D	21.4.-				5	0
E	28.4.93	8-9	50	10	2	0
F					6	0
G	21.4.-				3	0
H	28.4.93	8-9	10	10	2	0
I					4	0

Abundance of drifting mussel clumps. The wet weight of mussels caught in the collector fence showed distinct seasonal patterns which correlated well with the disturbance regime, namely the occurrence of storms (Fig. 3.7). During the calm summer months, only few clumps drifted into the fence. Prior to the 2 sampling dates with the highest capture of clumps (January 29 and November 22 , 1993, strong southerly winds (11-12 Bft during January 1993, 9-10 Bft in October 1993) were recorded (measurements by meteorological department, Institute of Marine Science).

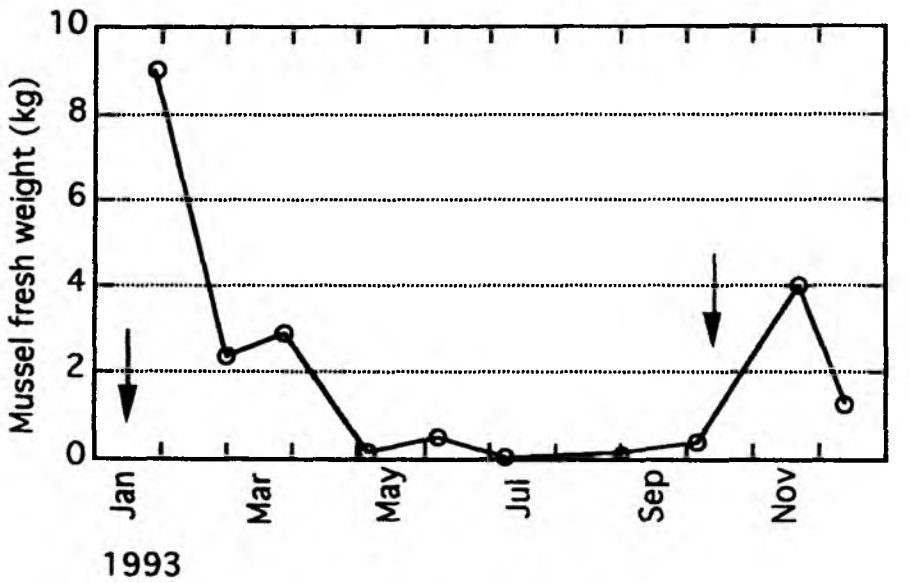


Fig. 3.7. Wet weight of mussel clumps caught in the drift collector fence. Data are pooled for all 3 sectors. Arrows indicate periods with heavy storms (January 1993 and October 11, 1993).

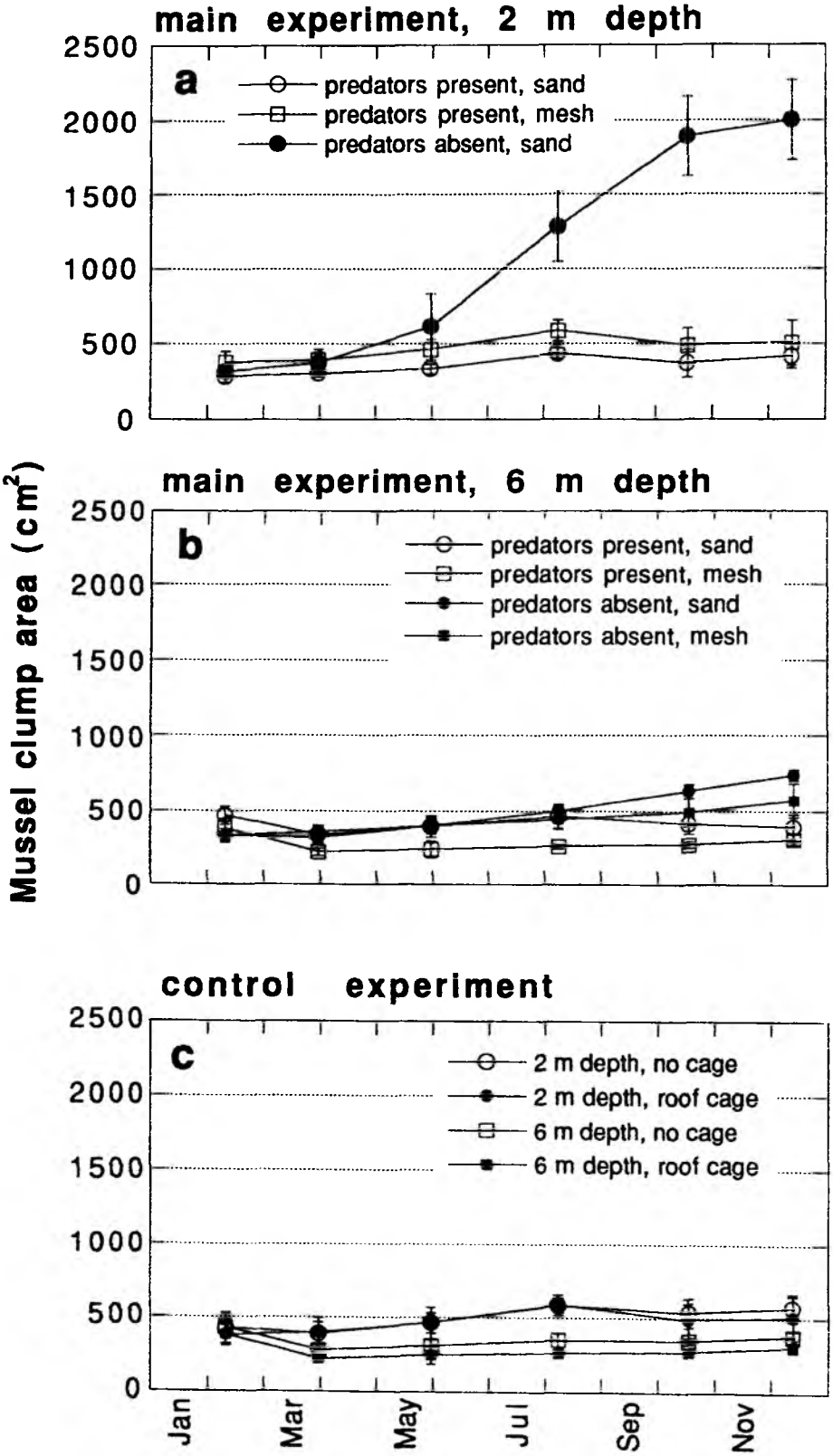
The fence which was installed in 4.5 m depth, collected roughly 21 kg wet weight of mussels during one year. Based on the wet weight biomass of *Mytilus* beds in 2 m depth, this corresponds to a bed area of approximately 1.5 m^2.

Mytilus transplantation experiment

Main experiment. The development of the clump areas under the different experimental conditions is shown in Fig. 3.8 a (2 m depth) and 3.8 b (6 m depth). All clumps survived the 10 mo experimental period. However, the areal development showed marked differences among treatments. Clumps under absence of predators in 2 m depth increased their area 6-fold (637±89%

SE). To a great extent mussels of the one-year age class which previously were hidden between interstices of the adult conspecifics contributed to this areal extension (Photo 5). Mussel clumps in 6 m depth without predators only increased their area by 133±21% and 71±20% on sand and mesh, respectively, over the 10 mo experimental period. Both treatments where predators were present in 2 m depth increased their area moderately until the final sampling date in December 1993. In contrast, deep clumps under access of predators showed a moderate decrease in clump size (area decrease ±SE 20±10% and 18±6%, on sand and mesh, respectively).

Fig. 3.8 (overleaf). *Mytilus* transplantation experiment: mean area (±1 SE, n=4) of clumps of main experiment in 2 m depth (a) and 6 m depth (b) and of control experiment in both depths (c) from February to December 1993.


main experiment, 2 m depth
a
predators present, sand
predators present, mesh
predators absent, sand
2500
2000
1500
1000
500
0
main experiment, 6 m depth
b
predators present, sand
predators present, mesh
predators absent, sand
predators absent, mesh
Mussel clump area (cm²)
control experiment
c
2 m depth, no cage
2 m depth, roof cage
6 m depth, no cage
6 m depth, roof cage
Jan
Mar
May
Jul
Sep
Nov

The results of the two statistical analyses applied on the response variable clump area was identical for the main effects but differed in the interaction terms. In the MANOVA (incorporating all sampling dates) and in the ANCOVA (on only the last sampling date in December 1993) the main effects "water depth" and "presence/absence of predators" were both found to have highly significant effects on *Mytilus* clump growth (Tab. 3.2 and 3.3). However, while the MANOVA detects a significant "depth*predators present/absent" interaction, the ANCOVA fails to detect a significant effect of this interaction (p=0.1003). In the ANCOVA (Tab. 3.3) the highly significant effect of the initial area (p<0.0001) indicates that the inclusion of the initial area into the analysis markedly reduced the error term and consequently, increased the power of the analysis.

Tab. 3.2. *Mytilus* transplantation main experiment: analysis of effects of water depth, presence/absence of predators and substratum type on *Mytilus* clump area over a period of 10 mo by 3-way MANOVA. Each of the 5 sampling dates was treated as one independent variable. Mussel clump areas were log-transformed. Multi-homoscedasticity and -normality was checked using a modified Hawkins-test (Johnson & Field 1993).

source of variation	Pillai Trace	F	Hyp. df	Error df	p	conclusion
water depth	0.5727	4.557	5	17	0.0081	**
predators present/absent	0.7364	9.498	5	17	0.0002	***
substratum type	0.3055	1.495	5	17	0.2432	ns
water depth*predators present/absent	0.5657	4.429	5	17	0.0091	**
water depth*substratum type	0.3332	1.699	5	17	0.1887	ns
predators present/absent* substratum type	0.2721	1.271	5	17	0.3212	ns

While it is obvious from the graph that predator exclusion in the shallow had a marked and significant effect on clump area this is not evident at first glance for deep treatments. A linear contrast by ANCOVA on clump areas in 6 m depth only, revealed that predator exclusion had a significant effect on clump area, i.e deep clumps grew larger under protection of cages ($F_{(1,12)}$=13.818, p=0.0029). A similar comparison using a MANOVA failed (Pillai trace=0.527, $F_{(5,10)}$=2.223, p=0.132).

In this context it is important to notice that the mean initial clump areas were not perfectly similar at the beginning of the experiment, although an ANOVA revealed that these differences were not significant. Mean clump size ±SE was 424±44 cm^2 and 327±26 cm^2 in deep plots with and without predators,

respectively (both n=8). Since in the ANCOVA, these lower initial areas of treatments without predators are taken into account, predator presence/absence had a significant effect in 2 m and 6 m depth in this type of analysis. As a consequence, the interaction term "water depth*presence/absence of predators" becomes non-significant because the effect of predator exclusion is independent of the level of factor depth. The MANOVA (recall that it was not legitimate due to significant treatment*covariate interactions) fails to detect a significant predator effect in 6 m depth. Hence, effects of predators are dependent of the level of the factor depth, i.e. an interaction occurs between depth and presence/absence of predators.

Tab. 3.3. *Mytilus* transplantation main experiment: analysis of effects of water depth, presence/absence of predators and substratum type on *Mytilus* clump area on the last sampling date (December 13, 1993) by 3-way ANCOVA. The initial area of transplanted clumps was covariate. Areas were log-transformed and meet assumptions of homoscedasticity tested by Cochran's test. Prior to the ANCOVA, a test of homogeneity of slopes was performed.

Analysis	source of variation	df	MS	F	p	concl.
Homogeneity of slopes	covariable*depth	1	0.0004	0.0229	0.882	ns
	covar*predators absent/present	1	0.0024	0.1531	0.700	ns
	covar*substratum type	1	0.0018	0.1129	0.741	ns
	covar*depth*predators absent/present	1	0.0239	1.535	0.232	ns
	covar*depth*substratum type	1	0.0019	0.1247	0.728	ns
	covar*predators abs/pres*substratum type	1	0.0150	0.9605	0.341	ns
	Error	17	0.0156			
		conclusion:		ANCOVA	legitimate	
Analysis	**source of variation**	**df**	**MS**	**F**	**p**	**concl.**
ANCOVA	covariate (initial area)	1	.3456	22.626	.0001	***
	depth	1	.3656	23.931	.0001	***
	predators absent/present	1	.9901	64.815	.0001	***
	substratum type	1	.0220	1.4391	.2443	ns
	depth*predators absent/present	1	.0454	2.9695	.1003	ns
	depth*substratum type	1	.0008	.0511	.8235	ns
	predators absent/present* substratum type	1	.0243	1.5928	.2214	ns
	Error	17	.0156			

Another means comparison was performed to test whether water depth had an significant influence in all plots with predators. An ANCOVA on the last sampling date as well as a MANCOVA revealed a significant depth effect (ANCOVA $F_{(1,13)}=12.36$, $p=0.0038$, MANCOVA Pillai trace=0.785, $F_{(5,9)}=6.552$, $p=0.0078$). In contrast to the whole data set, a MANCOVA was

legitimate on half of the whole data set including only incompletely caged plots in this case. Finally, the factor water depth was tested in a one-way MANOVA. Here, depth had no significant effect (Pillai trace=0.3967, $F_{(5,10)}=1.315$, p=0.332). This highlights again, that for the multivariate analysis a consideration of the covariate would have been much more appropriate, yet it was not justified for the entire multivariate data set.

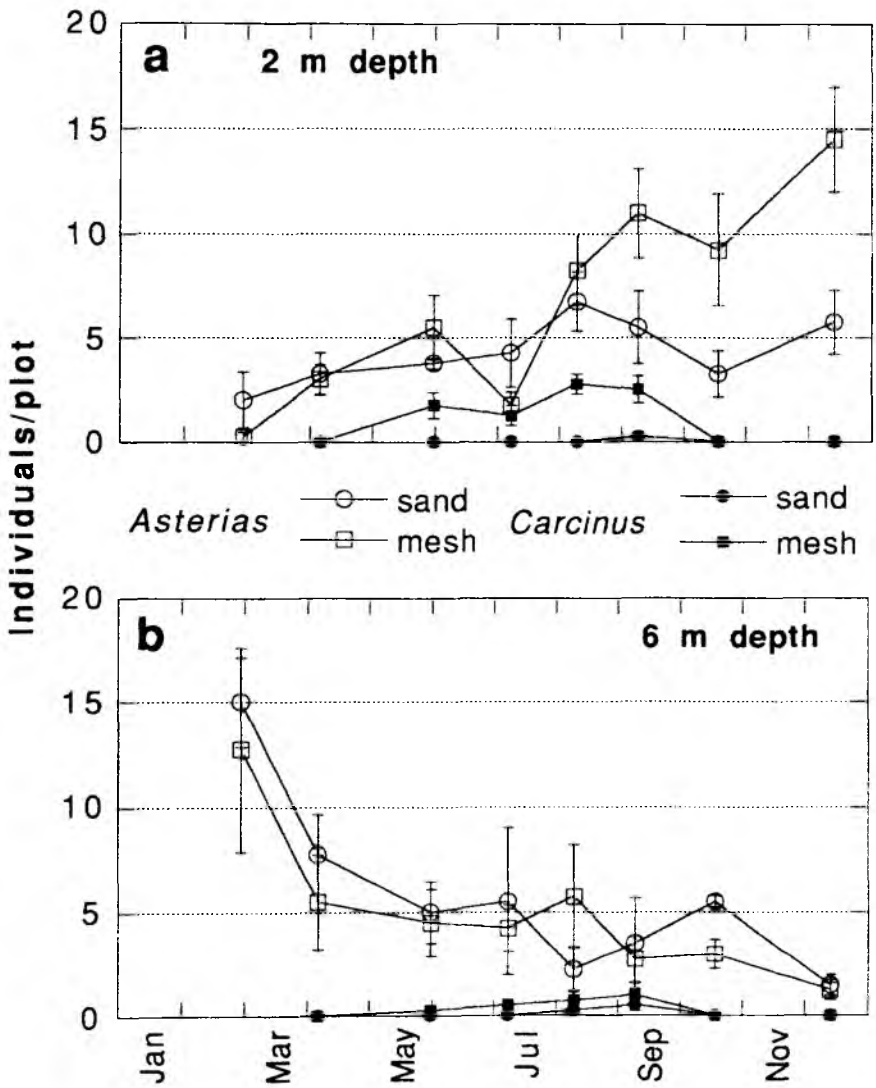


Fig. 3.9. *Mytilus* transplantation experiment: abundances of *Asterias* and *Carcinus* ±1 SE (n=4) on clumps of the main experiment in (a) 2 m depth and (b) 6 m depth.

With the results of the ANCOVA, I calculated the relative effect size ω^2. The presence or absence of predators explained 52% and water depth accounted for 17% of the total variance in clump area (variance contribution by covariate not considered).
A marked area decrease occurred from February to April 1993 in deep clumps and during autumn 1993 in shallow clumps in presence of predators. Both area decreases coincided with high abundances of *Asterias* on the mussel clumps (Fig. 3.9). On March 1, 1993 in 6 m depth, they attained densities ±SE of 14±1.9 ind/clump compared to only 1.5±0.8 ind/clump on mussel patches in 2 m depth. In October 1993, high absolute *Asterias* densities were found on clumps in 2 m depth (8.8±1.14, 7.4±1.34 and 8.8±1.6 ind/clump in September, October and December 1993, respectively). This suggests that feeding of *Asterias* was responsible for the observed area decreases.

Artefact control experiment. In the control experiment, no cage artefacts were evident comparing the response variable "clump area" among uncaged and roof caged plots (Fig. 3.8 c). A factorial (2x2) MANOVA on all 5 post-transplantation sampling dates revealed that the experimental factor "cage" was far from being significant (Tab. 3.4). Thus, it was legitimate to include the completely uncaged treatments "2 m depth*predators present*sand" and "6 m depth*predators present*sand" into the main experimental analysis (Fig. 3.4 b).
Since in the main experiment, the factor "substratum type" was not significant as main factor or in an interaction, I assume that cage artefacts neither occurred in experimental treatments on substratum type "sand".

Tab. 3.4. *Mytilus* transplantation control experiment for cage artefacts: analysis of the effects of water depth and presence/absence of cage on *Mytilus* clump area over a period of 10 mo by 2-way MANOVA. Each of the 5 sampling dates was treated as one independent variable. Mussel clump areas were log-transformed. Multi-homoscedasticity and -normality was checked using a modified Hawkins-test (Johnson & Field 1993).

source of variation	Pillai Trace	F	Hyp. df	Error df	p	conclusion
water depth	0.8395	8.371	5	8	0.005	**
cage present/absent	0.1867	0.3674	5	8	0.858	ns
water depth*cage present/absent	0.2749	0.6067	5	8	0.698	ns

Abundance of predators on clumps. A MANOVA on *Asterias* densities in the main experiment revealed that there was a statistically significant but biologically unimportant difference in *Asterias* densities among 2 m and 6 m depth (Fig. 3.9 a and b, Tab. 3.5). (5.3±0.65 ind/clump in 6 m depth, 5.5±0.56 ind/clump in 2 m, respectively). Substratum type had no effect on seastar density.

In the control experiment, the density of seastars was similar in open plots with roof cages and completely uncaged plots in both depths (Fig. 3.10 a). This is confirmed by a MANOVA on *Asterias* densities on all sampling dates which revealed that factor "presence/absence of cage" was neither significant as main factor nor in an interaction with factor "water depth" (Tab. 3.6).

Tab. 3.5. Mussel transplantation control experiment: two-way MANOVA on *Asterias* densities on uncaged mussel clumps on 8 dates. Depth and substratum type (presence/absence of a vexar mesh) were experimental factors. Since part of the data were compared in a second analysis (Tab. 3.6), the significance levels were Bonferroni-adjusted by dividing through the number of comparisons ($\alpha_{adj.}=\alpha/2$, ns $p\geq0.025$, * $0.025>p\geq0.005$, ** $0.005>p\geq0.0005$, *** $p<0.0005$). *Asterias densities* were (log+1)-transformed. Multi-homoscedasticity and -normality was checked using a modified Hawkins-test (Johnson & Field 1993).

source of variation	Pillai Trace	F	Hyp. df	Error df	p	conclusion
depth	.9545	13.11	8	5	.0058	*
substratum type	.5498	0.7632	8	5	.6511	ns
depth*substratum type	.8746	4.359	8	5	.0608	ns

In contrast, in plots of the control experiment *Carcinus* was more abundant underneath roof cages on all 4 sampling dates (Fig. 3.10 b). Non-parametric comparisons revealed that these differences were significant on 3 out of 4 dates (Mann-Witney U-test without Bonferroni-adjustment, July 1993 p=0.0235, August p=0.0059, September p=0.0373). For *Carcinus* only, the introduced structure of the roofed cages led to an artefact. It is clear that the roofs attracted *Carcinus* since they provided shelter to the crabs on the open sand flats.

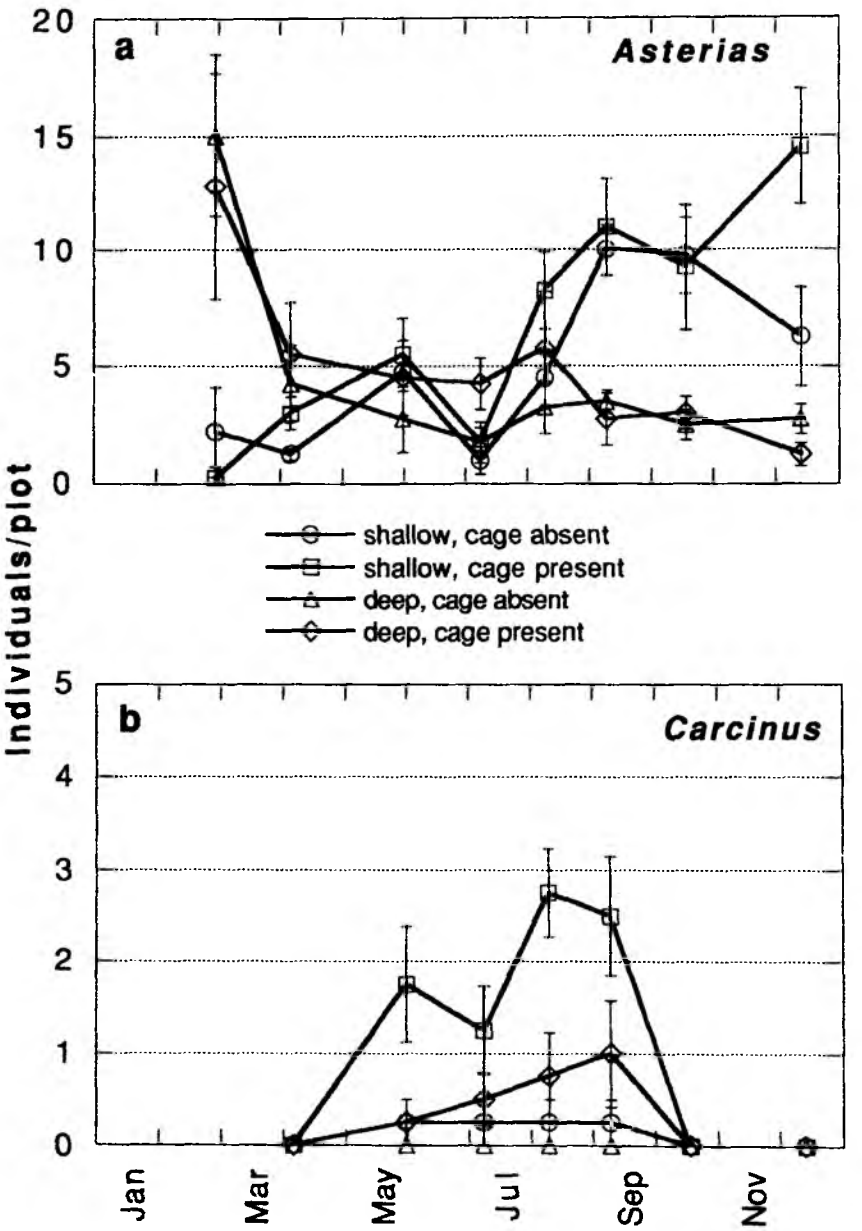


Fig. 3.10. *Mytilus* transplantation experiment: mean density ±1 SE (n=4) of (a) *Asterias* and (b) *Carcinus* on clumps of the control experiment.

Tab. 3.6. Mussel transplantation control experiment: two-way MANOVA on *Asterias* densities on 8 dates on all uncaged mussel clumps. Depth and presence or absence of a roof cage were experimental factors. Substratum type was always vexar mesh. See Tab. 3.5 for further details.

source of variation	Pillai Trace	F	Hyp. df	Error df	p	conclusion
cage present/absent	.6486	1.154	8	5	.4577	ns
depth	.9602	15.063	8	5	.0042	**
cage pres/abs*depth	.6168	1.006	8	5	.5223	ns

Drift of transplanted clumps. In contrast to the insignificant effects of substratum type on areal growth, the presence or absence of a stable substratum (mimicked by vexar meshes) had an overwhelming influence on the drift of clumps. Fig. 3.11 summarises drift events and distances of the transplanted mussel clumps ranging from 20 cm to 12 m. The presence of a vexar mesh as well as transplantation to 6 m depth completely prevented drifting. Therefore, only clumps which were transplanted onto sand in 2 m depth are shown. All 8 individual clumps of this treatment drifted at least once throughout the experimental period. In total, 22 drift events further than 20 cm were recorded. During the storm on October 10, 1993, 4 clumps could not be relocated. It is likely that they were dislodged over a distance >20 m. In 6 out of 22 cases (27%), drift of a clump was terminated after rolling into a *Zostera* or *Zostera/Mytilus* mixed patch. The influence of *Zostera* will be further discussed in chapter 4.

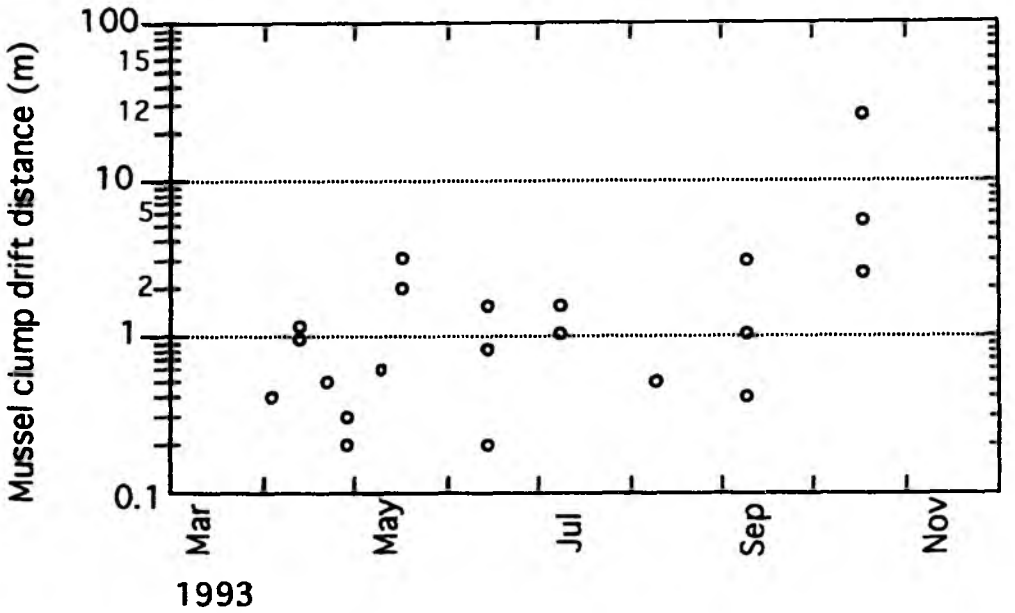


Fig. 3.11. Drift distances (log-scale) of 8 transplanted *Mytilus* clumps in 2 m depth on sand. Clumps attached to vexar meshes and those in 6 m depth are not shown since they never drifted. On October 18, 1993, six days after a strong storm (Bft. 10), 4 clumps could not be re-allocated and probably drifted further than 20 m.

Predation impact of *Asterias* vs. *Carcinus*. On three dates, recently opened mussels of the transplanted clumps were carefully examined for the presence of broken or intact shells. On March 10, 1993, all 50 mussels examined were eaten by *Asterias*. This was expected, since crabs were absent in the area during that time of the year. The following two censuses were done during summer when crabs were present in the experimental plots (Fig. 3.9 and 3.10). On June 26, 1993, 8.2% (8 out of 97) and on August 20, 16.5 % (23 out of 139) of recently opened *Mytilus* were eaten by crabs. Since their abundance on the experimental plots decreased markedly in September 1993, no further census was done later in the year.

On August 20, 1993, the proportion of crushed vs. undamaged opened mussels was assessed in all open plots. This enabled me to test whether the increased density of crabs underneath the roof cages resulted in a higher predation impact on the clumps in these same cages. Underneath roof cages, 8 of 36 mussels (22%) and on 16 open plots, 15 of 103 mussels (14.5%) were eaten by *Carcinus*. These proportion differences were found to be non-significant (χ^2=1.133, df=1, p=0.287). Thus, although *Carcinus* was attracted by roof cages, the increased density in these plots had no influence on the actual predation impact.

3.4 DISCUSSION

On soft substrata, the introduction of cages to exclude certain predator species has often produced severe cage artefacts (Arntz 1977). Careful experimental design and procedural controls have been proposed to minimise these risks (Virnstein 1978, Hulberg & Oliver 1980). During this study, I chose roof cages to test for potential cage artefacts. *Asterias* abundances were completely unaffected by their presence. Likewise, no evidence for cage artefacts was found in the control experiment for the response variable mussel clump area. Only crabs were more abundant underneath the cages. However, as could be detected, this did not alter the response in mussel clump area which was the variable I was primarily interested in.

The factors "presence/absence of predators" and "water depth" were found to interact with each other. However, this was statistically significant only in the MANOVA whereas the ANCOVA revealed that both factors were significant only as main factors. A thorough look into the data (Fig. 3.8 b) reveals that this differences in the outcome of both analysis types is due to differences in the mean initial clump area among treatment combinations. Since for example, the ANCOVA accounts for the lower starting area in deep clumps without predators, their area increase until December 1993 is significantly higher compared to the deep mussel clumps with predators.
Although the multivariate analysis without considering the covariate is obviously not fully appropriate I included this type of analysis because the underlying hypothesis being tested is different from the univariate ANCOVA. While the MANOVA tests the effect of experimental factors during the whole study period, the ANCOVA analyses effects on the last sampling date only.
Several authors claim not to consider main effects if an interaction is significant (e.g. Underwood 1981). However, in the multivariate analysis, main factor interactions would be non-significant if I could analyse the data with the more appropriate type of analysis, i.e. an analysis of covariance. Furthermore, all treatment means comparisons on parts of the data set using ANCOVAs and MANCOVAs revealed that both factors, depth and predators, showed significant effects in combinations with all levels of the other factor. That is, in all plots with predators, the growth of clumps was lower in 6 m

depth compared to the shallow treatments. Likewise, in both depths, the presence of predators was found to have a negative influence on clump area in open plots. The effect of predator exclusion was, however, much more pronounced in shallow water. Therefore I agree with Howell (1992, p.391) who states that it is perfectly legitimate to discuss main effects if the interaction only changes the magnitude of the main effect into the same direction.

However, no matter if the interaction "presence/absence of predators*water depth" is statistically significant, in shallow waters predation has obviously a much stronger effect than in 6 m depth. Statistically speaking, the ANCOVA suggests that both factors exert only additive effects on shallow clumps without predators while effects are multiplicative according to the MANOVA.

Why had predator exclusion a much stronger effect in 2 m compared to 6 m depth? Young mussels (10 to 30 mm) which contributed substantially to the 6-fold clump area increase in shallow treatments did not survive in any of the plots in 6 m depth, whether with or without predators. As a consequence, the large area differences between clumps with and without predators which were observed in 2 m depth could never occur. I hypothesise that in 6 m depth, young mussels inside the cages were smothered and suffocated by the markedly higher siltation compared to 2 m depth. In Kiel Fjord in 6 m depth, the exposure to wave induced water movement is greatly reduced. Additionally, the experimental site FO is completely protected against swells coming from the open Kiel Bight. Since tidal currents are absent in the area as well, the depth gradient of increased sedimentation is rather steep at FO. This is illustrated by observations made on the vexar nets: At the end of the experimental period, they were buried under 2-4 mm of silt. It is likely that small mussels hidden in the interstices of adults did not survive smothering by this high sedimentation. This is in concordance with results from the recruit samples taken on mussel aggregations in 6 m depth (chapter 2). Mussel spat was always rare compared to shallower depths. On mussel beds in 6 m, intermediate size classes are almost absent (Fig. 3.6), further suggesting that recruit survival is poor in 6 m.

A second possible explanation is that mussel recruits were eaten by small (<3 cm in diameter) seastars which were abundant on both open and caged deep plots. These small *Asterias* were not excluded by the 6x6 mm wire mesh openings of the cages. In contrast to the deep treatments, they were virtually absent in 2 m depth.

Although crabs are reported to control *Mytilus* distribution at some places (Kitching et al. 1959), I suggest that in Kiel Fjord, crabs contribute little to the total predation impact on mussels. First, *Carcinus* was only prominent from June to September, probably migrating to depths below 6 m during autumn and winter (Naylor 1962). Likewise Walne & Dean (1972) found a significant feeding impact of *Carcinus* from May to September only in Menai Street, Wales. Second, all area reductions of clumps occurred when crabs were absent from clumps, yet during the same period, *Asterias* densities were the highest during the experimental period.
Third, during the period when *Carcinus* was present on mussel patches, the proportion of mussels preyed on by crabs vs. preyed on by seastars was only 9 and 16.5%, respectively. This is in concordance with the non-significant effect of presence of roof cages on clump area. Although crabs were more abundant underneath roofs compared to completely open plots, this obviously did not result in an increased predation impact.

Although water depth moderately suppressed clump growth, this was not due to an increased predation pressure with depth. *Asterias* densities on natural beds were not significantly different among 2 m and 6 m depth.
Furthermore, the results of the statistical analysis (MANOVA) on *Asterias* densities on transplanted clumps revealed that Asterias was even more abundant in 2 m compared to 6 m depth. However, although being statistically significant, the absolute density difference of 0.2 ind/0.25 m^2 is probably biologically insignificant. This result was unexpected since for seastars, the risk of being dislodged by waves is markedly enhanced on soft substrata. In Kiel Bight, seastars can often be found washed onto the shore after storms (personal observations). This is concordance with diving observations made on stormy days. Frequently I observed dislodged *Asterias* which obviously had lost contact to the sandy substratum. However, the exposure found at the chosen depth of 1.8 to 2.0 m is obviously not enough to exert a significant effect on *Asterias* density. Furthermore, *Asterias* seems to exhibit behavioural responses which decrease its risk of being dislodged. During storms, *Asterias* never dwells on sand and prefers *Mytilus* beds possessing a current baffling *Zostera* canopy (Fig. 4.2).
The most detailed studies on the predation impact of seastars on mussel distribution were done in the intertidal zone. On rocky shores, the deeper

distribution limit of mussels is often set by seastar predation (Paine 1971, Menge 1976, Menge 1979, Christie 1983). In one of the few studies which were conducted in the subtidal zone, Himmelman & Dutil (1991) attributed the absence of blue mussels in the Gulf of St. Lawrence to depths below a few meters to predation by the seastars *Asterias vulgaris* and *Leptasterias polaris*. Both asteroids are scarce in the very shallow subtidal. In Kiel Fjord, however, mussel depth distribution is rather limited by the supply of drifting mussel aggregates since recruitment by settlement is poor below 5 m depth (chapter 2).

In the Baltic, diving ducks, especially the common eider (*Somateria mollissima*) may also exert a considerable feeding impact on mussel beds (Kirchhoff 1979, Kautsky 1981). However, they prefer mussel beds in the open Kiel Bight (Meißner 1992) and were seldom present at the experimental site.
In the central Baltic, flatfishes were reported to feed on blue mussels (Kautsky 1981). Fishes, which may consume mussels, were generally rare at the site. During two nocturnal dives, eelpout (*Zoarces viviparus*) and dab (*Limanda limanda*) were observed. The qualitative analysis of gut contents of 6 dabs of 22-38 cm length caught in August 1993 revealed that none of them had fed on adult or juvenile mussels, although the latter were abundant during that period. Instead, their stomach content consisted entirely of juvenile cockles (*Cerastoderma edule*).
Having grown beyond a size of approximately 5 cm, *Mytilus* individuals are almost safe against predation by *Asterias* (Photo 2). In laboratory feeding experiments, *Asterias* never fed on mussels beyond 5 cm in size as long as smaller adults were present. Only seastars which were larger than 12 cm in diameter were able to open large mussels, but they would only do so in no-choice experiments. Furthermore, seastars above 10 cm in diameter are scarce at the experimental site. In Lough Ine, Ireland, Kitching et al. (1959) and Ebling et al. (1964) found only very large mussels in the subtidal zone and hypothesised that they attained a refuge by body size. Paine (1976) observed a similar refuge from predation by size in the *Pisaster-Mytilus californianus* interaction. He only found few large mussel individuals subtidally where seastars are abundant and able to feed independently of tidal level.

In contrast to predators and water depth, the third main factor "substratum

type" had no influence on patch areal extension. Yet stable substratum, experimentally mimicked by vexar nets, had an overwhelming influence on *Mytilus* clump dispersal. Detachment and subsequent drift of mussel clumps was completely prevented by the presence of a stable substratum.
Contradictory to several studies which emphasise the role of physical disturbance for mortality of mussel patches on rocky shores (Harger & Landenberger 1971, Suchanek 1978, Paine & Levin 1981, Witman & Suchanek 1984, Denny 1987, Witman 1987), wave and current induced transport of clumps was found to be an important means of mussel dispersal at the experimental site. A total wet weight of some 20 kg of mussels was found caught in the collector fence during a period of one year, corresponding to approximately 50 clumps of an average size of 300 cm^2. Following the drift of the marked clumps of the transplantation experiment further supports the role drifting clumps may have in dispersal. All replicates of the treatment "2 m depth*predators present*sand" were lost at least once from their original position through physical disturbance. The majority of clumps could be re-allocated and had not drifted into unfavourable conditions. I hypothesise that at least some of the clumps would have give rise to the formation of new mussel patches. This is in concordance with observations made at another sheltered soft-bottom site in the Wadden Sea. In Königshafen, Sylt, (Thiel & Reise 1993) found a similar dispersal of mussel clumps of the same size range as in this study

On transplanted clumps, seastar densities varied markedly throughout the year. From February to April 1993, high seastar abundances led to an area decrease of mussel clumps in 6 m depth. Later in the year however, the seastar density decreased in 6 m depth and there was a complementary increase in shallow waters. The reasons for this remain speculative. It may be that *Asterias* sought shelter in deeper water from the very strong physical disturbance during January 1993 when three storms hit the experimental site.
It is well known that seastar densities vary markedly in time and space. In their review on seastar feeding biology, Sloan & Aldridge (1981) cite 12 references which describe mass aggregations of *Asterias*. During the study period, such aggregations of 10s of meters were also observed in the adjacent Kiel Bight. On October 29, 1992, an extended seastar front of at least 100 m in length and 5-10 m width preyed upon a subtidal mussel bank in 5.5 m depth at the entrance of Kiel Fjord (Pos N54°57,3' E10°13,0'). Only empty mussel shells

were left behind the seastar aggregation in which densities up to 800 ind/m^2 were found. In contrast to previous reports on mass aggregations which always reported them to occur during periods of warm water, in our case water temperature was only 8°C.
During the study period I recognised a second aggregation on July 29, 1993. *Asterias* ranging in density between 240 and 480 ind/m^2 led to a complete mortality of an one-year old mussel cohort (20-35 mm length) at Karlsminde (Pos N54°29,9' E9°57,5') in depths between 3 and 10 m. Therefore I suggest that massive feeding events are more common in structuring subtidal mussel beds than previously thought. These extreme biological disturbances are rare events sensu Gaines & Denny (1993), having a low chance of occurrence but a high impact on the community. In conclusion, I recommend great care in generalising the results of a one year predator-exclusion experiment for other years since fluctuations of seastar abundances in time and space appear to be very high.

On the transplanted clumps a predation caused areal decrease occurred only twice: during March in 6 m depth and during September/October 1993 in shallow plots. The number of predators which was necessary to produce a feeding impact which was higher than growth of clumps corresponded neatly to the expected feeding activity of seastars at different ambient water temperatures. In water of only 4°C, 14±1.9 individuals per clump were necessary to lead to a areal decrease whereas densities between 7.4 to 8.8 ind/clump were sufficient in 12°C warm water during September 1993. The latter water temperature falls within the range of the peak feeding rate of *Asterias* which is between 10 and 13°C (Hancock 1955, Hancock 1958). However, my observations demonstrate that a destructive feeding of *Asterias* on mussel beds is also likely to occur during the cold water season.

In Kiel Fjord at FO, *Asterias* densities regularly attained similar levels to those found during mass invasions in the open Kiel Bight that were destructive for mussel beds. In February 1993, 35 ind/0.25 m^2 were found on mussel beds in 2 m depth. On transplanted clumps in March and October 1993, 8 to 13 ind/clump, corresponding to 40 to 65 ind/0.25m^2 (corresponding to 160 to 260 ind/m^2) were present. How can mussel beds develop in Kiel Fjord despite such high abundances of potent predators, namely *Asterias*?
A similar paradoxical situation was described by Petraitis (1987, 1991) for

sheltered sites of the rocky intertidal in Maine, north-west Atlantic. Here, *Mytilus* is equally abundant at exposed and very sheltered sites. Dogwhelks and crabs are supposed to control *Mytilus* abundance under moderately exposed conditions (Menge 1976, 1978). These predators are absent or less efficient at exposed sites due to wave action. However, at sheltered sites predators are abundant as well as blue mussels. Petraitis (1987) proposed two hypotheses for this apparent contradiction: (1) the predators are outnumbered by the extremely high recruitment of mussels (2) chance effects lead to establishment of *Mytilus* patches which then are self-sustaining.

Both hypotheses can be applied to the situation found at FO. First, recruitment in the shallow water was high in both study years. Peak densities of mussel settlement on artificial substrata was 80,000 ind/131 cm^2 and 15,000 ind/131 cm^2 in 1992 and 1993, respectively (see chapter 2).

Petraitis' second hypothesis is also met at the site. Stochastic drift events by physical disturbance of mussel patches were found to be an important means of dispersal. These clumps consist of a matrix of larger mussels which are already much less susceptible to predation than are young individuals. In fact, none of the transplanted clumps died from predation over a period of one year. The second hypothesis states implicitly that, once mussels have attained a critical size, they are relatively safe against predation. This is in concordance with the present investigation. Mussels larger than 50 mm were never fed upon in laboratory trials and seldom in the field. Thus, according to Petraitis (1987), both conditions are met for allowing the establishment of mussel patches at a sheltered site with abundant predators such as Kiel Fjord.

Chapter 4
Mixed *Mytilus/Zostera* stands I: effects of eelgrass on mussel distribution

4.1 INTRODUCTION

In Kiel Fjord a higher proportion of mussel beds occurs associated with *Zostera marina* than in pure stands on sand (Fig. 4.1, 68% and 84% covers at FO and MOE, respectively). At the same time, uncolonised sandy patches as potential substrata for mussel beds are more abundant than are *Zostera* meadows (Photo 6). This suggests that *Zostera* may have a major positive influence on the ecological-scale distribution of *Mytilus edulis*.
It is well known that the abundances of infaunal as well as of epifaunal organisms are often higher within seagrass meadows compared to adjacent sand flats (Weinstein & Brooks 1983, Orth 1992). Bivalve densities have been found to be higher as well (Peterson 1986). In a recent review, Orth (1992) identifies 5 main hypotheses for this higher abundance: (1) habitat complexity and active habitat selection by vagile organisms (2) refuge from predation (3) stable substratum (4) increased recruitment due to hydrodynamic effects on larval supply or lower post-settlement mortality and (5) increased food supply. This study will focus on hypothesis (2), (3) and (5). Hydrodynamic processes which affect settlement rates into the meadow as well as higher post-settlement survival (hypothesis (4)) have been discussed in chapter 2.

In several studies it was shown that prey organisms find a refuge from predation inside seagrass meadows. Often the predation success of epibenthic and endobenthic predators is reduced through the above-bottom (Heck et al. 1981, Weinstein & Brooks 1983, Bell & Westoby 1986) or below-bottom-architecture of the meadow (Brenchley 1982). Predation on clams (Peterson 1982) and other infaunal bivalves (Blundon & Kennedy 1982) was found to be significantly reduced by the dense root/rhizome mat of *Zostera*. Caging experiments which were designed to test the impact of predation on infaunal organisms revealed insignificant effects of predation inside meadows compared to adjacent sand flats, suggesting that the meadow provides a refuge from predation (Summerson & Peterson 1984).

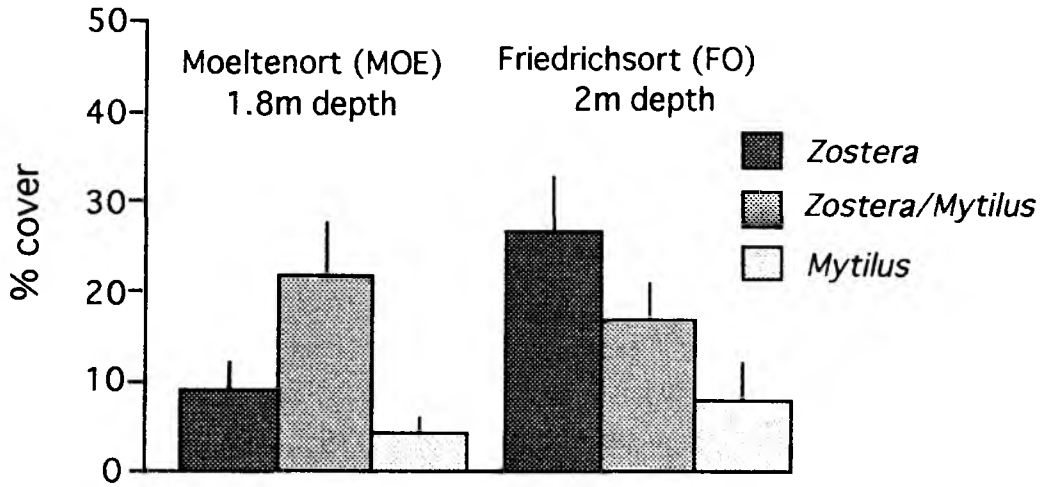


Fig. 4.1. Substratum coverage +1 SE at Friedrichsort (FO) and Möltenort (MOE) on March 20 and 25, 1993, respectively. 16 quadrates of 1x1 m were placed at random within a strip of 100 m length and 10 m width parallel to the shoreline.

At my study sites, the seastar, *Asterias rubens*, and the shore crab, *Carcinus maenas*, are prominent predators, which are known from the literature to be able to control *Mytilus* distribution (*Asterias*: Himmelmann & Dutil 1991, Seed 1993 and references therein. *Carcinus*: Ebling et al. 1964, Walne & Dean 1972). *Asterias* especially is very abundant in Kiel Fjord, ranging in density from 16 to 140 ind*m^{-2}. A different feeding impact among patches with or without *Zostera*. could be either due to altered predator densities and/or different feeding performances of predators.

Therefore, one objective of this study was to test whether the abundance of both predators varied dependent on presence or absence of *Zostera*. Additionally I examined whether the proportion of *Asterias* feeding on adult mussels differed among adult mussel beds in presence and absence of *Zostera*.

A second important source of mussel bed mortality which could be mediated by *Zostera* is the susceptibility of mussels to physical disturbance. Seagrass meadows are known to baffle currents and wave induced water movements due to their canopy friction (Fonseca et al. 1982, Fonseca et al. 1983, Fonseca & Fisher 1986, Gambi et al. 1990). Consequently they increase the sediment

stability and have a beneficial effect on the endobenthic community living below the canopy (Orth 1977b). When occurring on soft substrata, blue mussels are especially vulnerable to storm induced dislodgement, since the individuals are not fixed to primary, stable substratum but attached only to conspecifics. In the German Wadden Sea (North Sea), physical disturbance has been identified as a major structuring factor for intertidal mussel beds on a large scale of 100s of meters to kilometers (Nehls & Thiel 1993). In the western Baltic, storm impact on mussel beds has been found down to a water depth of 12 m (Brey 1989, Meißner 1992). However, in the Wadden Sea on a local scale, new mussel patches are frequently established by drift of dislodged mussel clumps (Thiel & Reise 1993). In Kiel Fjord, this mode of dispersion represents a major source of new patch formation (see chapter 3). Mussel aggregates are abundant in open Kiel Bight as well (personal observations). A second objective was therefore to find out whether (1) presence of *Zostera* decreases mussel bed mortality caused by physical disturbance and whether (2) presence of *Zostera* increases the chance for a clump to establish a new mussel bed.

A third process which potentially affects distribution of mussel beds may be an increased areal growth of *Mytilus* patches when co-occurring with *Zostera*. Patch growth is a function of recruitment onto existing patches and of growth of recruits and adult individuals of the patch. In chapter 2 it was shown that *Zostera* enhances mussel recruitment. Here, I restrict discussion to the question whether individual growth of *Mytilus* adults is different among beds in presence or absence of *Zostera*. Mussel growth may be affected positively or negatively by the presence of a seagrass meadow. Comparing the sizes of the suspension feeding bivalve *Mercenaria mercenaria*, Peterson et al. (1984) found a population structure which suggests a higher growth rate of this suspension feeding bivalve in the presence of a seagrass canopy. I estimated mussel growth rates from lengths distributions sampled on natural patches and from length distributions and areal extensions of mussel transplants placed on sand flat and into *Zostera* meadow.

4.2 MATERIAL AND METHODS

Estimating predation pressure. Seastars were counted and their feeding performance recorded as described in chapter 2. In brief, the individuals in quadrats of 50x50 cm were turned upside down, their prey item recorded and the body diameters were measured. The censuses were done on 9 dates (from June 1992 to October 1993) in 6 pure *Mytilus* patches and *Zostera/Mytilus* mixed patches. Patches were selected within a strip running 50 m parallel to the shoreline. Within the pre-selected patch, the sample area was allocated haphazardly by tossing a frame from 1 m height onto the sea-bottom. *Carcinus* individuals were counted together with *Asterias* in plots of 50x50 cm, recording only individuals above 2 cm carapace width.

Asterias densities were compared among substrata with a 2-way (2x9) ANOVA including 9 sampling dates. At 5 dates only, *Asterias* biomasses, which were calculated from their diameters using a regression equation ($AFDW(g) = 0.00452 * diameter(cm)^{2.667}$, $r^2=0.92$, n=42), were compared in a 2-way (2x5) ANOVA with the same factors.

Subsequent to the ANOVAs, linear contrasts were performed to identify group means which were responsible for significant interaction effects. Their significance levels were Bonferroni-adjusted because the data were already analysed as part of a larger ANOVA design in chapter 2.

For only very few seastars fed on mussels >30 mm length, substratum dependent differences in feeding impact on these mussel size classes had to be analysed using the proportions of seastars feeding on a given size class pooled over all dates. These proportions were analysed by contingency tables (χ^2-tests).

Carcinus densities were compared among substrata by Mann-Witney U-tests because densities in the selected quadrate size (50x50 cm) were too low to perform a parametric test.

Mussel clump drift experiment. I tested the effect of presence of *Zostera* on drift of mussels by transplanting clumps onto bare sand and into *Zostera* meadow.

In February 1993, 8 mussel clumps of 250 to 350 cm^2 area were transplanted. Their drift distances were recorded in approximately 4-weekly intervals. Sampling started on March 23, 1993. After each re-allocation, the clump was

replaced to its original position which was marked with a stake (Photo 8). The recording of drift distances was terminated on December 14, 1993.

Effects of physical disturbance on mussel beds. I tested the hypothesis that associations of *Zostera* and *Mytilus* are more stable in the face of physical disturbance than pure stands of blue mussels by comparing the loss of cover on permanent quadrats due to natural disturbance events among mussel beds with and without eelgrass. Permanent plots of 50x50 cm were marked within one narrow depth range (1.80 to 2 m) and followed through time. Since it is unpredictable when major disturbance events occur, I determined mussel cover every two months. Predation can be excluded as a major source of loss of cover since a mussel clump transplantation experiment running during the same time period revealed that none of the shallow clumps under access of predators decreased in cover (see chapter 3).

Two natural experiments were analysed. At FO, mussel coverages in 6 permanent *Zostera/Mytilus* and *Mytilus* plots were sampled on November 18, 1992 and on February 5, 1993. Between these dates, a series of 3 severe storms (Beaufort 11 to 12) from southerly to south-westerly directions represented a major natural disturbance event.

In September 1993, a new set of permanent quadrats of the same size (50x50 cm) was set up at 2 sites in Kiel Fjord, FO and MOE. At FO, 6 plots and at MOE, 7 plots of pure *Mytilus* and *Zostera/Mytilus* were marked. This set up was different from the previous one in that an experimental manipulated treatment was added by removing the eelgrass canopy from existing *Zostera/Mytilus* associations. Artificial pure mussel patches were created by pulling out all *Zostera* shoots in *Zostera/Mytilus* plots plus a strip of 25 cm around the plot. All plots were selected haphazardly within a strip of 50 m (FO) and 150 m (MOE) length parallel to the shore. Allocation of treatments to *Zostera/Mytilus* plots was done at random.

By chance, at both sites the last sampling date before the disturbance event was on October 10. On October 11, 1993, a severe storm (Beaufort 10) from south/south-westerly direction together with a sea level decline of 1.10 m below MWL provided a natural disturbance experiment. Post-disturbance sampling was done only a few days after the disturbance on October 13, 1993 at FO and on October 18, 1993 at MOE. Hence, all observed cover changes are due to physical disturbance and no other mortality source.

Sampling was done by underwater photography with the aid of a frame with flash. The colour-slides were processed into video-signals with a S-VHS video camera and analysed for coverage on a NeXT-computer with image analysis software (Huckriede 1992). Forty randomly generated dots were laid over the sample image. The points touching mussels were counted and percent cover calculated. Repeated determinations revealed an error <5 %.

No statistical analysis was applied to the data of the drift experiment, since differences in numbers and distances of drift events between clumps lying within *Zostera* meadow compared to those outside were very large. The effects of physical disturbance on established mussel patches were tested with two ANOVAs. One (2x2) ANOVA used data only taken at FO and analysed the effects of the factors "time interval" (i.e. November 1992 to February 1993 or October 1993) and "presence/absence of *Zostera*" on mussel cover after the disturbance event (data set (a)). A second (2x3) ANOVA was performed on mussel cover sampled at both sites in October 1993 and tested the effects of the factors "site" and "substratum type". In this design, "substratum type" had 3 levels: (1) *Zostera* canopy was absent due to experimental removal, (2) *Zostera* was originally absent, i. e. substratum was a pure *Mytilus* patch, and (3) *Zostera* was present (data set (b)). Originally it was planned to analyse the changes in mussel cover with ANCOVA models to account for the variation in initial coverage which was not always 100% but ranged between 75 and 100%. However, ANCOVAs were not justified since interactions between factors and the covariate (i.e. pre-disturbance cover) were significant and hence the assumption of homogeneity of slopes was not fulfilled. Therefore, I had to restrict analysis to ANOVAs which compared mussel coverage on the post-disturbance sampling date. Since the same cover data (at FO in October 1993) were used for two ANOVAs, the significance levels in both analysis were Bonferroni-adjusted, i.e. divided by 2. Before performing ANOVAs I checked whether differences in *Mytilus* cover existed among treatments prior to the disturbance event. This was not the case for both data sets (Data set (a): $F_{(3,20)}=0.275$, $p=0.844$; data set (b): $F_{(5,33)}=0.424$, $p=0.83$). All cover data were angular transformed ($x_{trans}=\sin^{-1}\sqrt{x}$) and checked for homoscedasticity by Cochran's test.

Mussel size-distribution and patch growth. Growth of mussels in the presence or absence of *Zostera* was estimated from size distributions of adults which were either sampled in the field or obtained from mussel transplants. In

contrast to other investigations in the Baltic it was not possible to determine the age of the individuals using checkmarks or age rings of the shells (Kautsky 1982a).

Mussels were sampled with cores of 14 cm diameter (0.015 m^2) on April 29 and May 3, 1993 in FO (N=4), on May 10 in MOE (N=3) and between August 23 and 29, 1993 in FO and MOE (N=6). In the laboratory, all mussels ≥5 mm length were measured with a vernier calliper to the nearest 1 mm. The mussel population at both sites showed a bimodal size distribution (Fig. 4.5) Therefore, and to account for higher densities of juvenile mussels in the presence of *Zostera* (Fig. 2.3), adult mussels were defined as those individuals larger than 30 mm.

In March 1993, mussel clumps originating from a larger mussel patch with known homogeneous size distribution (Fig. 4.6) were transplanted haphazardly into *Zostera* patches and onto patches of pure sand within a strip of 15 m length in 2 m water depth. The mussels transplants which were placed onto sand were allowed to attached to polyethylene-mesh quadrats (40x40 cm, 10 mm mesh size). They were fixed with stakes into the sediment. This was necessary since non-attached clumps were easily dislodged by waves and/or currents (see drift experiment). The height of mussels above the ground was no more elevated than in clumps lying on the sand. I tried to choose clump sizes as similar as possible (between 200 and 280 cm^2). The mussel clumps within *Zostera* patches were at least 50 cm apart from the meadow edge and from each other. At the start of the experiment, I derived the initial length from 124 adult mussels sampled in the large source patch for the transplants. Juvenile mussels which were distinguished from those being older than 1 year by colouration of shell were omitted from the calculation of initial length. If there were any differences in initial size distribution between the clumps, I assumed that they were randomly distributed between the two treatments (presence or absence of *Zostera*).

On November 18, 1993 on each of the plots 10 mussels were selected haphazardly and measured in the field with a vernier calliper to the nearest mm. No destructive sampling of clumps was done since they had be followed over another 2 months. Only those mussels at the clump edges were measured, omitting those in the clump center, since individual growth is dependent on mussel position within a patch (Okamura 1986).

On 5 dates, patch area was sampled using a camera attached to a frame with flash. Clump areas were obtained by encircling the digitised colour slide using an image analysing software running on a NeXT workstation (Huckriede 1992).

For statistical analysis mussel lengths were log-transformed, and the success of the transformation was tested by Cochran's test. Nested ANOVA models were used with core or plot nested in the factor "presence or absence of *Zostera*". The observational length/frequency data obtained in April/May and August 1993 were analysed with two separate 2-way (2x2) nested ANOVA with site (FO or MOE) as additional experimental factor and core nested in both factors. For the observational data only, the mussel number in some cores was reduced to the smallest sample size using random numbers to achieve a balanced ANOVA design.

The effects of *Zostera* presence or absence on clump area were analysed with a one-way MANCOVA, using initial clump areas in April 1993 as covariate and treating each of the subsequent 4 bimonthly sampling dates as dependent variables. Since only 4 out of 8 mussel clumps were re-allocated after storm dislodgement in October, 3 clumps from the same source patch which had been transplanted at the same time onto vexar meshes were selected at random and added to the treatment without *Zostera*. This was justified since the presence or absence of stable substratum (vexar mesh) had no significant effect on clump area (Tab. 3.2 and 3.3). Sample size was reduced at random to n=7 to achieve balance of data since a clump area in *Zostera* got lost on one date. Clump areas were log-transformed. Multivariate variance homogeneity and normality was checked by a modified Hawkins-test (Johnson & Field 1993) on the adjusted data (after regression on the covariate). The differences of the medians of the A_{ij} vectors among both groups never exceeded the critical value of 0.85 given by Johnson & Field (1993) for balanced designs. Prior to the MANCOVA, a test of homogeneity of slopes was performed.

4.3 RESULTS

Predator densities. *Carcinus* was only found during the summer months. From June to October on 4 sampling dates (June 18, June 23, September 10, October 20), their densities were lower than 1 ind/0.25 m^2 except on June 23, 1993 when density in *Zostera* attained 1.8±0.76 ind/0.25 m^2. On June 18 and 23, abundances of crabs on adult mussel beds in the presence of *Zostera* were higher compared to pure mussel beds. However, Mann-Witney U-tests performed on each of the dates revealed that none of these differences were significant.

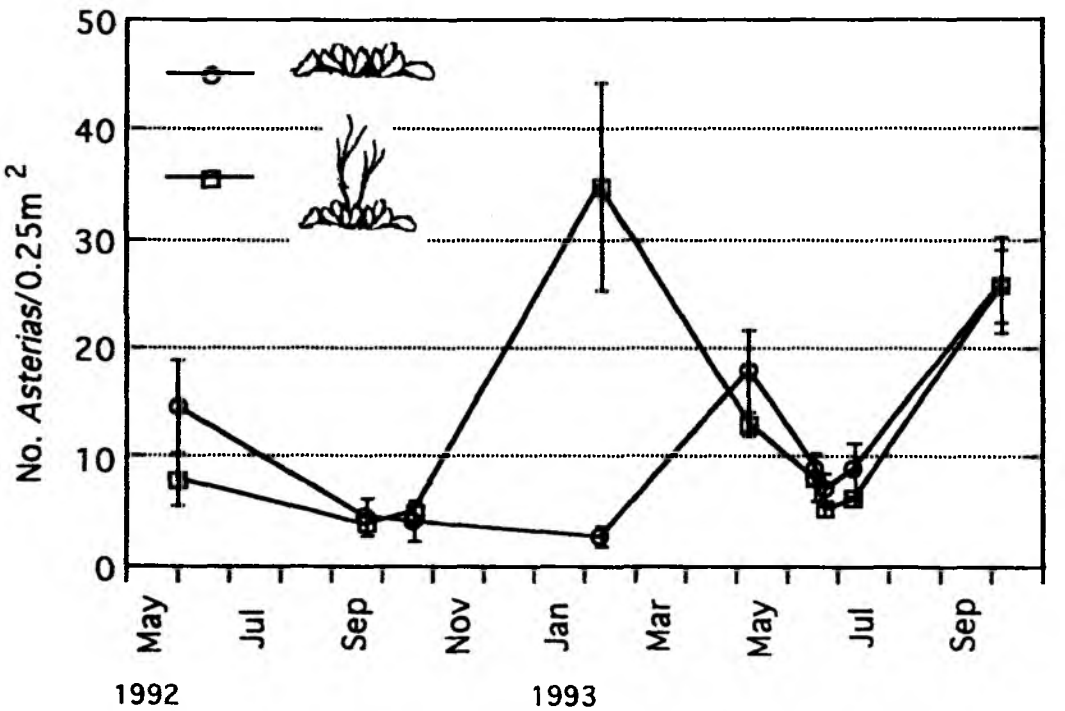


Fig. 4.2. Abundance of *Asterias* on mussel beds in presence (circles) or absence (quadrats) of *Zostera*. Error bars are ±1 SE, n=6 quadrats of 0.25 m^2.

Asterias was present on mussel beds throughout the year (Fig. 4.2). A (2x9) ANOVA comparing adult beds with and without *Zostera* canopy only, revealed that "presence or absence of *Zostera*" had no significant effect on seastar density (Tab. 4.1). However, the interaction "presence/absence of *Zostera**sampling date" was highly significant. A post-hoc means comparison

revealed that the significant interaction was produced entirely by the very high seastar densities under presence of *Zostera* on February 10, 1993 ($p<0.0001$, ***). If the February data were excluded from analysis, the interaction term is clearly non-significant ($p=0.9285$).

Tab.4.1. Two-way (2x9) ANOVA on the effects of presence or absence of *Zostera* and "sampling date" on *Asterias* density and biomass on adult *Mytilus* patches. Density was determined on 9 and biomass on 5 sampling dates, respectively. Biomasses were obtained from seastar diameters measured in the field using a regression equation between diameter and ash free dry weight. Sample size n=6 for each date and substratum. Counts were logarithmic (log) and biomasses (log+0.5)-transformed. Both data sets were checked for homoscedasticity by Cochran's test. Significance levels were Bonferroni-adjusted since parts of the data were in another ANOVA ($\alpha_{adj} = \alpha/2$, ns$\geq$0.025, * 0.025>$\alpha\geq$0.005, ** 0.005>$\alpha\geq$0.0005, *** α<0.0005).

density					
source of variation	**df**	**MS**	**F**	**p**	**conclusion**
Zostera present/absent	1	.1624	1.6571	.2013	ns
date	8	.9422	9.6162	<.0001	***
date*_Zostera_ present/absent	8	.4650	4.7459	<.0001	***
Error	90	.0980			
density					
Zostera present/absent	1	.1018	1.311	.2577	ns
date	4	1.1085	14.272	<.0001	***
date*_Zostera_ present/absent	4	.5131	6.607	.0002	***
Error	50	.0980			

A comparison of *Asterias* biomasses which were obtained from diameters using a regression equation gave the same results: the main effect of presence or absence of *Zostera* was non-significant, yet the interaction "presence/absence of *Zostera* "sampling date" was highly significant. Again, this was entirely due to the exceptional high densities *Asterias* showed on *Zostera/Mytilus*-patches in February 1993.

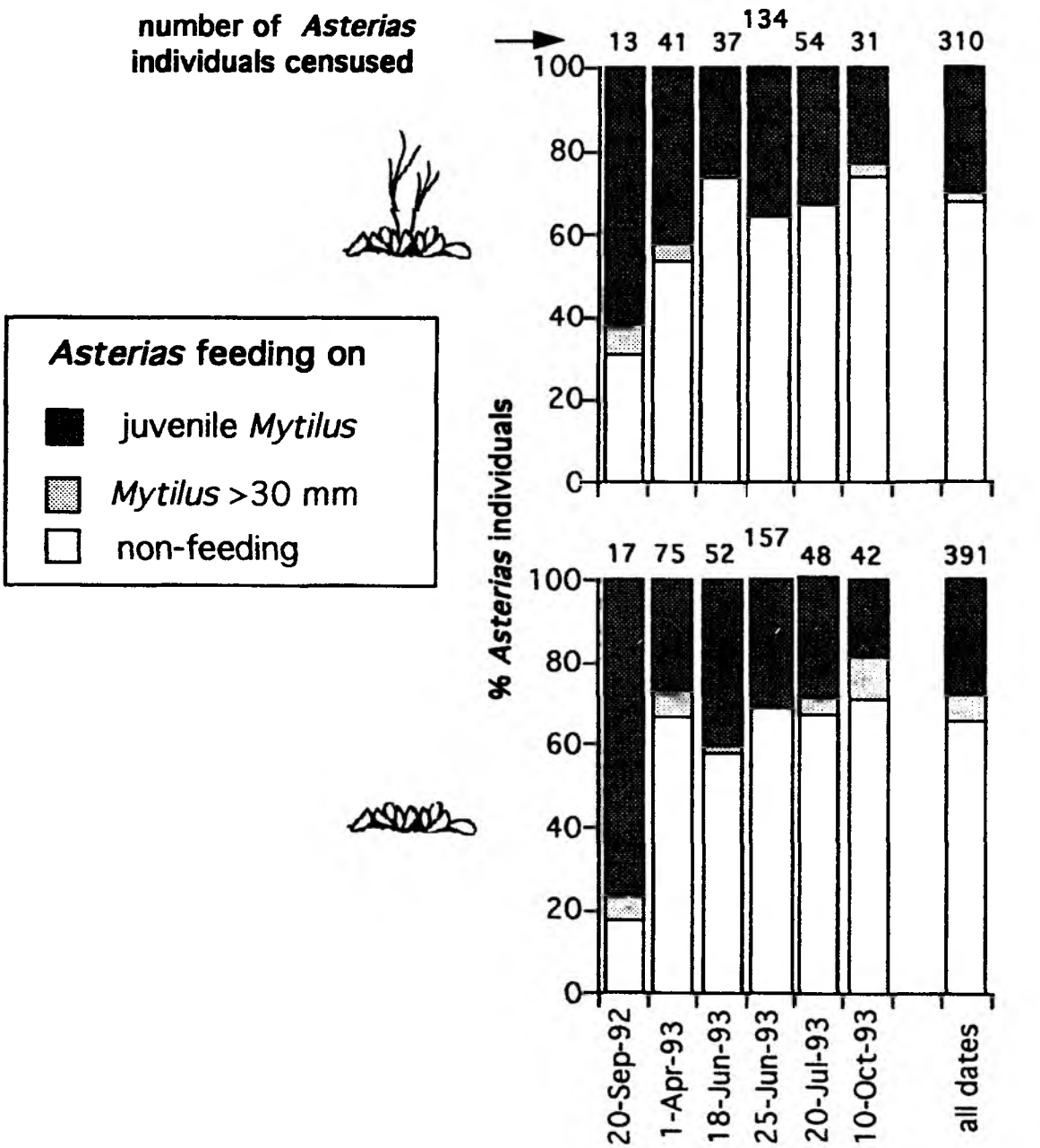


Fig. 4.3. Proportion of *Asterias* individuals found feeding on adult (≥30 mm) mussels on 6 dates on *Zostera/Mytilus* and pure *Mytilus* patches. All *Asterias* individuals in six 0.25 m^2 quadrats were censused.

Feeding performance. Fig. 4.3 shows the proportions of *Asterias* individuals which were found feeding on juvenile and adult (≥30 mm) mussels. The proportion of *Asterias* individuals feeding on juvenile (2 to 30 mm)

mussels have already been analysed in chapter 2. Here I compared only frequencies of *Asterias* preying on adult *Mytilus* individuals among mussel beds with and without eelgrass. A χ^2-test revealed that, in the absence of *Zostera*, a significantly higher proportion of all individuals present was feeding on adult *Mytilus* compared to *Zostera/Mytilus*-patches (χ^2=4.56, p=0.0381).

Drift of mussel clumps. Throughout the study period, mussel clumps which were transplanted onto sandy patches drifted away from their original position. In total, 22 drift events were recorded. Drift distances during approximately 4 weekly intervals ranged between 20 cm and 12 m for clumps in shallow water on sand. These data were already summarised in Fig. 3.11. In 6 out of 22 cases, drift was terminated after the mussel clump had rolled into a *Zostera* meadow. In contrast, only 2 out of the 8 clumps which were placed into *Zostera* patches drifted once for a distance of 10 and 20 cm, respectively, during the time interval from March 23 to April 7, 1993.

Effects of storm disturbance on mussel beds. The presence of *Zostera* significantly reduced loss of mussel cover due to wave induced disturbance (Fig. 4.4). The degree of destruction of the original mussel coverage (which was always near 100%) was substantial at both sites, ranging between 49% and 81% at FO and 17% and 42% at MOE in absence of *Zostera*.
In a first sub-experiment, two disturbance events in January and October 1993, respectively, were analysed at FO only (Tab. 4.2). "Presence/absence of *Zostera*" had a highly significant effect on mussel cover after the disturbance events. The interaction of time interval with presence or absence of *Zostera* was significant as well. Post-hoc means comparisons indicated that *Zostera* had no effect on loss of cover during storms in January 1993, i. e. pure *Mytilus* patches lost cover to the same extent as did mussel beds with *Zostera* canopy.

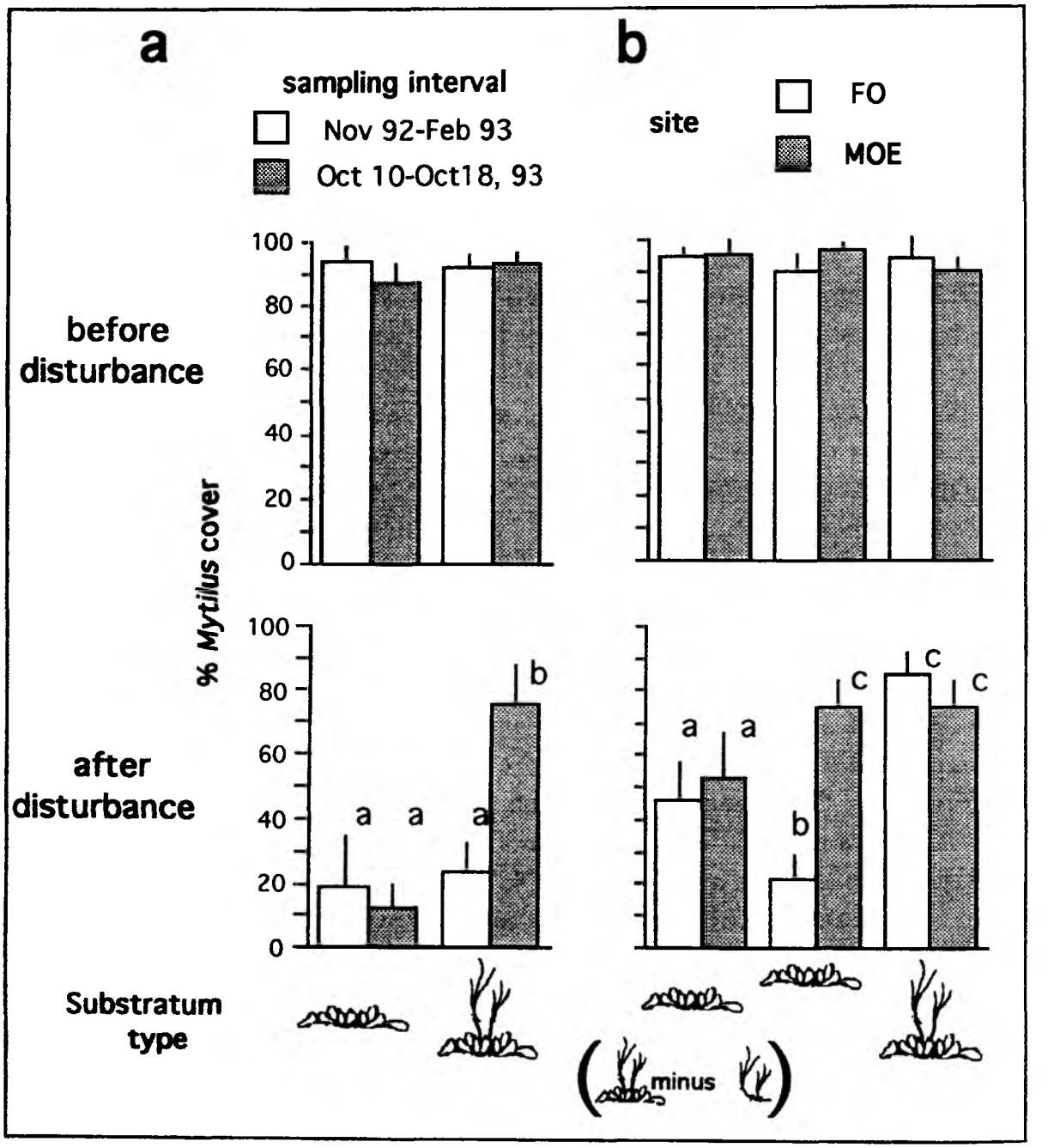


Fig. 4.4. Effects of *Zostera* on susceptibility of mussel beds to physical disturbance. Bars represent means (+1SE) of *Mytilus* cover in permanent quadrats before (above) and after (below) storm induced disturbance. Panels (a) compare two disturbance events among natural mussel beds and *Zostera/Mytilus* patches at FO only. Panels (b) compare effects of one disturbance event (October 1993) at two sites among pure mussel beds created by canopy removal, natural pure mussel beds and *Zostera/Mytilus* patches. Cover differences among treatments before disturbance were not significant. Letters indicate which treatment means differed significantly.

Tab. 4.2. Two-way ANOVA on the effects of "presence/absence of *Zostera*" and "time interval" on the loss of mussel coverage in permanent quadrats due to physical disturbance at FO. During 2 sampling intervals (November 22, 1992 to February 10, 1993 and October 10 to October 18, 1993) heavy storms hit the site. Prior to the disturbance, mussel cover ranged from 75 to 100%. However, no significant differences were found among groups. Significance levels were Bonferroni-adjusted since parts of the data (cover at FO in October 1993) were used for two ANOVAs ($\alpha_{adj} = \alpha/2$, ns$\geq$0.025, * 0.025>$\alpha\geq$0.005, ** 0.005>$\alpha\geq$0.0005, *** α<0.0005). Sample size n=6.

source of variation	df	MS	F	p	conclusion
time interval	1	.6387	3.3666	.0815	ns
Zostera present/absent	1	1.5718	8.2848	.0093	**
time interval*_Zostera_ present/absent	1	.8979	4.7330	.0418	*
Error	20	.077			

Tab. 4.3. Two-way (2x3) ANOVA: Analysis of effects of the factors "site" and "substratum type" on the loss of mussel coverage on permanent quadrats during one storm event on October 11, 1993. The factor "substratum type" had 3 levels: (1) *Zostera* was present (i.e. *Zostera/Mytilus* patch), (2) *Zostera* canopy had been removed from *Zostera/Mytilus* patches (3) mussel bed was naturally devoid of *Zostera* (Fig. 4.4). The design was slightly unbalanced in that 3 treatments had 6 and another 3 treatments had 7 replicates. For further details see Tab. 4.2.

source of variation	df	MS	F	p	conclusion
site	1	.5324	5.1122	.0305	ns
substratum type	2	.7395	7.1010	.0027	**
site*substratum type	2	.7123	6.8398	.0033	**
Error	33	.1041			

These results are in concordance with a second analysis on mussel cover data before and after a single disturbance event (between on October 10 and 18, 1993) now including both sites, FO and MOE, into analysis (Fig. 4.4 b, Tab. 4.3). A post-hoc contrast revealed that both treatments without *Zostera* had a significantly lower mussel coverage after disturbance compared to *Zostera/Mytilus* mixed stands. Approximately 50% of mussel coverage at FO and 42% at MOE were destroyed by the storm in October 1993 on plots which had received experimental removal of *Zostera*. A comparison of cover loss among *Zostera/Mytilus* patches and the experimentally produced pure *Mytilus* beds revealed, that the risk for mussels of being dislodged increased 11-fold at

FO and 3.5-fold at MOE after canopy removal. Besides a significant substratum effect on mussel cover, the interaction between substratum type and site was significant, too. Means comparisons by linear contrasts indicated that this interaction was significant since *Mytilus* cover of treatment "natural *Mytilus* patches at MOE" was not significantly different from cover in *Zostera/Mytilus* patches. In contrast, natural beds at FO suffered similar destruction than did experimentally produced mussel patches.
The main effect of site was almost significant, i.e. there was a trend of a higher loss of cover at FO compared to MOE.

Influence of *Zostera* on population structure and growth of *Mytilus*. Table 4.4 summarises the mean mussel lengths of natural mussel populations sampled on two dates at two sites, FO and MOE. The length/frequency distribution are shown in Fig. 4.5. No significant differences in adult mussel lengths among beds with *Zostera* compared to pure mussel beds were found in May and August at both sites, FO and MOE (Tab. 4.5 and 4.6).

Tab. 4.4. Mean lengths of *Mytilus* ≥30 mm at two sites (FO and MOE) in presence and absence of *Zostera*. SE = standard error, n = total sample size. For statistical analysis see Tab. 4.5 and 4.6.

site	FO						MOE					
Zostera	absent			present			absent			present		
	mean	SE	n	mean	SE	n	mean	SE	n	mean	SE	n
May	47.6	1.38	44	41.6	1.37	44	46.9	1.29	33	48.6	1.32	33
August	48.4	1.76	60	47.6	1.35	60	51.0	1.13	60	46.2	0.64	60

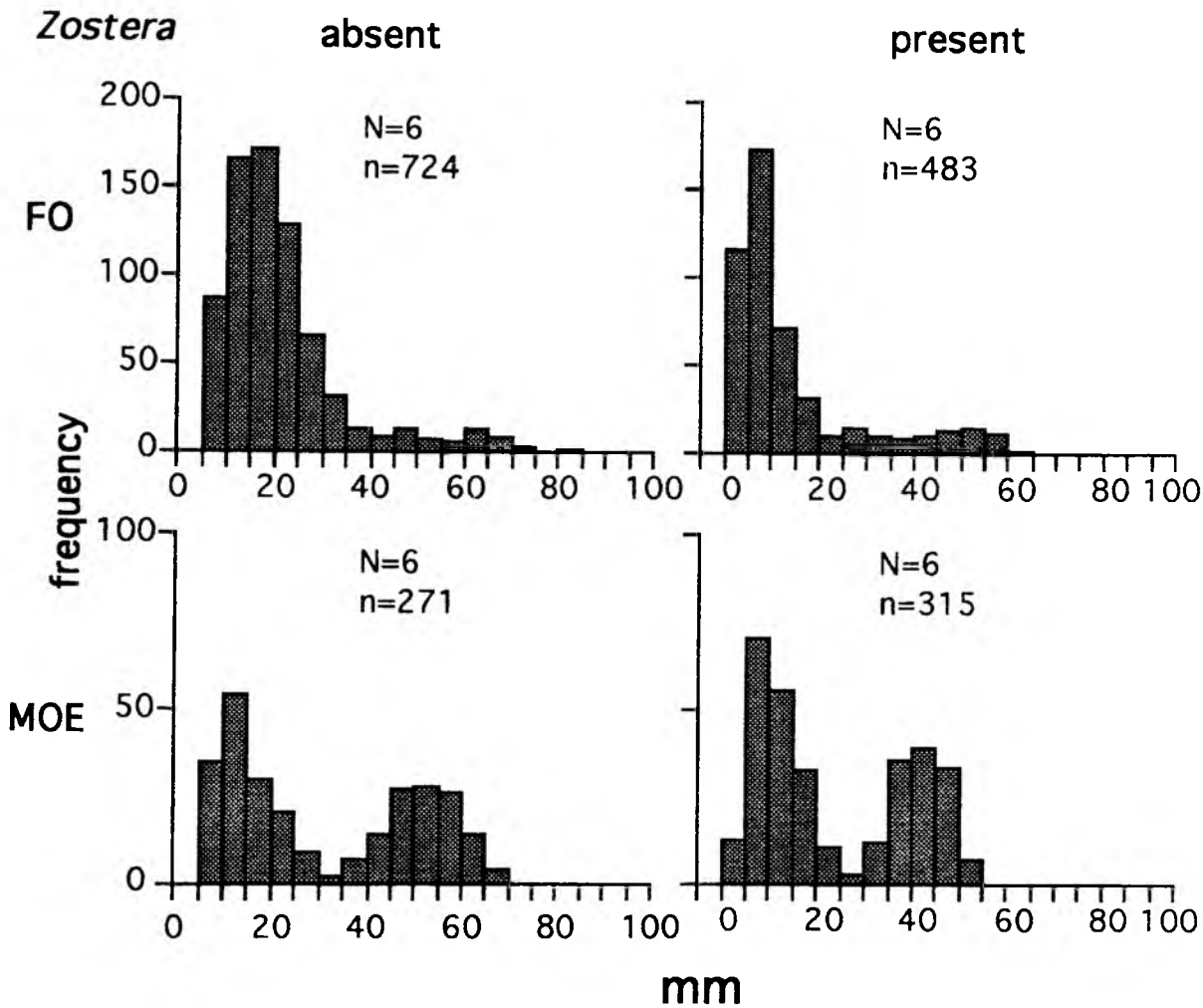


Fig. 4.5. Length/frequency distributions of natural *Mytilus* populations. Core samples (N=6) were taken between August 23 and 29, 1993 at two sites, FO and MOE in presence or absence of *Zostera*. Mussels smaller 5 mm were omitted. Number of mussels measured is given in each panel.

Tab 4.5. Two-way nested ANOVA: effects of site, presence or absence of *Zostera* and sample (nested in both factors) on *Mytilus* length obtained in April/May 1993. Eleven mussel lengths were chosen at random out of 4 core samples at FO and 3 samples at MOE, respectively. Only mussels ≥30 mm were included into analysis to account for different recruitment densities on both substrata. Lengths were log-transformed and checked for homoscedasticity using Cochran's test.

source of variation	df	MS	F	p	conclusion
site	1	.0432	3.7964	.0800	ns
Zostera present/absent	1	.0202	1.7734	.2125	ns
site*Zostera present/absent	1	.0519	4.5633	.0584	ns
sample (site*Zostera present/absent)	10	.0114	1.8438	.0583	ns
Error	140				

Tab 4.6. Two-way (2x2) nested ANOVA: effects of site, presence or absence of *Zostera* and sample (nested in both factors) on *Mytilus* length in August 1993. The lengths of 10 mussels were obtained at random out of each core sample. Number of cores N=6, thus total sample size was n=60. Only mussels ≥ 30 mm were included into analysis to account for different recruitment rates on both substrata. Lengths were log-transformed and checked for homoscedasticity by Cochran's test.

source of variation	df	MS	F	p	conclusion
site	1	.0130	.5911	.4510	ns
Zostera present/absent	1	.0227	1.0361	.3209	ns
site*Zostera present/absent	1	.0209	.9542	.3403	ns
sample (site*Zostera present/absent)	20	.0219	2.9629	.0001	***
Error	216	.0074			

Tab. 4.7. Nested ANOVA on *Mytilus* length with mussel clumps nested in factor "presence or absence of *Zostera*". In March 1993, mussel clumps originating from the same *Mytilus* bed were transplanted into *Zostera* patches and onto bare sand (N=6). On November 18, 1993 ten adult mussels were measured in each clump, thus n=60. Log-transformed data meet the assumptions of homoscdedasticity (tested by Cochran's procedure). See Fig. 4.6 for size distribution.

source of variation	df	MS	F	p	conclusion
Zostera present/absent	1	0.0896	12.434	0.0055	**
clump (*Zostera* pres/abs)	10	0.0072	2.0112	0.0389	*
Error	108	0.077			

However, mussel transplants stemming from the same mussel patch with known homogeneous size distribution showed a significantly greater length after having grown for 7.5 month on sand flat compared to those clumps situated within *Zostera* patches (Fig. 4.6, Tab. 4.7). The mean lengths ±95% confidence intervals were 52.1±1.72 mm and 46.1±1.8 mm on sand and within *Zostera* meadow, respectively.

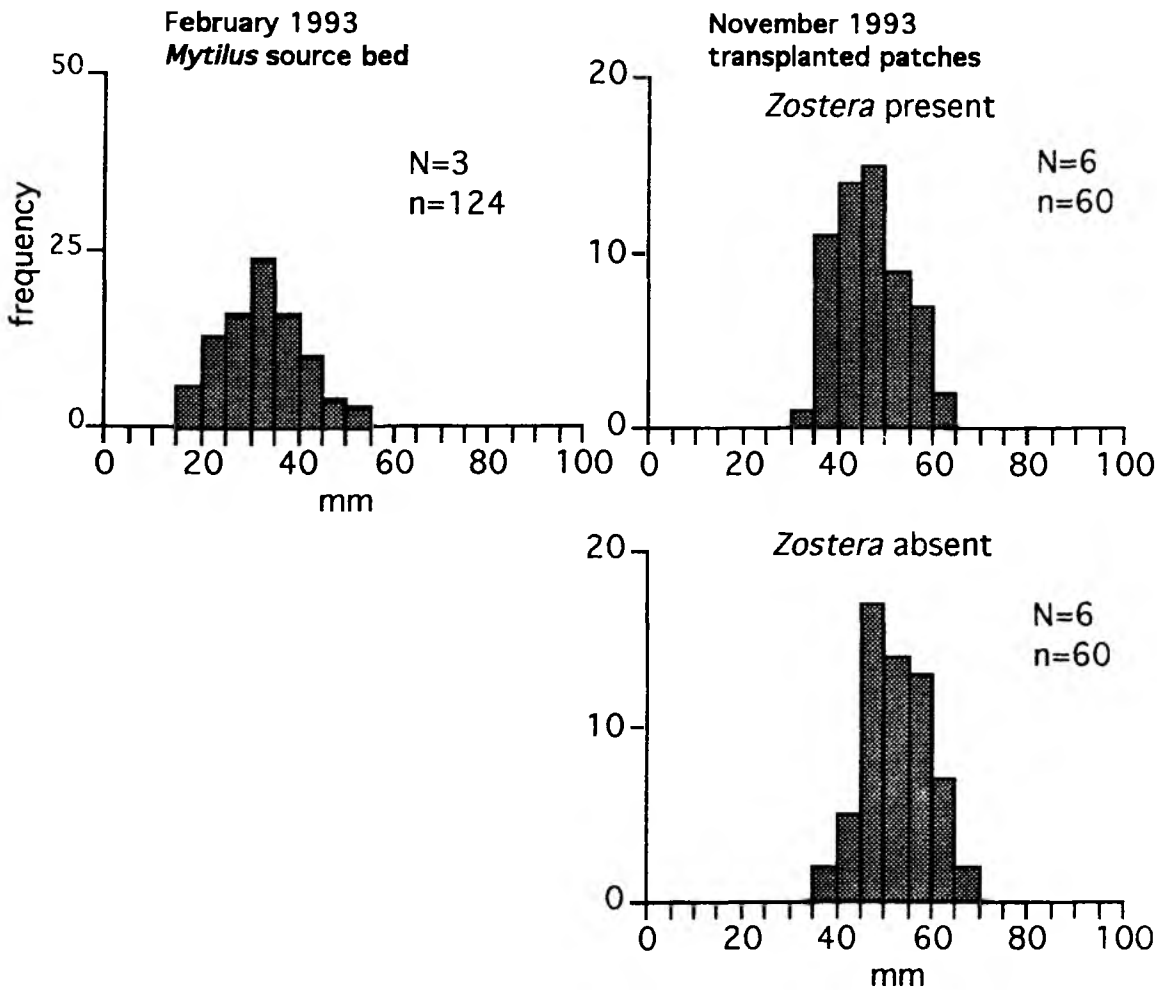


Fig. 4.6. *Mytilus* length distribution in transplanted clumps. Left: source bed for *Mytilus* -transplants in March 1993. Right: Length of 10 haphazardly selected mussels in each of 6 clumps after 7.5 mo exposure within (top) or outside (bottom) *Zostera* meadow. All juvenile mussels (<1 yr old) were omitted from measurement.

Also, the clump area of the transplants showed almost no increase inside the meadow (Fig. 4.6), whereas clump area increased by approximately 40% on sand. A MANCOVA revealed that the differences in areal development of clumps were significant (Tab. 4.8).

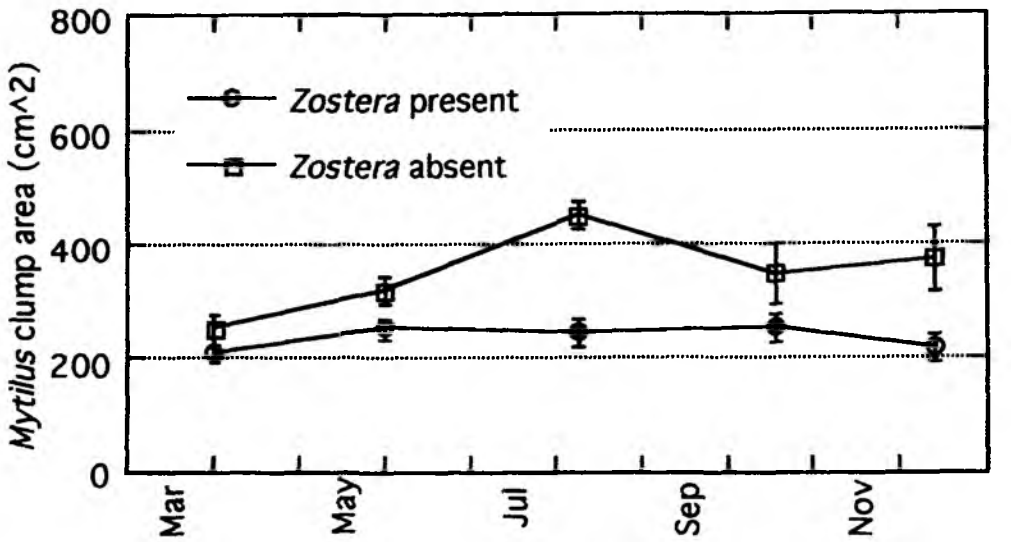


Fig. 4.7. Area of mussel clumps which were transplanted into *Zostera* meadow and onto sand flat from April to December 1993. Sample size n=7, error bars represent ±1SE. See Tab. 4.8 for statistical analysis.

Tab. 4.8. Analysis of the effects of "*Zostera* presence/absence" on clump area of transplanted *Mytilus* over a period of 8 mo (April to December 1993) by MANCOVA. Each of the 4 sampling dates after transplantation was treated as one independent variable. The initial clump area on April 10, 1993 was the covariate. Prior to the analysis, a test of homogeneity of slopes was done. Mussel clump areas were log-transformed. Multi-homoscedasticity and -normality were checked using a modified Hawkins-test (Johnson & Field 1993).

test of homogeneity of slopes						
source of variation	Pillai Trace	F	Hyp. df	Error df	p	conclusion
Zostera present/absent	.5062	1.7936	4	7	0.2346	
covariate (initial area)	.2620	.6213	4	7	0.6619	
Zostera present/absent* covariate (initial area)	0.5089	1.8135	4	7	0.2308	MANCOVA legitimate
MANCOVA						
Zostera present/absent	.8282	9.6432	4	8	0.0038	**
covariate (initial area)	.3705	1.1770	4	8	0.3898	ns

4.4 DISCUSSION

On all sampled substrata, densities of crabs (*Carcinus maenas*) were always low compared to those of *Asterias*. *Carcinus* was completely absent from mussel beds during winter until April 1993 and from November 1993 onwards. This is in concordance with censuses which were done on transplanted mussel patches (Fig. 3.9). Therefore, I feel safe in restricting the discussion of substratum dependent predation impact to *Asterias*.

On adult mussel beds, the presence of *Zostera* was found to have no effect on *Asterias* density and biomass and only minor influence on the feeding performance of *Asterias*. A trend was found, for adult mussels only, to be more susceptible to seastar predation outside *Zostera* meadows. However, this may be due to the 2-fold higher recruit densities within *Zostera/Mytilus* patches compared to pure mussel beds which dilute predation pressure on adults in favour of preferred juveniles (Fig. 2.3). Therefore, I do not suggest that foraging of *Asterias* on adult mussels is impeded by the presence of *Zostera* shoots. This is in concordance with results presented in chapter 2 which revealed that the presence of a *Zostera* canopy had no effect on the density or proportion of *Asterias* feeding on juvenile mussels.
In February 1993 only, the *Zostera* meadow in combination with mussel beds as secondary hard substratum had a different function for *Asterias*. After an extreme disturbance event, the highest seastar densities during the 18 mo study period were found on mussels beds having *Zostera* canopy (up to 60 ind/0.25 m^2). A few days prior to this sampling date, three intense storms hit the site. Therefore, I suggest that *Asterias* either migrated into the shelter of the canopy to escape from storm induced dislodgement or was drifted into *Zostera* patches.

Zostera was found to have a major influence on the residence time and drift distance of mussel clumps and on the stability of mussel beds against storm induced dislodgement. At FO during storms in January 1993, *Zostera* did not prevent loss of mussel cover. I attribute that to the markedly higher intensity of disturbance in January 1993. A series of 3 storms with peak wind speeds of Bft. 11-12, each lasting 2-3 days at least with Bft. 10, hit the site. In October 1993, wind force were 9-10 Bft. and the storm lasted for 24 h only. This

suggests that *Zostera* offers less protection to mussel beds against extreme disturbance events.

The second analysis included one single disturbance event (October 1993) at two sites. At MOE only, natural mussel beds did not respond in the same way as those artificially produced by canopy removal. Instead, their cover decreased only non-significantly compared to plots under presence of *Zostera*. The reasons why non-manipulated pure mussel beds persisted much better at MOE compared to FO remain speculative. It may be that at MOE, due to the exposure to northerly storms, natural beds developed a relatively higher byssal attachment strength compared to individuals within *Zostera* than at the more sheltered site FO. However, only taking the experimentally manipulated treatments into account, both sites show concordant results. In October, the main effect "site" was almost significant, i. e. at MOE, a trend was found for mussel cover to be significantly higher after disturbance compared to FO. I attribute that to the storm which came almost exactly from the south. Hence waves hit the shoreline perpendicular in FO but in an 80° angle at MOE. Therefore, the force exerted by breaking waves and the severity of the disturbance was probably much lower at MOE.

Adult mussels are seldom attached to *Zostera* shoots themselves by means of their byssus threads. Therefore, I hypothesise that *Zostera* stabilises *Mytilus* beds entirely by its ability to reduce current speed and baffle wave induced water movement by canopy friction. Although in the literature, canopy effects on current reduction have only been tested by laminar, unidirectional currents (e.g. Gambi et al. 1990), I suppose that these results apply also to orbital, wave induced water movements.

It is well known from the literature that *Zostera* has strong influence on the stability of the substratum and hence on the co-existing infauna. Manipulative removal of the leaf canopy resulted in a marked decrease of infaunal organisms within the meadow compare to adjacent sand flats (Orth 1977b). Whereas space itself is seldom limiting, stable substratum is often a premium in soft-bottom communities (Woodin 1978). The studied community provides another example to this model.

No influence of *Zostera* on the population size structure of *Mytilus* was found on two dates at two sites, FO and MOE, which would suggest a lower growth rate of mussels within *Zostera*. In contrast, individual mussels of transplanted

clumps were approximately 6 mm shorter than the control group which was growing on bare sand for 7.5 mo.

One solution to this apparent contradiction may be that the mean age of patches and hence of mussel individuals inside *Zostera* is higher. The canopy removal experiment showed that the risk of a pure *Mytilus* patch of being destroyed by a winter storm is much higher compared to a *Mytilus* patch living in association with *Zostera*. Approximately 73±9 % (±95%-confidence interval) of the original mussel coverage at FO and 17±8.2 % at MOE were destroyed by the storm in October 1993 on natural mussel beds. For beds without *Zostera* this corresponds to an 14-fold and 1.5-fold higher risk of being dislodged compared to mussels in association with eelgrass at FO and MOE, respectively. Therefore I assume that, at least at FO, mussels are older on the average when living inside *Zostera*.

Peterson et al. (1984) found enhanced growth of the suspension feeding bivalve *Mercenaria mercenaria* within a *Halodule wrightii* meadow. However, he cites Beal (1983) who found slower growth of *Mercenaria* at another site in North Carolina sounds and no effect at a third site. Peterson et al. (1984) further discusses the processes which may affect growth of suspension feeders under a seagrass canopy. Although the transport of suspended particles into the meadow decreases with decreasing current velocities, the actual food concentration in the benthic boundary layer which is available to suspension feeders like *Mytilus* or *Mercenaria* may increase. This is true especially at the meadow edge. Here suspended particles settle to the bottom due to rapidly declining current speeds. Thus, the available food for filter feeders may be either increased, decreased or not affected at a certain location within the seagrass meadow depending on the distance from the meadow edge, the prevailing current regime, and the density of shoots. Detailed observations on current modification by *Zostera* in flume tanks confirmed these hypotheses (Gambi et al. 1990). Recently Judge et al. (1993) proved that *Mercenaria* indeed encounters elevated food levels within a seagrass (*Halodule wrightii*) meadow. The increased food concentration above bottom consisted mainly of resuspended benthic diatoms.

In Kiel Fjord, tidal currents are absent and wind induced currents are generally feeble and seldom exceed 5 $cm*s^{-1}$ during the warm water period in summer when most of the mussel growth takes place (personal observations).

This may meet one of the conditions proposed by Peterson et al. (1984) and lead to poorer food supply to *Mytilus* within the meadow.
Furthermore, all experimentally transplanted clumps were at least 50 cm apart from the meadow edge and received thus a higher food depletion compared to individuals at the meadow edge. Yet, the core samples to obtain *Mytilus* length distribution of unmanipulated populations were placed haphazardly in pre-selected mussel patches. Hence, in the case of mussel beds in presence of *Zostera*, samples were taken in central parts of patches as well as at the meadow edge. This led to a dilution of the potentially lower mean length inside the meadow by mussel individuals which encounter food conditions comparable to those outside the meadow.
As a result of slower individual mussel growth, the transplanted clumps showed almost no areal extension from April to December 1993. However, based on the arguments proposed above I suggest that the actual growth reduction and hence reduction of natural mussel patch areal extension is probably smaller in the real world than the data of the transplanted clumps suggest since only few parts of the natural beds are 50 cm or more away from the seagrass meadow edge.
I suggest that this problem deserves a further thorough experimental investigation which should include the transplantation of individually marked mussels to different distances to the meadow edge and current measurements.

In summary, a moderate growth reduction occurs in central positions under a *Zostera* canopy at the experimental site, with an absolute length difference among individuals transplanted onto sand and *Zostera* which is only 2 mm between both 95%-confidence intervals. This is probably not very significant for the distribution of *Mytilus*.
Zostera affects *Mytilus* distribution mainly through its ability to modify the physical environment in the shallow subtidal. *Mytilus* has the tendency to fasten in the *Zostera* meadow when being drifted around. For established beds, the energy of storm induced disturbance is markedly reduced by presence of *Zostera* and hence the destruction of mussel patches is decreased. The high percentages of mussel beds which were destroyed during both disturbance events suggest that patch fluctuation is high at both sites.

Chapter 5
Mixed *Zostera/Mytilus* stands II: mussels do not interfere with eelgrass but fertilize shoot growth through biodeposition

5.1 INTRODUCTION

The co-occurence of blue mussels (*Mytilus edulis*) and eelgrass (*Zostera marina*) is a widespread phenomenon at sheltered sites of the shallow subtidal of Kiel Bight (e.g. Kiel Fjord, Schwenke 1969, personal observation). Besides pure *Zostera* meadows and pure *Mytilus* banks, there are mixed stands. These combinations form a mosaic of patches, which are interspersed with sand (Photo 6).

There is anecdotal evidence for deleterious effects which *Mytilus* may have on *Zostera*. In intertidal seagrass meadows of the Wadden Sea (North Sea), a rapid succession from meadows of *Zostera marina* and *Z. nana* to mussel beds is frequently observed (Ruth 1991 and personal communication). In Kiel Bight, Gründel (1980) observed the rapid conversion of an eelgrass meadow to a mussel bank within one year following heavy settlement of juvenile mussels. At the experimental site of the present study in Friedrichsort, Kiel Fjord, Kobarg (1993) transplanted *Zostera/Mytilus* patches to greater water depth (3.5 and 5 m) to study the light limitation of *Zostera*. After three months in deep water, *Zostera* was destroyed by *Mytilus* and Kobarg (1993) attributed this to a mechanical damage of the shoots by the growing and extending mussel individuals. Observations made at the study sites revealed that in unmanipulated patches, lateral growth extensions of the dense mussel understory frequently bent *Zostera* shoots aside (Photo 7).

In the intertidal of rocky shores, mussels are often the top space competitors which restrict macroalgal distribution (Dayton 1971, Paine 1971, Paine 1974, Menge 1976). In contrast, for soft-bottom communities competition for space has seldom been shown to structure the community (Woodin 1976, Peterson 1977, Brenchley 1982). Spatial interference is thought to be rare because the 3-dimensional space on soft-bottom provides spatial refuges in excess. Moreover, on soft-bottom no fixed attachment points exist from which sessile organisms may push or squeeze competitively inferior organisms off the substratum (Peterson 1979), except in very rare events where infaunal

molluscs settle in such a high density that they push conspecifics out of the sediment (Dijkema et al. 1987).
However, mytilid mussels are known to compete intraspecifically for space if occurring in epibenthic beds or clumps of conspecifics. The forces individuals may exert on their neighbours suppress growth (Fréchette & Lafaivre 1990) and may even lead to shell deformation (Harger 1972, Bertness & Grossholz 1985).
One major goal of this study is to test whether there is any deleterious effect of *Mytilus* on *Zostera*. I hypothesise that *Zostera* shoot density declines over time if interference competition occurs. In an experimental manipulation of *Mytilus* coverage, I assess the effects of *Mytilus* on *Zostera* densities. With a series of permanent plots over adjacent patches, I test if the vegetative propagation of *Zostera* is inhibited by the presence of an adjacent mussel bank.
Besides having a potential competitive role, mussels are reported to fertilize co-occurring algae by their excretion of nitrogen (mainly as ammonium) and phosphate (Kautsky & Wallentinus 1980). Therefore, the second objective of this study is to test whether *Mytilus* enhances *Zostera* growth by fertilization. In the case of marine angiosperms, not only water column excretion but also nutrient enrichment of the sediment by the mussels may be responsible for potential growth effects (Bertness 1984), since seagrasses obtain the greatest fraction of their nutrient demands via roots from the sediment (Barko et al. 1991). The biodeposits of pseudofaeces and faeces of Baltic blue mussels were shown to be high in nitrogen-content despite having passed through the mussel intestine (Kautsky & Evans 1987). Therefore, the effects of experimental changes of *Mytilus* densities on the sediment nutrient content will be assessed as well.

5.2 MATERIAL AND METHODS

Study period and sites. Observations were carried out from June 1992 until October 1993 using SCUBA diving. The experiments were run during one *Zostera* growth period from April 1993 until October 1993 at Friedrichsort (FO), and additional observational data were obtained at Moeltenort (MOE) which is situated opposite to FO on the eastern side of Kiel Fjord (Fig. 1.1). The distribution depth of the *Zostera/Mytilus* association is between 1.2 and 2.5 m in FO and 1.0 and 2.2 m in MOE. Further down to a

depth of approximately 4 m pure patches of *Zostera* occur. The shape of the patches is irregular, ranging from ellipses to narrow, elongated structures which are mostly oriented perpendicular to the shoreline. Their extension on the longest axis of both pure *Zostera* and *Zostera/Mytilus* patches ranges from 0.5 to approximately 5 m, with a high percentage of patches measuring between 1 and 3 m. Those sizes were chosen for the experimental manipulations.

On the gentle slopes at both sites, the depth band with co-occurring *Zostera* and *Mytilus* is approximately 30 m wide. The coverage of the substratum with eelgrass, pure mussel banks and the *Zostera/Mytilus* association is shown in Fig. 4.1. In March 1993, at FO, 39% and at MOE, 71% of the *Zostera* meadows possessed an understory of mussels. Typically, they form an almost continuous, epibenthic layer underneath the *Zostera* canopy, and they are not hummocked (Photo 7). The byssus threads of the mussels are rarely attached to *Zostera* shoots or rhizomes but usually to other mussels. This allowed the removal of *Mytilus* without damaging *Zostera* plants (see below).

Field observations

Determination of plant parameters of *Zostera*. At both sites, the plant morphology was determined between August 25 and September 2, 1993, comparing plots with and without *Mytilus* from the same depth range from 1.8 to 2 m. In each of the 7 plots of 50x50 cm, 6 plants were chosen haphazardly by blindly pointing into the plot with a ruler, thus total sample size is n=42. Only adult, fully grown plants were measured, whereas those which had recently developed from the rhizome were ignored.

The length of the largest photosynthetic active leaf was measured to the nearest cm and its width to the nearest 0.5 mm. The leaf area was calculated by multiplication assuming a rectangular shape. The width of the leaves was constant over the whole length (personal observation). In concordance with studies on Danish Baltic seagrass meadows (Sand-Jensen 1975), I found that the largest photosynthetically active leaf of *Zostera* was in most cases the 4th youngest.

All shoot densities were determined in areas of 50x50 cm. Each leaf bundle, including those recently formed, counted as one shoot. To make counts as accurate as possible, the plot area was subdivided with two stakes into strips of 10 cm width. To determine the accuracy of the method, counts of shoot density

on three plots were repeated three times in April. The error was smaller than 5%. All counts were made by the same observer.
To determine the ratio of above ground to below ground biomass, and the length of the roots in pure *Zostera* compared to the *Zostera/Mytilus* association, 5 destructive core samples (250 cm^2, 15 cm depth) were taken at MOE on September 1, 1993 on each substratum type. The samples were divided into leaves (above ground biomass) and rhizomes plus roots (below ground biomass), rinsed with fresh water and weighed after drying at 80 °C for 24 h. Ten roots in each core were chosen at random and measured from attachment base at the rhizome to the tip to the nearest 1 mm.

Sediment analysis. Sediment samples were taken in 50 ml plastic vials (5 cm i.d.) which were inserted 5 cm into the sediment. On August 2, 1993, three samples were taken in each of the 5 control plots of a *Mytilus*-addition/removal experiment at FO. The organic content of the sediment was determined as loss of ignition (LOI) by drying the sample at 100 °C and determining the weight loss after heating at 500°C for 12 h in a muffle furnace.
Porewater was sampled in triplicate on August 26, 1993 in all 20 experimental plots at FO and, on September 2, 1993, at MOE in 5 *Zostera* plots each in the presence and absence of *Mytilus*. The samples were obtained in situ with 10 ml plastic syringes. A plastic tip was perforated several times and a 20 µm mesh gauze wrapped around it. At three randomly chosen points, they were inserted 5 cm into the substratum using a new syringe for each sample. By gently sucking over a period of approximately 30 s, 10 ml of porewater were sampled from the 4 to 6 cm depth horizon. The chosen depth lies within the densest root/rhizome development (personal observations). Samples were deep frozen on board the dive boat. Since the concentration of ammonium in the porewater is generally > 20 µM, changes in concentration due to freezing were considered non significant. In the laboratory, the samples were diluted 1:5 with distilled water and analysed for nitrate/nitrite, dissolved ammonium and soluble reactive phosphate (SRP) after the methods of (Grasshoff 1976), (Koroleff 1976a, Koroleff 1976b) modified for a smaller sample volume. In concentrations >150 µM, H_2S may interfere with determination of ammonium and lead to false positive results of 7-14 % (Koroleff 1976a). However, I assumed the H_2S-concentrations in the porewater to be markedly below this

value since core samples never smelled sulfidic. The photometric measurements were corrected for turbidity.
Shoot density, leaf length and width, and nutrient concentrations in the porewater were compared between sites (FO and MOE) and between substrata with a 2x2 nested ANOVA with site and presence/absence of *Mytilus* as factors and plot nested in both factors. The response variables, leaf length, width and area, were log-transformed, nutrient concentrations were cubic-root and shoot densities square root-transformed to remove heterogeneity of variances. Cochran's test was applied to test the success of the transformation. The three leaf parameters measured were considered as parts of one mensurative experiment on general differences in leaf morphology. Therefore, to minimise the chance of committing a type I error, the significance levels were Bonferroni-adjusted by dividing α (probability of making a type I error) by the numbers of comparisons, i.e. 3.

Regression of sediment nutrients on *Zostera* leaf length. During late August 1993, 20 triplicate porewater determinations were performed at FO and 10 determinations at MOE, half of each on *Zostera* plots with and without a mussel understory. Simultaneously I measured length of the largest photosynthetically active leaf of *Zostera* in the same plots between August 26 and September 3, 1993. I estimated relative differences in *Zostera* growth between treatments from the lengths of the largest intact leaves (Hamburg & Homann 1986). To do this, I assumed that the rate of new leaf formation (the plastochrone interval) and hence the age of the leaves until they stop growth is similar among the treatments. If there is acceleration with nutrient enrichment, increases in leaf growth rate would be underestimated by this method.
In concordance with work done by Sand-Jensen (1975) I observed that leaves stop growing when they become the 3rd youngest leaf of one shoot.
Since the relation between eelgrass growth and nutrients is not linear, but follows a saturation-type function (Dennison et al. 1987, Williams & Ruckelshaus 1993), a Monod curve was calculated between the corresponding sample means of sediment porewater (n=3) as the independent and the leaf length (n=6) as the dependent variable using a least square approximation method. For ammonium as dependent variable only, a Woolf linear transformation (leaf length/ammonium concentration vs. ammonium concentration) was used to test the significance of the regression by an ANOVA.

Observations on patch boundaries. Permanent plots were followed through time to gain information on whether (a) the presence of adjacent mussel beds impedes vegetative propagation of eelgrass and (b) fertilization by co-occuring mussels accelerate the rate of vegetative propagation compared to pure eelgrass stands. No *Zostera* seedlings were found throughout the study period in the water depth investigated. Thus, extension of *Zostera* patches occurred only through vegetative propagation.

The positions of borders of approximately 50 cm length were sampled photographically in quadrats of 50x50 cm. An accuracy of 1 cm was achieved using marking stakes at two diagonal edges. Ten plots on the following combinations of patch boundaries were chosen haphazardly within a strip of 80 m parallel to the shoreline in the 1.8 to 2 m depth: (1) pure *Zostera* vs. sand (2) pure *Zostera* vs. *Mytilus* (3) *Zostera/Mytilus* vs. *Mytilus* and (4) *Zostera/Mytilus* vs. sand. Border type (2) could not be sampled because a severe storm destroyed most of the pure mussel banks on October 10, 1993. The remaining permanent areas were carefully examined three days after the disturbance event to exclude every border which was apparently damaged by the storm, for I were interested only in border shifts due to growth processes. Due to the storm, the final sample size had to be reduced from a planned 10 to 8 independent pairs of adjacent patches.

The positions of borders were sampled on April 5 and on October 18, 1993. Non-destructive sampling using a camera with flash attached to a frame was feasible since *Zostera* canopy and shoot density were sufficiently low on the chosen sampling dates, that is before and after the growth period. The colour slides were then digitised using a S-VHS-Video-camera plugged into a NeXT workstation. Using the digitised image, in each replicate plot, patch boundaries were selected in the following way: to be included into a patch, no shoot could be more than 12 cm away from a conspecific. Spring and autumn boundary positions were drawn into a co-ordinate system. The border shifts were quantified by measuring the smallest distance between the spring and the autumn border at 5 randomly chosen points of the spring border within each plot. Image analysis software was developed in our department. In cases of doubt, the colour slide was investigated using a stereo-microscope.

Five distances were obtained for each of the 8 replicates of one border type, thus the total sample size was n=40 propagation distances for each border type. The distances were (log+1)-transformed to remove heterogeneity of variances. A Cochran test for homoscedasticity was performed to confirm the success of

the transformation. The three different border types were compared with a one-way ANOVA nesting the five distances obtained for each replicate plot within the factor "border type" to account for large variation within one border type.

Experiments

Changing *Mytilus* densities. Two sub-experiments were carried out. In a *Mytilus*-addition experiment, mussels were transplanted into pure *Zostera* plots and thus artificial *Zostera/Mytilus* associations were produced. In a *Mytilus*-removal experiment mussels were removed from existing associations (Fig. 5.1 a). The chosen depth range was narrow (1.8 to 2 m) and identical to the other observational sampling sites. The experimental layout was not completely randomised, because preliminary observations revealed a high variability in shoot density and plant size among patches in the same water depth. Therefore, each sub-experiment was performed as a randomised block design (Hurlbert 1984, Fig. 5.1 b). Within a strip of 50 m length and 10 m width parallel to the shoreline, 5 blocks were selected. The size and density of *Zostera* was chosen to be as homogeneous as possible. The coverage of mussels in the *Zostera/Mytilus* plots was always 100% before the experimental manipulation. Within each block, the positions of treatment and control plots were chosen at random. The plots of 50x50 cm were placed diagonal to each other without any intermediate space to minimise sediment and exposure variability within each block (Fig. 5.1 a). Since both plots have contact only at a corner, I assume that interference between treatment and control is probably small.

All mussels were removed from *Mytilus/Zostera* patches. In 3 removal plots, the number of *Zostera* shoots was counted before and after treatment to account for treatment effects. As greatest care was taken in removing the mussels without diving gloves, losses of shoots were minimised to between 2 and 7%, and therefore considered as unimportant for the outcome of the experiment. The number of *Zostera* shoots after experimental manipulation counted as the initial value for the experiment.

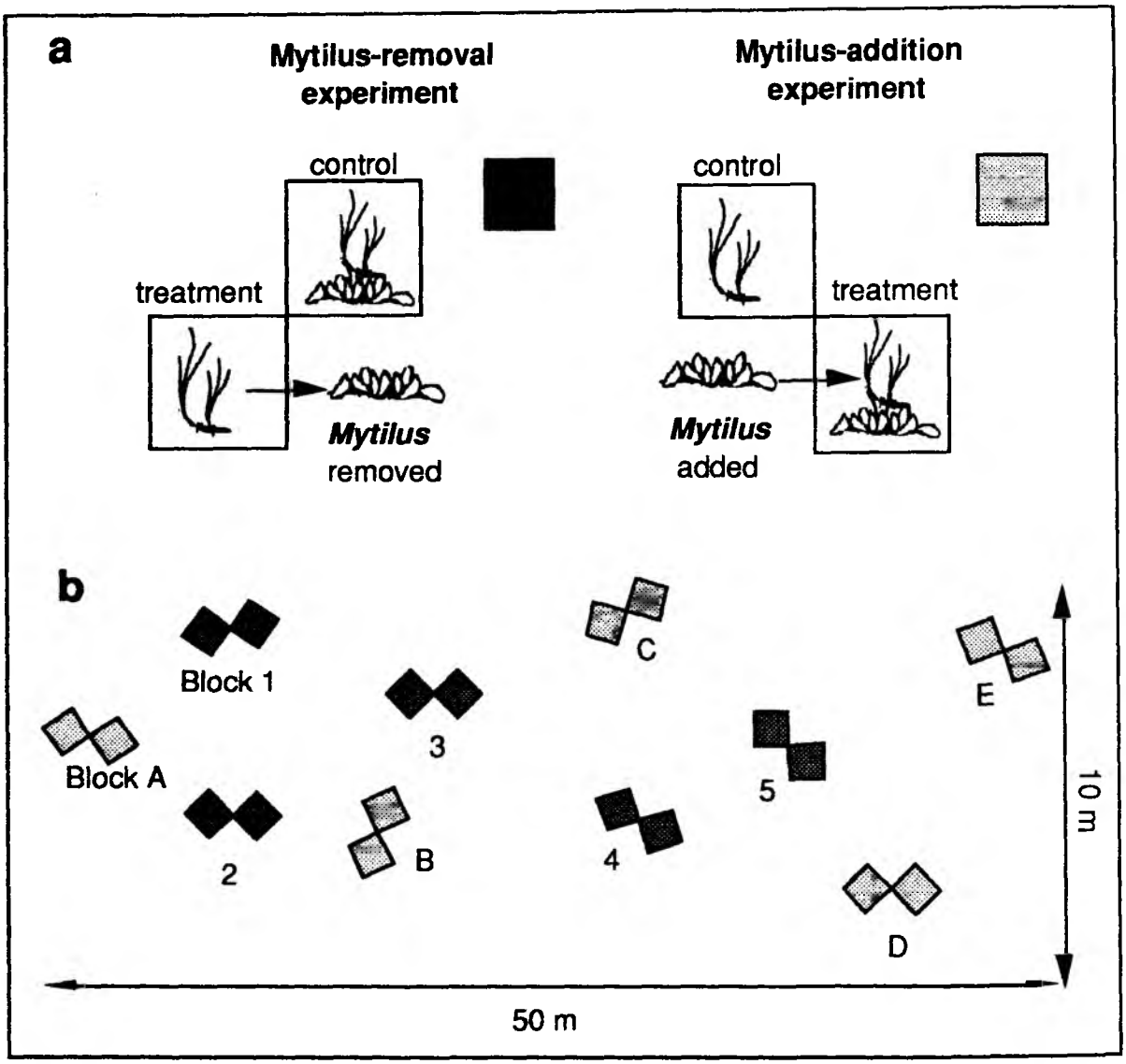


Fig. 5.1. Experimental treatments and controls (a) and representation of the experimental block design (b) of the *Mytilus*-addition and -removal experiment. Block A to E and 1 to 5 belong to different sub-experiments. The size of the quadrates is 50x50 cm.

The removed mussels of the first sub-experiment were immediately transplanted into the pure *Zostera* plots which were chosen to receive the treatment of *Mytilus* addition. For both experiments, the volume of mussels removed and subsequently added to another plot was about 4 dm^3. Before transplanting, the mussel clumps were broken into smaller aggregates because (a) this facilitated the homogenous dispersion on the bottom, (b) prevented the

Zostera shootlings from being bent to the ground by bigger clumps, and (c) provided a stimulus for byssus secretion and attachment to conspecifics (personal observations). During the first week only, wire fences of 10x10 mm mesh size and 10 cm height surrounded plots which received mussels to prevent the unattached animals from being washed away from the treatment plots due to wave action. After that period, most mussels had attached to their neighbours and no difference between natural and artificially generated *Mytilus/Zostera* associations was apparent. The experiment lasted for 7.5 mo from April 10 to October 27, 1993. In all plots, mussel cover remained at >90% during the experimental period.

In both sub-experiments, response variables were (1) the number of *Zostera* shoots censused every 6 weeks as described above (2) length, width and area of the largest photosynthetic active leaf determined as described above on August 28, 1993 (3) porewater nutrient concentrations sampled in triplicate in each plot on August 26, 1993.

Statistical analysis. Two different hypotheses were formulated on the effects of mussels on shoot density. The first is that the manipulation of *Mytilus* cover led to differences in *Zostera* density after 6 mo of experimental duration, i.e. on the last sampling date (October 27). Therefore, October densities were analysed with two separate univariate analyses of covariance (hereafter ANCOVA), using the initial density as covariate.

The second hypothesis states that there is a difference in *Zostera* density as result of experimental manipulation throughout the entire growth period (June to October). To test for this hypothesis, shoot densities were analysed with a multivariate analysis of variance (MANOVA), treating each of the 4 post-manipulative sampling dates (June 2, July 21, September 2, October 27) as one dependent variable (Farrell 1989, Howell 1992, p.472). This multivariate analysis has the advantages of having a greater power of detecting a real difference. At the same time, it minimises the risk of committing a type I error and eliminates the problem of non-independence among consecutive sampling dates (Johnson & Field 1993). In fact, the 4 vectors of dependent variables were not independent but highly correlated among each other as can be expected in a repeated measure design. I tested this by comparing the covariance matrices of both treatments and both experiments against the identity matrix (which assumes no correlation) with a likelihood test (Fahrmeir & Hamerle 1984, p. 74ff).

The MANOVA assumptions of multi-normality and multi-homoscedasticity were tested independently by two procedures. The 4-dimensional normality was checked on the basis of a modified Choletzky decomposition, simultaneously testing kurtosis and skewness vectors of the dependent variables with a Chi-square distribution (Lütkepohl 1991). Multi-homoscedasticity and -normality were tested simultaneously using Hawkins' test (Hawkins 1981, proposed by Johnson & Field 1993). In both analyses, the differences in the medians of the tails of the F-distribution (i.e. the difference of the medians of A_{ij}s of each group, Hawkins 1981) did not exceed the critical value of 0.85 (Johnson & Field 1993). Therefore, I conclude that it is legitimate to perform a MANOVA.

For hypothesis testing, I chose the Pillai Trace-statistic and its F-approximation. It is recommended by Johnson & Field (1993) as being the most robust against violations of multi-normality and multi-homoscedasticity compared to other multivariate statistics (e.g. Hotelling's Trace, Wilk's Lambda).

On the same data sets, I also performed MANCOVAs (=multivariate analyses of covariance) with initial shoot densities as covariates. In both analyses, the effect of the initial density (=covariate) was not significant. If this is the case, including the covariate into the analysis does not increase the power of the test but wastes degrees of freedom due to over-parametrization (Bernstein 1987, p. 342). Hence, the outcomes of the MANCOVAs (which were not different from the MANOVAs considering the factor *Mytilus* present/absent) are not shown and interpretation of the results was entirely based on the MANOVAs.

Additionally, the shoot densities of the 5 unmanipulated control plots of both sub-experiments were analysed for all 5 sampling dates (including the initial density on April 10) with a multivariate analysis of variance (MANOVA), treating each sampling date as one dependent variable. Response variable as well as covariate shoot densities were square root transformed to remove heterogeneity of variances.

Effects of presence or absence of mussels on *Zostera* leaf parameters and sediment porewater were analysed with two sets of ANOVA models with blocking factor for each sub-experiment. The three leaf parameters measured were considered as parts of one mensurative experiment on general differences in leaf morphology. Therefore, to minimise the chance of committing a type I error, the significance levels were Bonferroni-adjusted by dividing α

(probability of making a type I error) by the numbers of comparisons, i.e. 3. Leaf length, width and area were log-transformed and nutrient concentrations were cubic-root -transformed to remove heterogeneity of variances. Cochran's test was applied to test the success of the transformation.

5.3 RESULTS

Field observations

Shoot density. The shoot densities in August at FO and MOE were not significantly different in the presence or absence of *Mytilus* (Fig. 5.2 a, Tab. 5.1). The site had a significant effect on shoot density, but the interaction term site**Mytilus* absent/present was not significant, i.e. the effect of mussels on *Zostera* density is site independent.

Plant morphology. In contrast to density, plant morphology was dependent on the presence or absence of *Mytilus*. At both sites, the length, width, and area of the largest photosynthetically active leaf (in most cases the 4^{th} youngest leaf) were higher when *Zostera* grew with an understory of mussels. The effect of the site was also highly significant but not the interaction term site*absence/presence of *Mytilus*, i. e. the effect of *Mytilus* on *Zostera* morphology is independent of site (Tab. 5.1, Fig. 5.2 b to d)

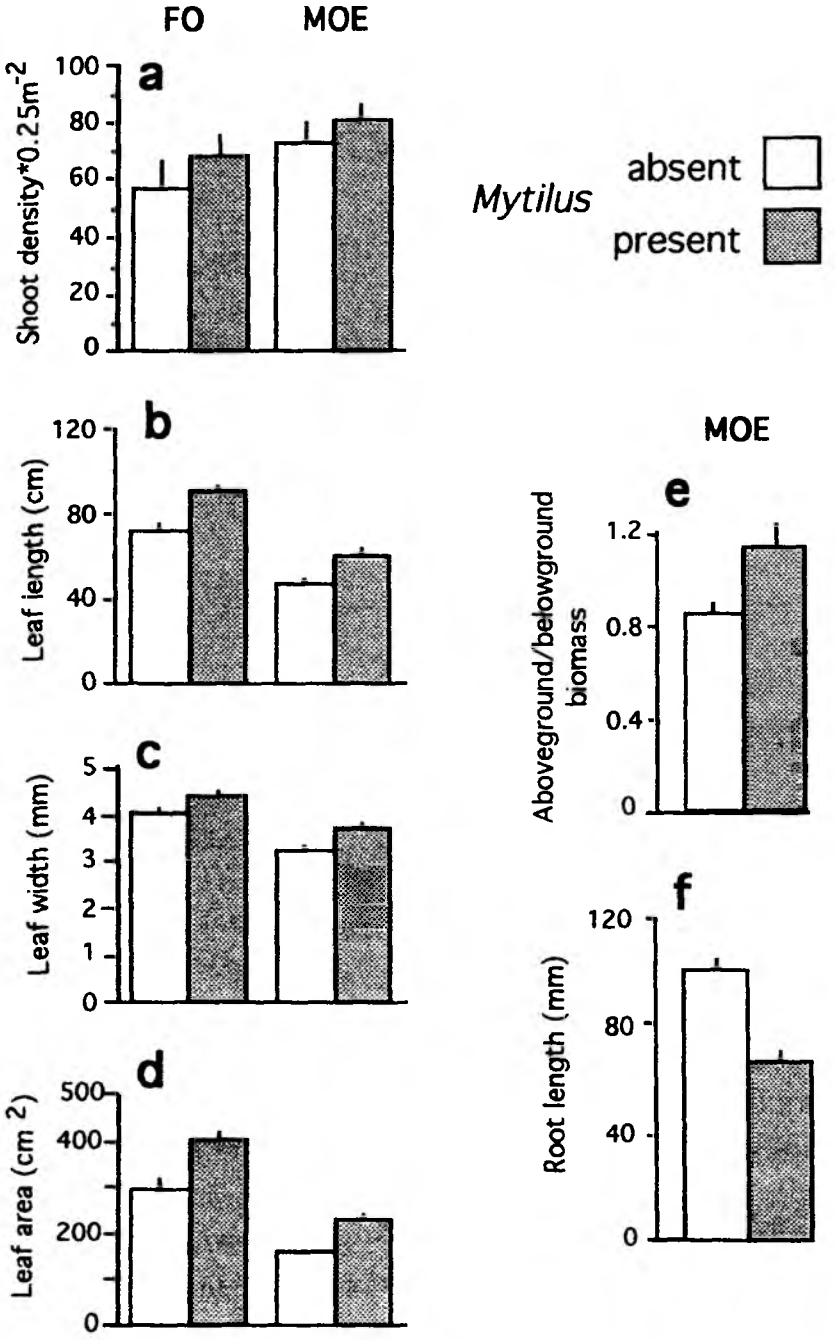


Fig. 5.2. Comparison of shoot density (a), and length (b), width (c), and leaf area (d) of the largest photosynthetic active leaf of *Zostera* in presence and absence of *Mytilus* at FO and MOE. Data from destructive core samples at MOE (250 cm^2) compare the ratio of above ground to below ground biomass (e) and the root length of *Zostera* (f) dependent of absence/presence of *Mytilus*. The sampling period was between August 25 and September 2, 1993. Sample size is n=7 for shoot density. The leaf parameters were determined in 6 haphazardly chosen, adult plants on 7 replicate plots, thus the total sample size is n=42. Sample size for biomass ratio (e) is 5. Ten randomly chosen root length (f) were determined in 5 core samples, summing up to a total sample size of n=50. Error bar is +1 SE. For statistical analysis see Tab. 5.1.

Destructive sampling of *Zostera* in MOE revealed that the ratio of above ground to below ground biomass was higher and the roots of *Zostera* were significantly shorter if co-occurring with *Mytilus* (Fig. 5.2 e and f, Tab. 5.1).

Tab. 5.1 (overleaf). Summary of observational data on sediment characteristics and on shoot density and plant morphology of *Zostera* at two sites, FO and MOE, in presence or absence of mussels. The following ANOVA models were used: a two way 2x2 ANOVA for the shoot densities with site and *Mytilus* absent/present as factors, and a two way 2x2 nested ANOVA with plot nested in both factors, site and *Mytilus* absent/present, for sediment porewater concentrations (ammonium and phosphate) and for shoot morphology of *Zostera* (length, width, area of largest leaf). The root lengths of *Zostera*, at MOE only, were analysed with a one-way nested ANOVA with *Mytilus* absence or presence as factor and plot nested in the factor, and the ratio between above ground to below ground biomass was analysed with a simple one-way ANOVA. Transformations of the dependent variables are given. After transformation, all data fulfil Cochran's test of homogeneity of variances. Note that 3 samples from different plots were not analysed for phosphate since the sample volume was too small. Therefore, the nested design became unbalanced, i.e. 3 plots contained only 2 instead of 3 replicates. Cochran's test was done with the more conservative value of $G_{(crit)}$ for a group size of n=3. For leaf parameters only, the significance level was Bonferroni-adjusted to $\alpha_{adjusted}=\alpha/3$ (ns $p\geq 0.0166$, * $0.0166 > p \geq 0.0033$, ** $0.0033 > p \geq 0.00033$, *** $p<0.00033$).

Dependent variable/ transformation	Source of variation	df	MS	F	p	
Shoot density	Site	1	6.481	4.392	0.0468	*
$x = \sqrt{y}$	*Mytilus* absent/present	1	3.060	2.074	0.1628	ns
	site**Mytilus* abs/pres	1	0.2323	0.1574	0.6950	ns
	Error	24	1.4757			
Porewater	Site	1	0.4935	0.4377	0.5177	ns
ammonium	*Mytilus* absent/present	1	9.1693	8.1321	0.0115	*
$x = \sqrt[3]{y}$	Site**Mytilus* abs/pres	1	0.1434	0.1272	0.7260	ns
	Plot No.(site, *Mytilus* absent/present)	16	1.1275	4.7691	0.0001	***
	Error	40	0.2364			
Porewater	Site	1	0.1797	2.589	0.1272	ns
phosphate	*Mytilus* absent/present	1	0.3195	4.605	0.0476	*
$x = \sqrt[3]{y}$	Site**Mytilus* abs/pres	1	0.0004	0.0059	0.9398	ns
	Plot No.(site, *Mytilus* absent/present)	16	0.0694	1.288	0.2557	ns
	Error	37				
Leaf length	Site	1	1.406	34.984	0.0001	***
x = log(y)	*Mytilus* absent/present	1	0.468	0.468	0.0023	**
	Site**Mytilus* abs/pres	1	0.001	0.022	0.8842	ns
	Plot No.(site, *Mytilus* absent/present)	24	0.040	4.486	0.0001	***
	Error	139	0.009			
Leaf width	Site	1	0.318	48.574	0.0001	***
x = log(y)	*Mytilus* absent/present	1	0.088	13.405	0.0012	**
	Site**Mytilus* abs/pres	1	0.002	0.349	0.5601	ns
	Plot No.(site, *Mytilus* absent/present)	24	0.007	1.296	0.1774	ns
	Error	139	0.005			
Leaf area	Site	1	3.061	76.986	0.0001	***
x = log(y)	*Mytilus* absent/present	1	0.961	24.182	0.0001	***
	Site**Mytilus* abs/pres	1	0.0003	0.008	0.9276	ns
	Plot No. (site, *Mytilus* absent/present)	24	0.040	1.742	0.0252	ns
	Error	139	3.174			
Destructive core samples at MOE						
Root length	*Mytilus* absent/present	1	0.9682	11.902	0.0087	**
x = log(y)	Plot No.(*Mytilus* absent/present)	8	0.0813	3.9394	0.0005	***
	Error	90	0.0206			
above ground/ below ground biomass	*Mytilus* absent/present	1	0.3133	10.693	0.114	ns
no transformation	Error	8	0.0293			

Sediment parameters. Fig. 5.3 summarises the differences of various sediment parameters between *Zostera* patches with and without *Mytilus*. At FO, the organic content of the upper sediment horizon (0-5 cm) is generally low (means±1SE: 1.02±0.12% LOI in pure *Zostera* patches, 1.60±0.13% LOI in *Zostera/Mytilus* patches). The difference in LOI between *Zostera* patches in presence or absence of *Mytilus* is significant (one-way nested ANOVA, number of patches N=7, total number of samples n=21, $F_{(1,12)}=8.324$, p=0.0137).

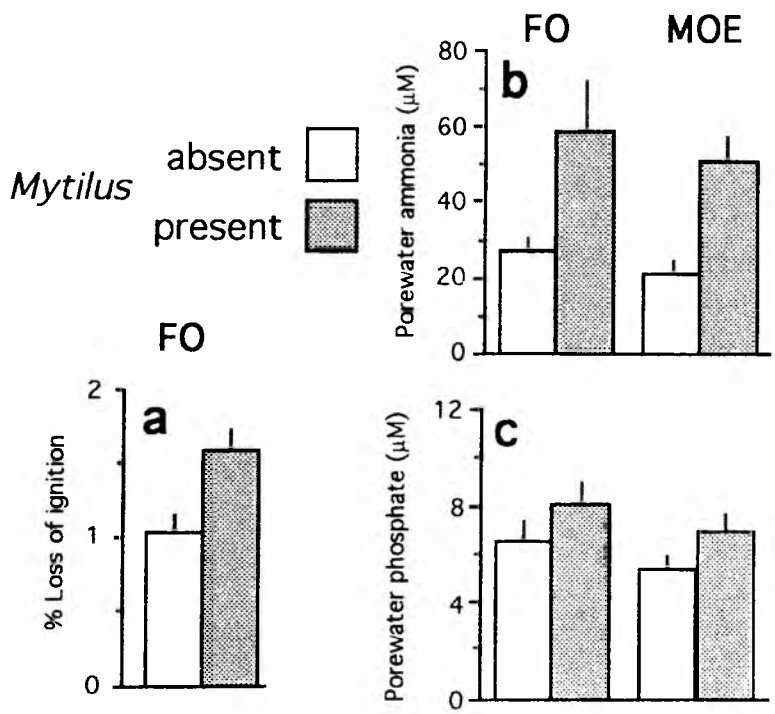


Fig. 5.3. Sediment parameters on *Zostera* plots in absence and presence of *Mytilus* at Friedrichsort (FO) and Moeltenort (MOE). Means of loss of ignition LOI (a), sediment porewater concentration of ammonium (b), and of soluble reactive phosphate SRP (c) are shown +1 SE. Three subsamples were taken in 7 plots for determination of organic content (LOI), thus total sample size n=21; triplicate porewater subsamples were taken on 5 plots, thus the total sample size n=15 for porewater phosphate and ammonium. For statistical analysis of data see Tab. 5.1.

At both sites, the porewater of the sediment horizon (3-6 cm) in the *Zostera/Mytilus*-association contains significantly more ammonium and phosphate than pure *Zostera* plots (Fig. 5.3 b and c, Tab. 5.1). Since the chance of committing a type I error is increased in the unbalanced phosphate analysis, the significant treatment effect of mussels (p=0.0476) has to be

interpreted with caution. Nitrate plus nitrite concentrations were always at the detection limit (<1 μM). As it can be expected in reduced sediments, they contribute very little to the total inorganic nitrogen available to the rhizosphere of *Zostera* and were therefore excluded from further data analysis.

Regression between sediment nutrient concentration and growth. Plotting the ammonium porewater concentrations against leaf length results in a saturation-type, hyperbolic function which levels off at approximately 75 μM ammonium at MOE and 100 μM at FO (Fig. 5.4 a). The calculated regression equation according to a Monod model explains 71% and 34% of the variation in leaf length at MOE and FO, respectively. The ANOVAs on the Woolf linearized data were highly significant for both sites (at FO $p<0.00001$, at MOE $p=0.0004$, Fig. 5.4 b).

In contrast to ammonium, no such relationship exists between porewater phosphate concentrations and the leaf length of *Zostera*. (Fig. 5.4 c). Except for three higher values, all concentrations are found within a range of 3 to 11 μM soluble reactive phosphate in the porewater. No regression formula was calculated because of this obvious lack of correlation.

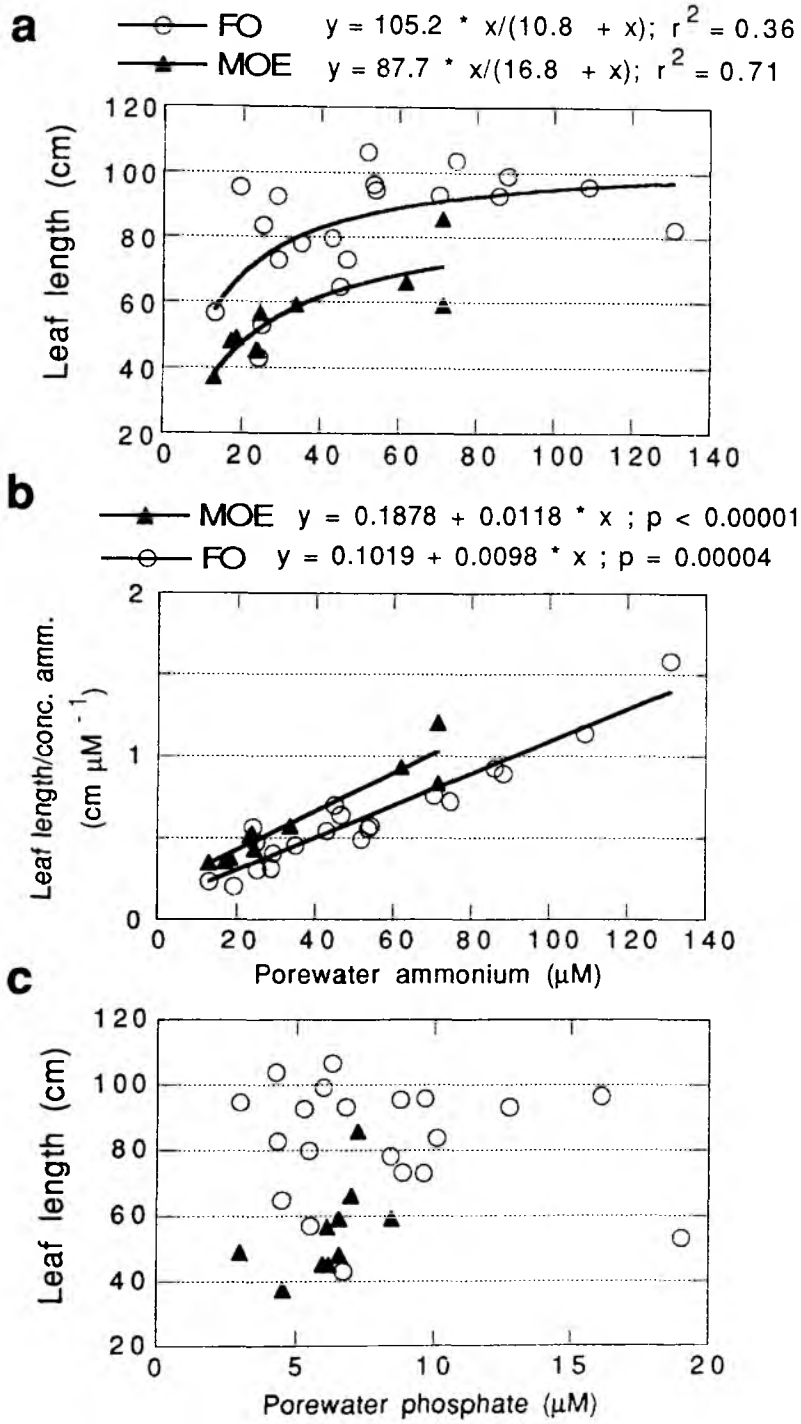


Fig. 5.4. Leaf lengths of *Zostera* measured between August 26 and September 2, 1993 as function of the ammonium (a and b) and phosphate concentrations (c) in the sediment porewater at the stations FO (circles) and MOE (triangles) on unmanipulated plots. Half of them had a mussel understory. For ammonium, the corresponding Monod equation was determined by a least square approximation and is given (a). Panel (b) shows a Woolf linear transformation of the same data (length/ammonium concentration vs. ammonium concentration). The significance of the linear plot was checked by ANOVA. Their p-values are given. Each data point represents the mean of 3 nutrient determinations and 6 leaf measurements. No equation or linearization was calculated for phosphate because of the apparent lack of correlation.

Observations on *Zostera/Mytilus* borders. There was no evident effect of adjacent *Mytilus* patches on the vegetative propagation of *Zostera* when analysing the propagation distances with a one-way ANOVA with plot nested in border type (Fig. 5.5, Tab. 5.2). Furthermore, *Zostera* did not propagate faster when co-occurring with *Mytilus*. There was a considerable variation among the sampled plots which were nested within one border type. This was largely due to the irregular shape of the propagating meadow edge. Hence within one plot, some propagation distances were zero while other rhizomes propagated some 30 cm. However, absolute propagation rates were very similar among levels of the factor "border" (n=40, mean propagation ±SE from April 4 to October 18, 1993: *Zostera/Mytilus* into *Mytilus* 13.27±0.96 cm, *Zostera/Mytilus* into sand 14.6±1.45 cm, *Zostera* into sand 13.3±1.50 cm).

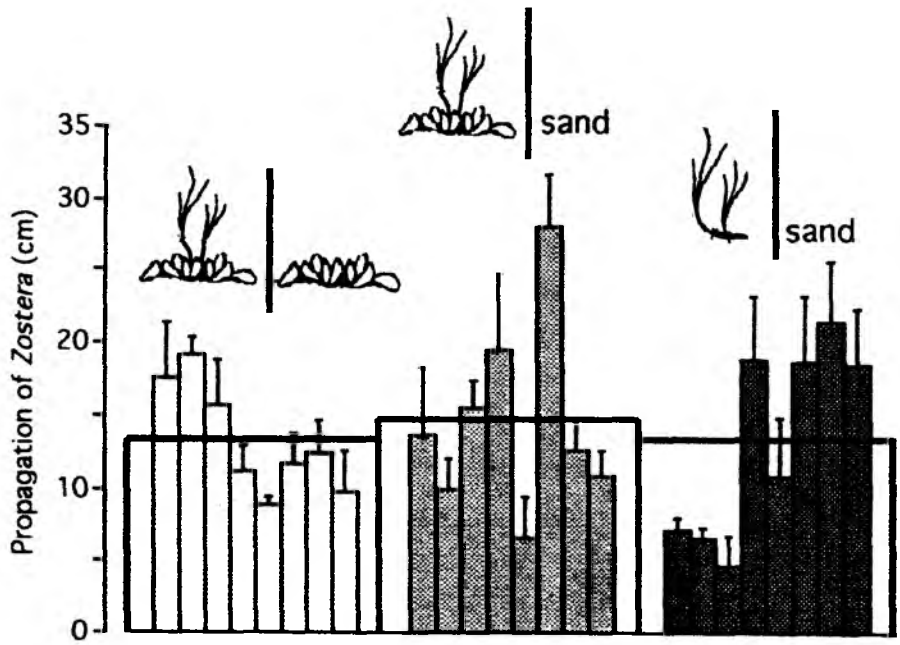


Fig. 5.5. Comparison of the vegetative propagation of different borders of *Zostera* patches over 6 month. In each of the 8 independent replicate plots on one border type, 5 propagation distances of the meadow edge were randomly obtained between the position of the patch border on April 4 and October 18, 1993. The total sample per border type is 8 replicates * 5 distances per replicate =40. The means of the replicate plots +1 SE are shown separately to emphasise the considerable scatter within one border type. The unfilled large blocks represent the overall means for one border type. Their SEs are given in the text. See Tab. 5.2 for statistical analysis.

Table 5.2. One-way nested ANOVA comparing the vegetative propagation of *Zostera* patches from April 4 to October 18, 1993 among 3 different border types: (1) *Zostera/Mytilus* association propagating into *Mytilus*, (2) *Zostera/Mytilus* association propagating into bare sand, and (3) *Zostera* propagating into bare sand. Five distances between April and October border position obtained at random in each replicate plot were nested in factor border type. Distances were (log+1)-transformed to fulfil Cochran's test of homogeneity of variances.

Source of variation	df	MS	F	p	
Border type	2	0.062	0.266	0.7689	ns
Plot-No.	21	0.233	3.022	0.0001	***
Error	96	0.077			

Experiments

Experimental effects of *Mytilus* on *Zostera* density. The *Mytilus*-addition/removal experiment showed no negative influence of *Mytilus* on *Zostera* density (Fig. 5.5 a and b). Neither the addition of *Mytilus* to *Zostera* patches nor the removal of mussels from existing *Zostera/Mytilus*-associations resulted in significant changes of *Zostera* shoot density at the final sampling date. The results of the analyses are summarised in Tab. 5.3 (*Mytilus*-addition experiment) and Tab. 5.4 (*Mytilus*-removal experiment). Both ANCOVAs detected no significant difference in shoot density on the final sampling date (October 27). None of the interactions between initial density and *Mytilus* absent/present were significant, i.e. the ANCOVAs were legitimate.

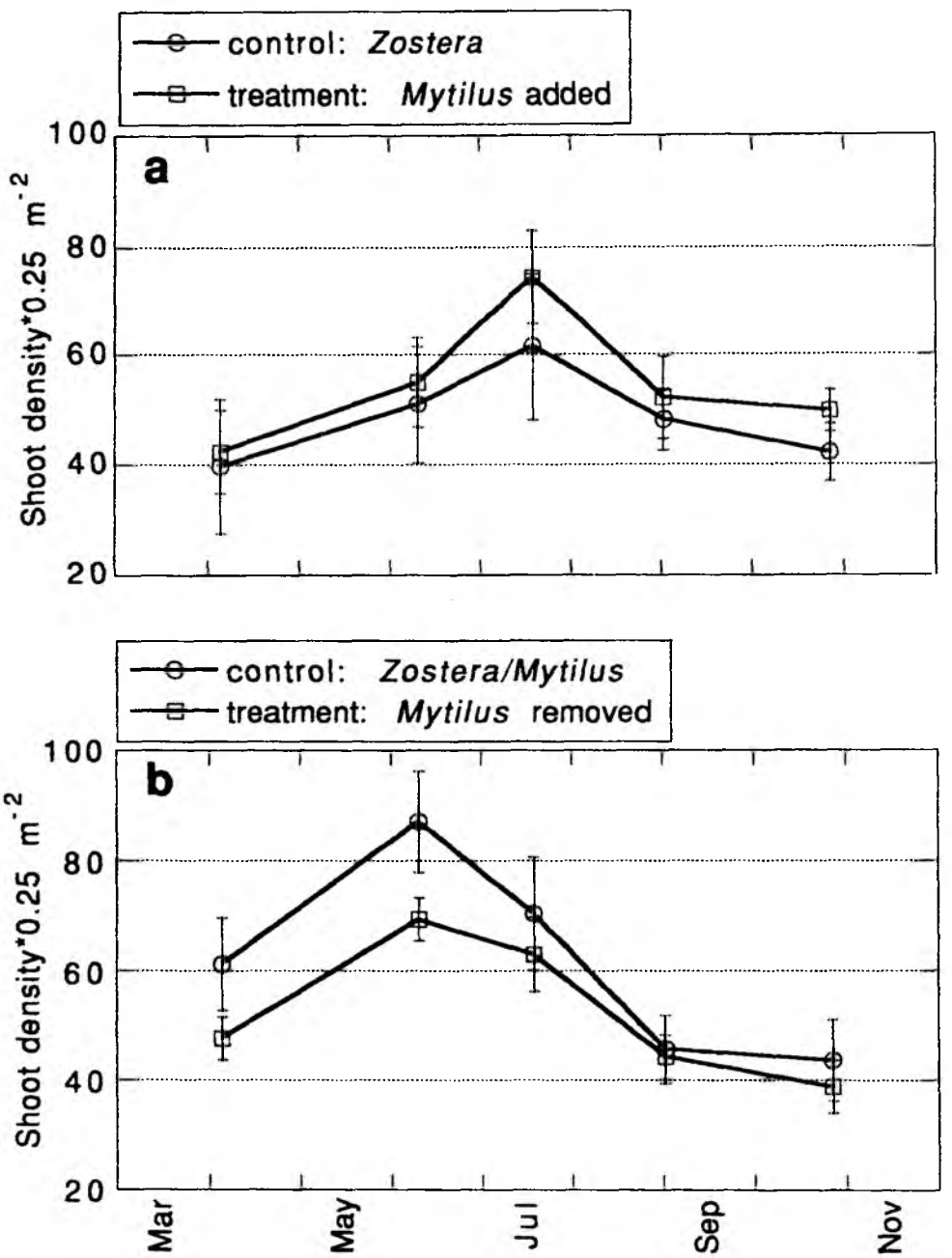


Fig. 5.6. *Zostera* densities ±1 SE in 50x50 cm plots (n=5) during one growth period from April 10 to October 27, 1993. The experimental effects of the addition of *Mytilus* to *Zostera* plots (a) and of the removal of *Mytilus* from *Zostera/Mytilus*-association plots (b) on density of *Zostera* are shown compared to the unmanipulated controls. For statistical analysis see Tab. 5.3 and 5.4.

Table 5.3. Univariate analysis of covariance (ANCOVA) and multivariate analysis of variance (MANOVA) on the effect of *Mytilus*-addition on *Zostera* shoot density. The ANCOVA tests if shoot densities are different on the final sampling date (October 27), taking into account the initial, post-manipulative shoot density as covariate. A test of homogeneity of slopes was done prior to the analysis. In the MANOVA, each of the 4 post-manipulative sampling dates (June 2, July 21, September 2, October 27, 1993) is treated as one dependent variable. Shoot numbers as response variable as well as the initial density in the case of the ANCOVA were square root transformed to remove heterogeneity of variances. The univariate data fulfil Cochran's test of homogeneity of variances and the multivariate data fulfil a modified Hawkins' test of multi-normality and -homoscedasticity (Johnson & Field 1993).

ANCOVA

Analysis	Source of variation	df	MS	F	p	concl.
Homogeneity of slopes	Initial density* *Mytilus* absent/present	1	0.157	0.442	0.531	ns
	Error	6	0.356			
ANCOVA	Initial density	1	2.471	7.551	0.029	*
	Mytilus absent/present	1	0.536	1.637	0.241	ns
	Error	7	0.327			

MANOVA

source of variation	Pillai Trace	F	Hyp. df	Error df	p	concl.
Mytilus absent/present	0.2747	0.473	4	5	0.756	ns

Both MANOVAs revealed that there was also no effect of *Mytilus* on *Zostera* density throughout the whole experimental period (April to October).
Before manipulation on April 10, the 10 *Zostera/Mytilus* plots of the *Mytilus*-removal experiment showed a trend of having a higher shoot density compared to the pure *Zostera* plots before manipulation (one-way ANOVA, shoot density square root transformed n=10, $F_{(1,18)}=3.199$, p=0.0905). However, this difference was not consistent with the outcome of a MANOVA, considering the shoot densities in the control plots on all 5 sampling dates as dependent variables. This analysis rejected the hypothesis that *Zostera* has a higher density in presence of *Mytilus* during the entire growth period (one-way MANOVA, Pillai Trace=0.829, $F_{(5,4)}=3.889$, p=0.106). These results are in concordance with the observational data on shoot densities described above (Fig. 5.2 a, Tab. 5.1).

Table 5.4. Separate univariate analysis of covariance (ANCOVA) and multivariate analysis of variance (MANOVA) on the effect of *Mytilus*-removal on *Zostera* shoot density on the last sampling date only in case of the ANCOVA, and on all 4 sampling dates during the growth period (June 2, July 21, September 2, October 27, 1993) in case of the MANOVA. For further details see Tab. 3.

ANCOVA

Analysis	Source of variation	df	MS	F	p	concl.
Homogeneity of slopes	Initial density* *Mytilus* absent/present	1	0.003	0.004	0.953	ns
	Error	6	0.798			
ANCOVA	Initial density	1	4.377	6.398	0.039	*
	Mytilus absent/present	1	0.216	0.316	0.592	ns
	Error	7	0.684			

MANOVA

source of variation	Pillai Trace	F	Hyp. df	Error df	p	concl.
Mytilus absent/present	0.4351	0.425	4	5	0.501	ns

Effects of *Mytilus* on *Zostera* leaf morphology and porewater nutrient concentrations. As a consequence of the experimental treatment, all measured characteristics of plant morphology, i.e. the length, width and area of the largest leaf, changed significantly (Fig. 5.7 c to e, Tab. 5.5 and 5.6). Where *Mytilus* was added, the leaf area increased by 35% compared to *Zostera/Mytilus* control plots, and this is almost precisely the difference in plant size in similarly configured unmanipulated plots at FO (leaf area is 36 % higher with *Mytilus* at FO, and 48 % at MOE, respectively, Fig. 5.7 e). The removal of *Mytilus* revealed a smaller effect: the decrease in leaf area in mussel free plots was only 16% and the decrease in leaf width not significant at all (Fig. 5.7 d and e, Tab. 5.6).

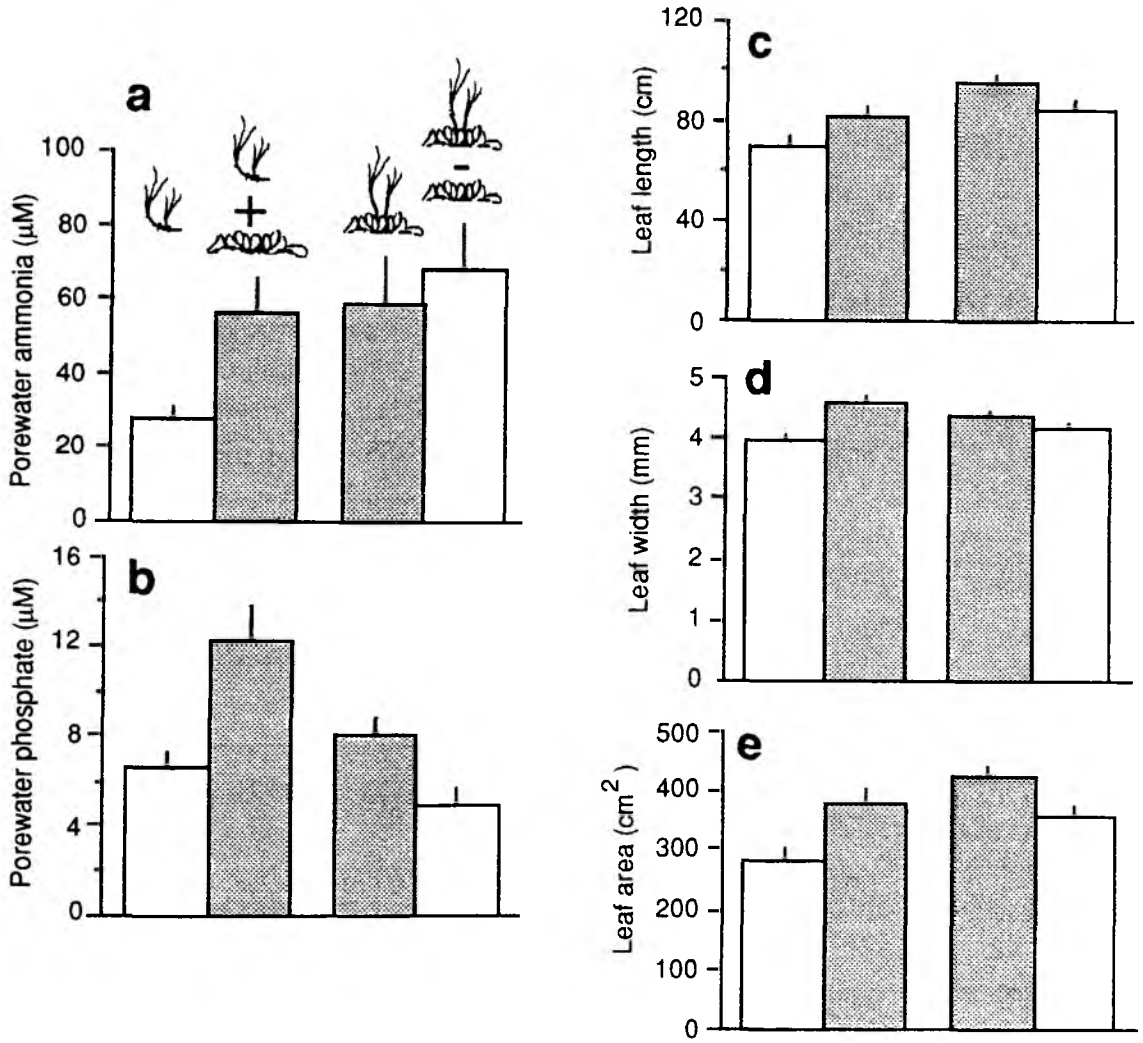


Fig. 5.7. Effects of experimental addition and removal of *Mytilus* on sediment porewater concentrations of ammonium (a) and phosphate (b) compared to unmanipulated controls, and on leaf parameters of *Zostera* (c to e). Measurements of plant morphology and sediment porewater were done between August 26 and 28, 1993. Triplicate sediment samples were taken and 6 adult plants were measured in each plot, thus sample size is n=15 for porewater analysis and n=30 for leaf morphology. Error bar is +1 SE. See Tab. 5.5 and 5.6 for statistical analysis of data.

Table 5.5. One-way ANOVA (with blocking factor) on the effects of experimental addition of *Mytilus* to *Zostera* patches on nutrient concentrations of sediment porewater and on morphology of the largest photosynthetic leaf of *Zostera*. The block*treatment interactions were tested in advance and are not shown. None of them was significant. After transformation, which is given below, all dependent variables fulfil Cochran's test on homogeneity of variances. Note that three samples from different plots were not analysed for phosphate. Thus, the design became unbalanced, i.e. 3 experimental plots had only 2 replicates. This increases the chance of committing a type I error. Nevertheless, the analysis is shown since the outcome is highly significant. The Cochran test was performed with a $G_{(crit)}$ for a group size of n=3.

For leaf parameters only, the significance level was Bonferroni-adjusted to $\alpha_{adjusted}=\alpha/3$ (ns $p \geq 0.0166$, * $0.0166 > p \geq 0.0033$, ** $0.0033 > p \geq 0.00033$, *** $p < 0.00033$).

Dependent variable transformation	Source of variation	df	MS	F	p	
Porewater ammonium x = log(y)	*Mytilus* absent/present	1	0.6271	12.30	0.0018	**
	Block	4	0.0373	0.7305	0.5800	ns
	Error	24	0.0510			
Porewater phosphate x = log(y)	*Mytilus* absent/present	1	0.4053	10.643	0.0037	*
	Block	4	0.0593	1.558	0.2223	ns
	Error	21	0.381			
Leaf length x = log(y)	*Mytilus* absent/present	1	0.0917	9.431	0.0033	**
	Block	4	0.1514	15.58	0.0001	***
	Error	54	0.0097			
Leaf width x = log(y)	*Mytilus* absent/present	1	0.0490	11.25	0.0015	**
	Block	4	0.0016	0.3767	0.8243	ns
	Error	54	0.0044			
Leaf area x = log(y)	*Mytilus* absent/present	1	0.2747	12.52	0.0008	**
	Block	4	0.1731	7.889	0.0001	***
	Error	54	0.0219			

Observational differences in sediment nutrient characteristics and plant morphology between *Zostera* stands with and without an understory of mussels are in concordance with the experimental results. The porewater concentrations of both ammonium and phosphate almost doubled after the addition of mussels (Fig. 5.7 a and b). The removal of mussels caused the phosphate concentrations to decrease in the manipulated plots. Only for porewater ammonium in the *Mytilus*-removal experiment. did I fail to detect a significant difference between plots with and without *Mytilus* (Fig. 5.7 a, Tab. 5.6).

Thus, the *Mytilus* addition/removal experiment provides evidence that the morphology of individual plants is in fact dependent on the presence or absence of mussels and not on an unknown covarying factor, and that in addition, sediment characteristics are altered by the presence of *Mytilus*.

Table 5.6. One-way ANOVA (with blocking factor) on the effects of removal of *Mytilus* from *Zostera/Mytilus* associations on nutrient concentrations in the sediment porewater and on the morphology of the largest photosynthetic leaf of *Zostera*. Only for leaf width, was there a significant block*treatment interaction (p=0.0497). Note that the design is unbalanced for phosphate data, since two samples from two different plots were not analysed. See Tab. 5.5 for further details.

Dependent variable transformation	**Source of variation**	**df**	**MS**	**F**	**p**	
Porewater ammonium $x = \sqrt[3]{y}$	*Mytilus* absent/present	1	0.6077	1.5361	0.2272	ns
	Block	4	3.3065	8.3575	0.0002	***
	Error	24	0.3956			
Porewater phosphate x = log(y)	*Mytilus* absent/present	1	0.4645	18.274	0.0003	***
	Block	4	0.0757	2.9794	0.0416	*
	Error	22	0.0254			
Leaf length x = log(y)	*Mytilus* absent/present	1	0.0546	8.414	0.0054	*
	Block	4	0.0401	6.183	0.0004	**
	Error	54	0.0065			
Leaf width x = log(y)	*Mytilus* absent/present	1	0.0048	1.756	0.1907	ns
	Block	4	0.0029	1.051	0.3995	ns
	Error	54	0.0028			
Leaf Area x = log(y)	*Mytilus* absent/present	1	0.0920	7.147	0.0099	*
	Block	4	0.0397	3.083	0.0233	ns
	Error	54	0.0129			

5.4 DISCUSSION

Competition

The experimental results concerning the change of *Mytilus* densities, as well as field observations, showed no negative effect of mussels on the shoot density and plant morphology of *Zostera*. This also holds true for the vegetative propagation of *Zostera* patch margins which are not influenced by the presence of an adjacent mussel patch. The rate of the margin projection into bare sand compared to projection into *Mytilus* patches during one growth period showed only small, non-significant differences.

Why is it that interference competition between mussels and the co-occuring macrophyte *Zostera* does not occur? In fact, spatial competition has seldom been found to structure soft-bottom communities. The key to these community regulation differences between soft- and hard-bottom lies in the mechanisms by which mussels may competitively exclude macroalgae or sessile organisms. Peterson (1979) distinguishes two principal mechanisms of interference competition on hard substrata: (1) heavy settlement and overgrowth and subsequent suffocation and starvation of the overgrown organisms, and (2) direct interference by crushing or prying other organisms off the surface of the primary substratum. Despite heavy settlement of *Mytilus* plantigrades in summer 1992 and 1993 (personal observations), mechanism (1) was not observed during the study period in Kiel Fjord or in the adjacent Kiel Bight at several subtidal stations. Direct interference is rare according to Peterson (1979), since on soft-bottoms, competitively inferior organisms may easily find a spatial refuge from competition in the three-dimensional space which is available.

However, the community studied differs from a true soft-bottom situation because both organisms are restricted wholly (*Mytilus*) or partially (*Zostera*) to the two-dimensional sediment surface. Thus, available space is reduced to two dimensions. This increases the likelihood for space to become a limiting resource compared to endobenthic, three-dimensional soft-bottom communities. In this respect, the *Zostera*/*Mytilus*-association represents an intermediate between a true soft-bottom and a hard-bottom situation. Moreover, mussels are known to suppress the growth of conspecifics if occurring in beds or clumps, not only by competition for food, but also via spatial competition (Harger 1972, Bertness & Grossholz 1985, Fréchette & Lafaivre 1990). To do this,

they need not be anchored to a primary rocky substrate. Therefore, squeezing and crushing of *Zostera* shoots may be a potential mechanism by which mussels affect eelgrass (Photo 7).

Direct interference of *Zostera* by mussels was observed by Ruth (1991 and personal communication) in intertidal *Zostera* meadows of the Wadden Sea and by Kobarg (1993) who transplanted *Zostera* in boxes to greater water depths to study the light limitation. While the situation in the Wadden Sea may be completely different from the Baltic, our results seem to contradict Kobarg's observations. Interference competition by mussels squeezing the shoots of *Zostera* seems only plausible if space is limiting and mussel patches can not extend further. I believe that this was the case in Kobarg's experiments, since the mussels covered the experimental plots completely and attached to the edges of the plastic boxes. The forces they could exert on the shoots were higher compared to mussel patches which have the possibility of extending towards sandy edges (Photo 6). Instead, space for epibenthic plants or animals is never limiting in the depth range investigated. Approximately 50% of the area at FO and 60% at MOE consists of bare sand devoid of *Zostera* and *Mytilus*.

The ultimate reason for a lack of interference competition may be the frequent biological and physical disturbance of mussel patches which never let coverage by mussels increase beyond 20%. The recruitment of *Mytilus* and hence patch extension is primarily controlled by predation from the seastar *Asterias rubens*, whereas physical disturbance is the main source of mortality for mussel adults (Reusch & Chapman in prep.) During the winter 1992/93, most of the marked pure mussel patches neighbouring *Zostera/Mytilus* patches were destroyed by storms (personal observations). Furthermore, in 4 out of 8 marked *Zostera/Mytilus* patches, mussels were washed away while *Zostera* remained intact. As a consequence, mussel patches inside or outside eelgrass meadows rarely attained a size larger than 2 m diameter. I assume that this is below the limit at which forces exerted by the cumulative growth of *Mytilus* individuals harm eelgrass shoots.

Although several studies showed that mytilid mussels interfere with macroalgae in the intertidal zone (Dayton 1971, and Paine 1974 for *Mytilus californianus*; Paine 1971 for *Perna canaliculus*; Menge 1976 for *Mytilus edulis*), there is recent experimental evidence that *Mytilus edulis* is not competitively superior to fucoid algae on North-Atlantic rocky shores (Janke 1990, McCook & Chapman 1991).

It may be questioned whether the time scale, i.e. one growth period from spring to autumn, is sufficient to exclude the possibility of competition occurring between mussels and eelgrass over a longer period. I found no evidence for this, since none of the above mentioned 4 *Zostera/Mytilus* plots, in which *Mytilus* coverage survived the winter storms, developed into a pure mussel bank over a period of 17 months.

Fertilization of *Zostera*

Instead of damaging eelgrass, mussels have a positive effect on *Zostera* growth. The mechanism of this facilitation is the biodeposition of nutrient rich material by the mussels onto the sediment surface. The mineralization of the organic material increases the amount of nutrients available to the rhizosphere of *Zostera.*

The significant differences in plant morphology and size which were produced by the experimental removal and addition of mussels give strong evidence that *Mytilus*, and not an unknown covarying factor, is responsible for an increased growth of *Zostera.* Although actual growth rates were not measured due to time constraints, I believe it to be legitimate to correlate plant morphology with growth because the experimental blocks were chosen to be as homogeneous as possible. Therefore, I assume that in April, all plants started to grow from the same average size.

It is well known that leaf morphology is a function of the nutrient conditions to which *Zostera* is exposed to (Short 1983b). Plants are smaller and the leaves are narrower under nutrient deficiency (Philip 1936, Short 1987). The ratio between above ground and below ground biomass becomes smaller and the length of the roots increases (Barko et al. 1991). All these morphological characteristics are concordant with the results of the present study and I conclude that growth of *Zostera* is nutrient limited in Kiel Fjord.

The responses of shoot densities to nutrient enrichment vary in the literature. Whereas Short (1983b) found a significantly higher shoot density in nutrient poor sediments, Orth (1977a) observed increased density after experimental fertilization of *Zostera.* My data indicate no effect of higher sediment nutrient levels on the density of *Zostera.*

There is an ongoing debate concerning the relative importance of nitrogen vs. phosphorus limitation in seagrasses. Growth was found to be nutrient limited in several studies (Harlin & Thorne-Miller 1981, Short 1983a, Short 1983b, Williams & Ruckelshaus 1993). However, Murray et al. (1992) reported increased growth in *Zostera marina* after phosphorus addition to the sediment. My data indicate that nitrogen is limiting for eelgrass growth on the organically poor sediments of the very shallow subtidal (1-2.5 m depth) of Kiel Fjord. I infer this from the lack of a correlation between porewater phosphate concentration and leaf lengths in this study, indicating that phosphate is of minor importance at the study site.

The saturation concentrations for porewater ammonium (75 µM in FO and 100 µM in MOE), which were derived graphically from the calculated regression equations, fall well within the range of concentrations documented for growth saturation of *Zostera* in the literature (Short & McRoy 1984, Dennison et al. 1987, Williams & Ruckelshaus 1993). These concentrations of porewater ammonium are never encountered at MOE and very seldom at FO.

Recently, Pedersen & Borum (1993) fertilized a Baltic *Zostera* population with a combined N:P:K-fertilizer. In a non-replicated experiment, they found a moderate, but significant (7% to 24%) increase in leaf elongation rate in fertilized plots compared to control plants. Since, during summer, the sediments of their study site had a markedly higher ammonium concentration in porewater than my sediments (240 to 300 µM compared to 17 to 110 µM at FO and 16 to 70 µM at MOE) a nitrogen limitation of *Zostera* growth in the Kiel Fjord is very likely.

The removal of *Mytilus* from *Zostera/Mytilus* associations showed a smaller effect on plant parameters compared to the addition treatment (Fig. 5.7 c to e). Where *Mytilus* was experimentally removed, plants attained a larger size than those in *Zostera* control plots. This suggests the presence of a pool of biodeposited organic matter in the sediment which mineralizes over a longer period and continues to fertilize *Zostera* for some weeks after mussel removal. In the *Mytilus*-addition treatment, the direct excretion of ammonium and the production of rapidly degradable biodeposits by mussels starts immediately after the addition.

If *Mytilus* occurrence is a major source of variation in the sediment nutrient status and, as a consequence, for plant morphology, the high plot to plot variability among *Zostera* as well as *Zostera/Mytilus* patches may reflect the history of a patch. It is probable that pure *Zostera* patches with relatively large

plants once had a *Mytilus* understory for a certain time before mussels were washed away by winter storms. Likewise, in *Zostera/Mytilus* patches having small plants, *Zostera* may exist in association and thus under nutrient enrichment for a few weeks only. Storms not only destroy associations, but can change a *Zostera* patch within a few hours into an association through drifting adult mussel clumps. They are as important for the formation of *Zostera/Mytilus*-associations as is mussel recruitment (see chapter 3).
Similarly, the high rate of mussel patch fluctuation may have influenced the comparison of propagation rates. In contrast to studies by Kenworthy & Fonseca (1977,1992) and Williams (1990) who reported that the rate of seagrass colonisation of bare sand is accelerated with fertilization, I was not able to detect differences in propagation rates among *Mytilus*-fertilized eelgrass and pure eelgrass stands. One possible explanation is that time delay between fertilization and plant response in the form of increased vegetative sprouting is longer than one vegetation period. Since patch fluctuation of mussel beds is high at both sites, the time period of co-occurrence with mussels of the selected *Zostera*-patches may be too short to detect a response. The propagation rates I found attained on the average 30% of the maximal rhizome elongation rates reported for *Zostera* (Duarte 1991), but in some of my plots these maximal propagation rates of 30 cm were attained.

For soft-bottom colonising angiosperms, very few other facilitating non-consumer plant-animal interactions have yet been studied experimentally. (Bertness 1984) worked on the interaction between the cord grass, *Spartina alterniflora* and a mytilid mussel, *Geukensia demissa* in north-east American salt marshes. In accord with the present study, *Spartina* benefited from the fertilization by the mussel through a higher net production and an elevated ratio of above ground to below ground biomass.

Ecological implications

Since 1950, the Western Baltic has received increasing nutrient input from human activity (Larsson et al. 1985). As a consequence, the biomass of macrozoobenthos and especially filter feeding molluscs has increased above the halocline due to increased food supply (Cederwall & Elmgren 1980). In some regions the *Fucus vesiculosus* community of the Baltic proper has been replaced by a mussel-red algal community (Kautsky et al. 1992). In Kiel Bight,

the macrozoobenthos biomass in general, and especially of blue mussels, has increased since 1960 (Brey 1986). Eutrophication may favour filter feeders, while seagrasses including *Zostera* are known to be weakened by eutrophication induced turbidity in many parts of the world (Orth & Moore 1983, Giesen et al. 1990, Walker & McComb 1992). Although few hard data are available, these processes are also likely to have occurred in Kiel Fjord since this site receives even more anthropogenic nutrients than the open Kiel Bight due to the discharge of the river Schwentine (Stienen 1986).

My data from Kiel Fjord indicate that the two processes, the decline of eelgrass and the increase of mussel biomass, do not reinforce each other. Instead, an understory of mussels mitigates nutrient limitation of *Zostera*. Since the depth distribution of eelgrass has moved upwards due to light limitation (Kobarg 1993), the principal distribution range of *Zostera* in Kiel Fjord becomes more and more restricted to the very shallow subtidal (1-3 m depth). In these depths, the sediments are often sandy and organically poor since organic matter never accumulates due to wave exposure.

Additionally, mussels may even improve the light transmittance to eelgrass by decreasing water turbidity through their filtering activity.

This study presents evidence that deterioration of *Zostera* stands by mussels does not occur in two shallow subtidal sites. This may change if, after a series of calm winters without major disturbances, most of the sand became covered by mussels. I hypothesise that large mussel patches which develop in this way may be able to destroy *Zostera* simply by force of their combined growth extensions.

I suggest that future work should be directed to test the hypotheses whether (1) there are conditions under which an understory of mussels may harm eelgrass and (2) the co-occurrence of *Zostera* and *Mytilus* is a trade-off between beneficial effects for eelgrass through mussel fertilization and negative effects through interference.

Chapter 6
General summary and conclusions

As predicted by Kautsky (1981), in the Western Baltic in contrast to the Baltic proper, the presence of epibenthic predators may control mussel abundance. During the study period, the seastar *Asterias rubens* was found to be the most important epibenthic predator on mussels. The shore crab *Carcinus maenas* accounted for at most 15% of the predation caused mussel mortality during the summer months and was totally absent during autumn and winter. Predator exclusion had a marked effect on areal growth of mussel patches. In the statistical analysis, predation explained the largest proportion of the experimental variance. Calculations of the relative effect size ω^2 revealed that presence or absence of predators accounted for approximately 52% of the total variation in clump size. Water depth was the second significant main effect and explained 16% of the variance.

Predation acted primarily on young (<1 yr old) mussels which was evident from both predator exclusion experiments. The first experiment was performed in autumn 1992 on substratum bare sand after an intense spatfall and revealed that young mussels did only survive under protection of cages. In the 1993 mussel clump transplantation experiment, young mussels which previously were hidden in the interstices of the mussel matrix, contributed largely to a 6.3-fold increase in clump area during the experimental period of 10 mo (Photo 5). Data on the feeding preferences of *Asterias* and length/frequency distributions of mussel recruits further supported that especially juvenile mussels suffer from a strong predation pressure.

An areal decrease of clumps which could be attributed to heavy predation occurred twice during the 10 mo of observation. The corresponding critical densities of seastars were approximately 240 ind*m^{-2} in March/April (3 to 4°C water temperature) and 180 ind*m^{-2} in September (12°C water temperature). These rather high values may provide a first estimation of those seastar densities under which a destructive feeding on mussel beds in Kiel Fjord might be expected.

However, whereas *Asterias* regulates the overall abundance of mussels at the sites, it does not account for patchiness in mussel distribution. Following permanent quadrats marked on mussel beds, I never observed seastars creating bare patches by their feeding activity. Another evidence comes from the transplanted clumps. I expected that some of them would have been consumed by seastars and others not due to the patchy distribution of *Asterias*. However, all clumps survived throughout 10 mo.

Instead, patchiness in *Mytilus* distribution (Photo 1) is mainly produced by stochastic storm events which disrupt mussel beds and disperse clumps over the area. Storms are also responsible for a considerable downslope transport of mussel clumps to depths were recruitment of *Mytilus* is poor. Patchiness is maintained by a preferential recruitment of juvenile mussels onto existing beds.

Stable substratum was found to have no influence on mussel clump growth. The availability of primary hard substratum seems to control mussel distribution entirely by mediating the impact of physical disturbance. Although both study sites are sheltered, the impact of physical disturbance on cover of mussel beds was considerably and unexpected to this extent. For example at FO, storms removed roughly 75% cover of the marked mussel beds in January 1993 and, on a new set of permanent plots, half of the original coverage during October 1993. I suppose that the byssal attachment strength of mussels at these sites is weak compared to e.g. those beds in the Wadden Sea which are able to withstand a much stronger disturbance regime.

In contrast to mussels, *Zostera* meadows were found to be much more persistent to storm disturbance. Their cover decrease in 8 permanent plots during a period with 3 storms of Bft. 11-12 in January 1993 was only 26% of the original (mostly 100%) cover and even no loss of *Zostera* cover was detectable during the storm in October 1993. These differences in stability between both pure stands, *Zostera* and *Mytilus*, were highly significant in an ANCOVA. Therefore I suggest that eelgrass is the more important structuring element in this shallow water environment. The presence of eelgrass allows the formation of mussel beds which otherwise would be much more scarce.

Whereas Kobarg (1993) showed that the lower distribution limit of eelgrass in Kiel Fjord is set by light availability, I can only speculate how patchiness of *Zostera* beds is maintained within the shallow water zone (1 to 3 m). It may be

that the eelgrass coverage of 50% and 30% found at FO and MOE, respectively, reflects the time *Zostera* needs to recover from the last destructive ice winter in 1986/87. The relatively slow rate of vegetative propagation (13 cm in one vegetation period) found in this study and the absence of germlings in one to 3 m depth support this contention.

Abiotic as well as biological factors were found to structure the shallow subtidal of Kiel Fjord. This result itself is not very surprising since in only a few community a single factor (Paine 1971 and 1974, keystone predator concept) the sole determinant of community structure. The community studied shows that the separation into biological and non-biological structuring factors is highly artificial. Both, biological and physical factors have strong interlocking effects on community structure. Blue mussels and eelgrass are epibenthic species which strongly modify their physical environment. In this way, in *Zostera/Mytilus* mixed stands, the presence of *Zostera* as well as of mussel beds have marked effects on each other.

The predation impact at least of *Asterias* on juvenile mussels was found to be similar on mussel beds with and without eelgrass. Therefore, I suggest that *Zostera*'s effect on mussel recruitment is primarily due to its modification of the hydrodynamic regime which increases the rate of primary and especially secondary settlers. Furthermore, *Zostera* provides secondary hard substratum for mussel recruits and probably decreases the risk of burial and dislodgement during storms.

On adult beds, *Zostera* has a beneficial effect on mussels due to its capability to baffle wave induced current velocities by canopy friction. I was able to demonstrate experimentally that the loss of established mussel beds through storm dislodgement is markedly decreased in the presence *Zostera*. Also, the chance for dispersed mussel clumps to become established within the meadow is markedly increased compared to areas of bare sand.

Mussels modify the environment mainly by their filter feeding activity which transfers large amounts of organic matter from the pelagic zone to the benthos via faeces and pseudofaeces. These biodeposits then become mineralized by bacterial activity and, as a consequence, the nutrient concentrations of the sediment porewater increase. In this way, the presence of a mussel understory mitigates situations of nutrient limitation in eelgrass. My data suggest that, in particular,

nitrogen in form of ammonium is growth limiting for eelgrass in Kiel Fjord. I hypothesise that the proportion of *Zostera* meadows which suffer from nutrient limitation is increasing since its principal distribution range has shifted to shallower water as a consequence of eutrophication caused light limitation. Yet, in the very shallow subtidal, the sediments are often poor in organic material due to wave exposure and an erosion regime which prevents any accumulation of organic material.
The observed higher abundance of mussels inside seagrass canopy is not due to a refuge against predation. No alteration of the predation regime for juvenile or adult mussels was found in the presence of a *Zostera* canopy. The above bottom architecture of the eelgrass meadow does not seem to interfere with the foraging activity of seastars. Likewise, no negative effects of mussel beds on vegetative propagation or shoot density of eelgrass were evident.

Only data of a mussel clump transplantation experiment revealed a moderately depressed growth rate of mussels inside the eelgrass canopy. However, I suggest that the advantages *Mytilus* encounters through the presence of an eelgrass canopy by far outweigh these shortcomings. Therefore, in summary, the interactions between mussels and eelgrass in the shallow subtidal of Kiel Fjord provide an example for a facultative mutualism (Fig. 6.1).

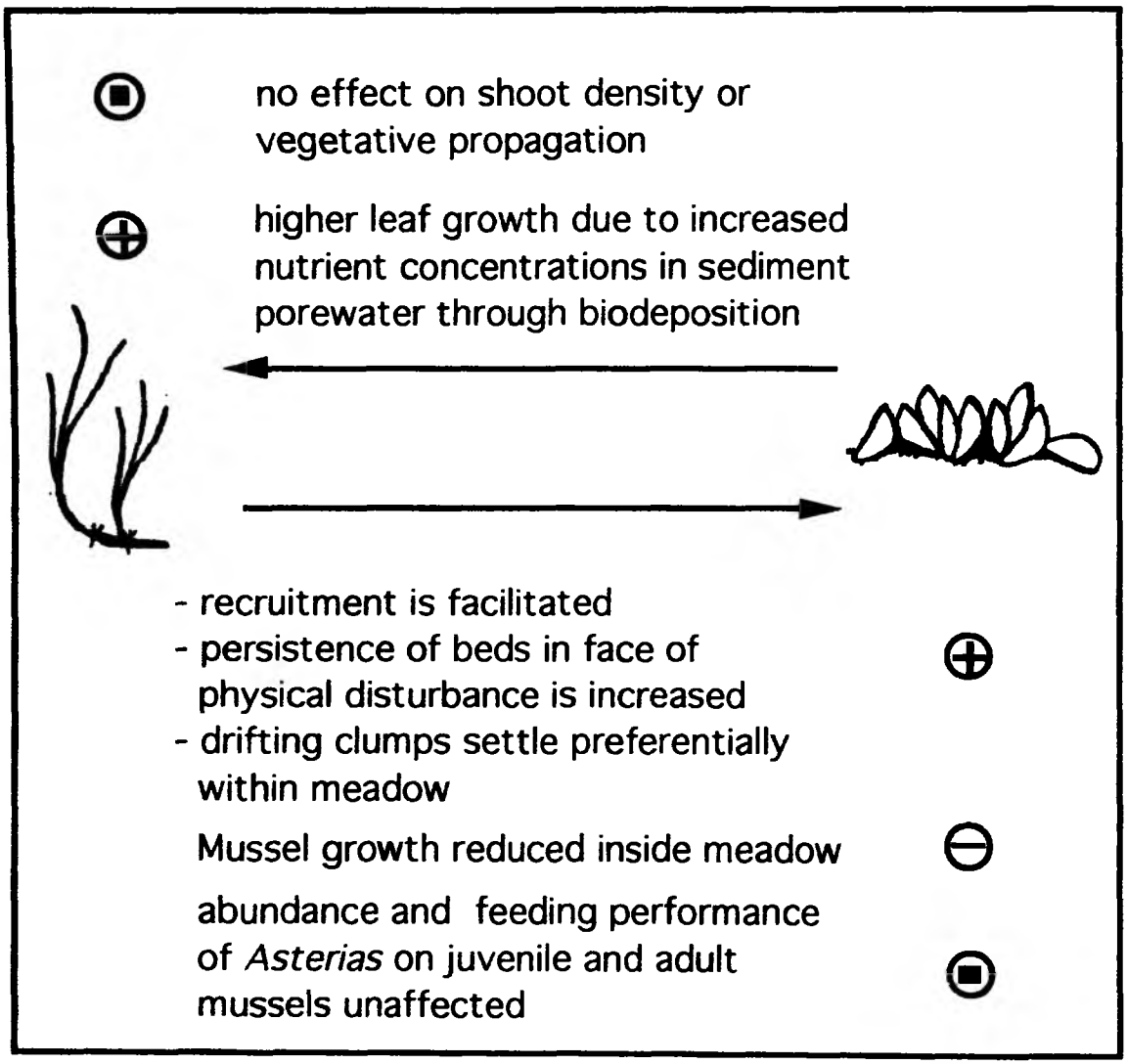


Fig. 6.1. Summary of interactions between eelgrass and blue mussels in Kiel Fjord.

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