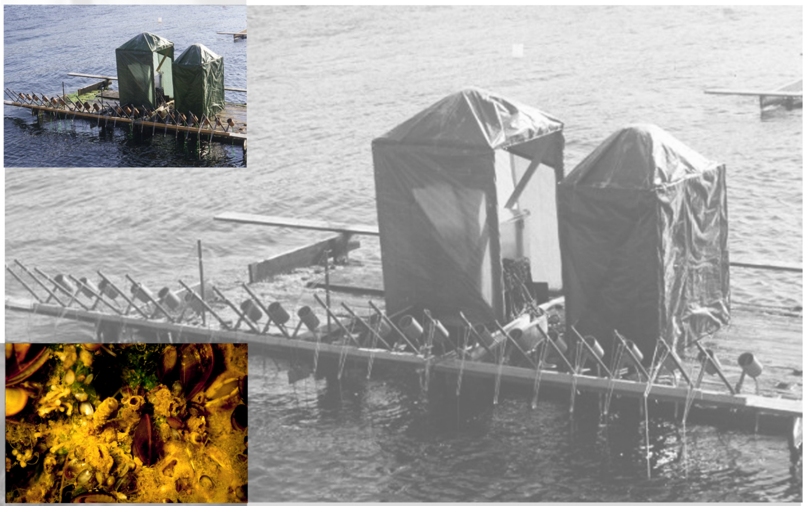
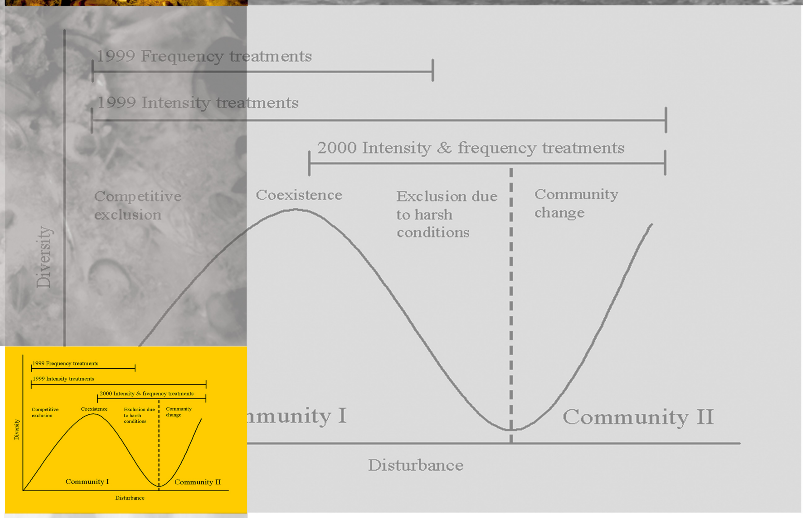
An experimental test of the intermediate disturbance hypothesis: influence of two disturbance types on the structure of established Western Baltic fouling communities





Dissertation zur Erlangung des
Doktorgrades der Mathematisch-
Naturwissenschaftlichen
Fakultät der Christian-Albrechts-
Universität zu Kiel

vorgelegt von Mark Lenz

Kiel 2003

An experimental test of the intermediate disturbance hypothesis: influence of two disturbance types on the structure of established Western Baltic fouling communities

Dissertation zur Erlangung des
Doktorgrades der Mathematisch-
Naturwissenschaftlichen Fakultät
der Christian-Albrechts-Universität
zu Kiel

vorgelegt von Mark Lenz

Kiel 2003

Table of contents

Appendix II: raw data

Summary

The intermediate disturbance hypothesis (Connell 1978) is a widely accepted concept in community ecology. It assumes disturbances as a potent agent to override the competitive exclusion principle (Gause 1937) and to facilitate the long-term coexistence of competitively inequal species. It states that diversity is highest at an intermediate level of disturbance while it is reduced under weak disturbance conditions due to competitive exclusion. Due to harsh environmental conditions, it is reduced under severe disturbance regimes as well. The model was developed with regard to species rich and oligotrophic systems like tropical rain forests and coral reefs. Despite its ubiquitous importance in the diversity-related discussion, it has rarely been tested in an experiment. The aim of this study is to verify the predictions of the concept in a eutrophic, species-poor system, as it is represented by the Western Baltic, in an *in situ* experimental approach. In two discrete experimental series, established hard-bottom communities were submitted to various levels of emersion and exposure to enhanced UVB radiation. The experiments were conducted with communities of two successional stages in Kiel Fjord. Fouling assemblages established on PVC-settlement panels and underwent 3 or 12 mo of undisturbed maturing before they were exposed to experimental manipulation. Species richness, Shannon index, evenness and community composition were recorded in order to measure the disturbance impact on community structure.

The blue mussel *Mytilus edulis* is known to be one of the dominant space competitors in the Western Baltic, and a 1 yr long observation of undisturbed succession at the study site confirmed this picture. Mussels dominated all vertically orientated communities and lowered their diversity within 2 mo after the first mussel spat fall.

Emersion treatments were subdivided into two disturbance components: disturbance frequencies, defined as 15 min long periods of emersion that were applied with various frequencies d^{-1}, and disturbance intensities, defined as various durations of continuous exposure to the air d^{-1}. The study on 3 mo old communities was firstly conducted in 1999 and repeated with an improved experimental design in 2000. The predicted unimodal relationship between disturbance and diversity was observed for both disturbance components in the first study year. The dominant competitor was impaired by all emersion treatments. In the second year, however, disturbance-diversity relationships were non-significant, monotonously increasing or inversely unimodal (U-shaped). Significant effects of the applied disturbance regimes on the dominant blue mussels were almost absent. This was presumably due to a modification of disturbance effects through colder and cloudier climatic conditions in 2000. The divergence of patterns was also due to a restricted dominance of the top competitor on the

undisturbed control panels in the second study year. The unimodal pattern was not observed in the study on the 1 yr old communities as well.

Disturbance frequencies and intensities were similar with regard to the direction of their forcing but differed in effect size. Intensity treatments had a more severe impact and led to a more pronounced pattern of the respective disturbance-diversity relationships. With regard to disturbance sensitivity as a function of community age, an unexpected picture was observed: under similar disturbance regimes, the initially more diverse 1 yr old assemblages experienced a greater decline in diversity in the intermediate disturbance range than younger communities. This was true for both disturbance components. In all experiments a diversity-enhancing change in community composition at the extreme end of the emersion disturbance gradient was observed. This observation was translated into an extended model of the classical unimodal relationship. The proposed sinusoid curve includes the disturbance-induced increase in diversity under conditions of extreme disturbance. This new model provides also an explanation for U-shaped disturbance-diversity relationships that have been found in this and other studies, which are incongruent with the classical concept.

In the study on the effects of UVBR, ambient irradiance regimes were elevated by 100 % on average by the use of fluorescent UVB tubes. UVBR treatments were designed as various periods of continuous exposure to enhanced UVBR doses d^{-1}. Assemblages established on PVC-panels and underwent maturing for 3 or 12 mo. During the maturing period as well as the experimental phase settlement panels were horizontally orientated. In contrast to the vertically orientated communities used in the emersion experiments, these were dominated by red algae while blue mussels were scarce. UVBR-experiments on communities of both successional stages were conducted in one year and were not repeated. UVBR treatment effects were transient and did not generate a unimodal disturbance-diversity pattern. Though treatment effects were not persistent, a general tendency for green algae to increase and for red algae to decrease with increasing daily UVBR exposure length was observed.

The results of this study deepen our understandings of the effects of disturbances on communities and extend the IDH with regard to diversity-enhancement, due to disturbance-induced change in community structure, at the extreme end of a disturbance gradient. This sinusoidal model accounts for all disturbance-diversity patterns that have been reported up to date. This study also throws light on restrictions in the testability of the concept due to fluctuations in environmental factors that modify the effects of disturbances. The predicted intermediate disturbance range of maximum diversity can shift along the applied disturbance gradient when the disturbance applied interacts with environmental factors. This observation

emphasizes the importance of repeated experiments in the *in situ* investigation of ecological models. The latter is mandatory in times of global change when ecological concepts are an indispensable tool of forecasts in management programs and conservation projects.

Zusammenfassung

Die von Connell (1978) formulierte „Intermediate Disturbance Hypothesis (IDH, deutsch: Theorie der mittleren Störungshäufigkeit)“ ist ein weithin akzeptiertes Konzept in der Synökologie. Es betrachtet Störungen als einen Faktor, der das Konkurrenzausschlussprinzip (Gause 1937) außer Kraft setzt und die langfristige Koexistenz konkurrenzungleicher Arten in einer Lebensgemeinschaft ermöglicht. Es besagt, dass die Diversität in einem Bereich mittlerer Störungen maximal ist, während sie zu den beiden Enden eines Störungsgradienten hin abnimmt. Zu schwache Störungen sind nicht in der Lage den Konkurrenzausschluss zu verhindern, während zu starke Störungen alle Arten, außer einigen wenigen besonders robusten Pionierformen, verdrängen. Das Modell wurde ursprünglich für artenreiche und oligotrophe Systeme, wie tropische Regenwälder oder Korallenriffe, entwickelt. Trotz seiner weitreichenden Bedeutung und seiner Relevanz in der wissenschaftlichen Diskussion um Diversitätsmuster wurde es nur selten experimentell getestet. Das Ziel dieser Studie ist es daher, die Gültigkeit der Voraussagen des Modells in einem experimentellen Ansatz, für ein artenarmes und eutrophes System, wie es die Westliche Ostsee darstellt, zu prüfen. In zwei getrennten Ansätzen wurden etablierte Aufwuchsgemeinschaften verschiedenen Behandlungsstufen der Störungen „Trockenfallen“ und „erhöhte UVB-Einstrahlung“ ausgesetzt. Zur Erfassung der Behandlungseffekte wurden die Diversität und die Zusammensetzung der Gemeinschaften unter dem Einfluss der Störungen und in einer ungestörten Kontrolle erhoben. Die Versuche wurden mit 3 und 12 Monate alten Gemeinschaften, die sich ungestört auf PVC-Siedlungsplatten entwickelten, durchgeführt. Alle Versuche fanden in der Kieler Förde statt.

Die Miesmuschel *Mytilus edulis* ist einer der dominanten Raumkonkurrenten in der Westlichen Ostsee, und ein einjähriges Monitoring der ungestörten Entwicklung von Aufwuchsgemeinschaften am Versuchsort hat dieses Bild bestätigt. Alle vertikal aufgehängten Siedlungsplatten wurden innerhalb von zwei Monaten nach einem Larvenfall von Miesmuscheln dominiert und die Diversität der vorhandenen Gemeinschaften nahm im Zuge dieser Entwicklung ab.

Innerhalb des Störungstypus „Trockenfallen“ wurde zwischen den Störungskomponenten Frequenz und Intensität unterschieden. Frequenzbehandelte Gemeinschaften wurden verschieden häufig am Tag für jeweils 15 Minuten aus dem Wasser gehoben, während Intensitätsbehandlungen in verschieden lange Perioden einer kontinuierlichen Exposition pro Tag unterteilt waren. Die Studie, die sich mit 3 Monate alten Gemeinschaften befasste, wurde zuerst 1999 durchgeführt und dann mit einem verbesserten Versuchsdesign im darauf

folgenden Jahr wiederholt. Der von der Theorie vorhergesagte, unimodale Zusammenhang zwischen Störung und Diversität wurde im ersten Versuchjahr sowohl für frequenz- als auch für intensitätsmodulierte Gemeinschaften beobachtet. Die Miesmuschel als dominanter Konkurrent wurde auf allen Behandlungsstufen von der Störung beeinträchtigt. Im zweiten Versuchsjahr wurde dieses Muster jedoch weder für die 3 Monats- noch für die 12 Monatsgemeinschaften beobachtet. Die Beziehungen zwischen Störung und Diversität waren nicht signifikant, monoton steigend oder u-förmig (umgekehrt unimodal). Die Miesmuscheln wurden nur von den stärksten der applizierten Störungen negativ beeinflusst. Dies ging vermutlich auf eine Abschwächung der Störungsstärke aufgrund kühlerer klimatischer Bedingungen im Jahre 2000 zurück. Das abweichende Bild in den Diversitätsmustern zwischen den Studienjahren beruhte zudem auf der eingeschränkten Dominanz der Miesmuscheln auf den ungestörten Kontrollplatten im zweiten Jahr. Die Störungskomponenten Frequenz und Intensität waren vergleichbar in ihrer Wirkrichtung, unterschieden sich aber in ihrer Effektstärke. Intensitätsbehandlungen hatten stärkere Auswirkungen auf die Gemeinschaftsstrukturen und führten zu einer deutlicheren Ausprägung der jeweiligen Störungs-Diversitätsbeziehungen. Die älteren Gemeinschaften waren, im Hinblick auf ihre Diversität, unerwarteterweise empfindlicher gegenüber den applizierten Störungen als die jüngeren. Die anfänglich artenreicheren, älteren Gemeinschaften erfuhren einen stärkeren störungsbedingten Rückgang der Diversität im Laufe des Versuchs als die jüngeren. Dies galt für beide Störungskomponenten.

In allen Versuchsserien wurde am harschen Ende des Störungsgradienten ein Wandel in den Gemeinschaftszusammensetzungen festgestellt, der mit einer Erhöhung der Diversität einherging. Diese neue Beobachtung führte zu einer Erweiterung des Modells: ein sinusförmiger Kurvenverlauf berücksichtigt den Diversitätsanstieg unter extremen Störungsbedingungen. Dieses neue Modell bietet auch eine Erklärungsmöglichkeit für den in dieser und bereits in anderen Studien beobachteten, umgekehrt unimodalen Zusammenhang zwischen Störung und Diversität, der mit dem klassischen Konzept unvereinbar ist.

Im Rahmen der Versuche zum Einfluss von UVB-Strahlung wurde die Umgebungsstrahlung durch UVB-emittierende Lampen um durchschnittlich 100 % erhöht. Die Behandlungsstufen umfassten verschieden lange Perioden erhöhter UVB-Einstrahlung pro Tag. Die Gemeinschaften reiften ebenfalls für die Dauer von 3 und 12 Monaten, wobei die Siedlungsplatten, entsprechend ihrer Position im Experiment, horizontal orientiert waren. Die unterschiedliche räumliche Orientierung der Besiedlungsplatten führte zu stark abweichenden Ausgangsgemeinschaften: horizontal orientierte Zönosen wurden von Rotalgen dominiert während Miesmuscheln fast völlig fehlten. Gemeinschaften beider Sukzessionsstufen wurden im selben Versuchsjahr manipuliert und die Experimente wurden nicht wiederholt.

Die Effekte der UVB-Behandlungen waren vorübergehend und verschwanden nach dreimonatiger Versuchsdauer. Ein Muster, wie es die IDH vorhersagt, war zu keinem Zeitpunkt zu beobachten. Trotz dieser Tatsachen lies sich ein allgemeiner Trend, nach dem Rotalgen mit zunehmender Behandlungsstärke ab- und Grünalgen zunahmen, feststellen. Dieses Bild stimmt gut mit den Resultaten vergleichbarer Studien überein.

Die Ergebnisse dieser Studie erweitern das Verständnis für die Auswirkungen von Störungen auf die Struktur von Lebensgemeinschaften, im besonderen in Bezug auf extreme Störungsstärken, die einen Gemeinschaftswechsel herbeiführen können. Die vorgeschlagene, sinusförmige Erweiterung des gängigen Modells bietet eine Erklärungsmöglichkeit für alle bisher gefundenen Beziehungen zwischen Störung und Diversität, einschließlich des umgekehrt unimodalen Verlaufs.

Im weiteren weist diese Untersuchung auf die mit der experimentellen Prüfung des Modells verbundenen Schwierigkeiten hin. Umweltfaktoren modifizierten die Stärke der applizierten Störungen im Fall der Emersionsbehandlungen in den zwei aufeinander folgenden Versuchsjahren. Dies zeigt, dass der Bereich der mittleren Störung entlang eines festen, vom Experimentator festgelegten Störungsgradienten wandern kann. Die zeitliche Replizierung ökologischer Feldstudien ist daher oftmals notwendig und sinnvoll, um die Interaktion des manipulierten Parameters mit fluktuierenden Umweltfaktoren richtig abschätzen zu können. Im Hinblick auf die IDH ist solches Wissen vor allem dann relevant, wenn es um die praktische Anwendung des Konzeptes im Rahmen von Konservierungs- und Managementprogrammen geht.

1. General introduction

1.1 The intermediate disturbance hypothesis

During the last 4 decades the question how diversity is generated and maintained in ecological communities, and the search for causes of patterns of species diversity were hotspots in the discussion among community ecologists. Hutchinson (1959) formulated the core question being the stimulus for a conceptual development in community ecology by asking, “Why are there so many kinds of animals?”; and a few years later MacArthur (1965) simply stated, “Patterns in species diversity exist”. These putative simple observations resume perfectly the problems community ecologists try to address since then. Tilmann (1982) even considered Hutchinson’s question as: “The most fundamental question that an ecologist can ask.”.

Hutchinson‘s and others‘ observations were in contrast with the Competitive Exclusion Principle (Gause 1937, in the following abbreviated as CEP), one of the central paradigms in community ecology, which assumes that competitively inferior species will be excluded by better adapted competitors while succession proceeds. Species number therefore declines while an equilibrium state, dominated by a single or a few highly competitive species, is approached.

A variety of explanatory concepts (reviewed by Palmer 1994) have been developed to describe the mechanisms that permit the long-term coexistence of competitively inequal species. Palmer (1994) suggested to classify these hypotheses with regard to the way they violate the conditions of the CEP. Following Palmer (1994) these conditions are: (1) time has been sufficient to allow exclusion, (2) the environment is temporally constant, (3) the environment has no spatial variation, (4) growth is limited by one resource, (5) rarer species are not disproportionately favoured in terms of survivorship, reproduction, or growth, (6) species have the opportunity to compete, (7) there is no immigration. Corollary: the greater the degree to which these conditions are broken, the greater the number of species that coexist.

An overall classification of theories concerning biodiversity differentiates between equilibrium and non-equilibrium concepts. The equilibrium view assumes that most of the communities observable in nature are at the end of their successional process. Species richness and composition are constant over a long time span and oscillate around a theoretical equilibrium point. To reach equilibrium the first two conditions of the CEP must be fulfilled while conditions 3 - 7 must be violated to allow high diversity in an equilibrium system. Spatial heterogeneity (violation of condition 3) enables species to coexist on a small spatial scale. This assumption is embedded in the concepts of **environmental heterogeneity**, **habitat diversity** and **spatial variability**. If species differ in their basic requirements, growth is not limited by one resource (violation of condition 4). This case is treated in the **resource ratio** and the **niche diversification hypothesis**. Invalidation of condition 5 increases diversity when competition-unrelated mortality disproportionately impairs abundant species. This mechanism is formulated in the **compensatory mortality hypothesis**. If habitat structure precludes competition (violation of condition 6), e.g. when landscape barriers inhibit contact between two potentially competing species, species number is higher than the number of available resources. Consequently diversity will increase with increasing number of intrahabitat barriers. Finally, species immigration (violation of condition 7) has the potential to maintain diversity over long time spans.

The universality of the equilibrium concept has been increasingly doubted in ecological sciences during the second half of the 20th century. It became common sense that communities are often kept away from equilibrium by perturbing factors that interrupt the course of succession and set back the ecological clock. Observations of ecosystems in a non-equilibrium state amassed, a fact that led Begon et al. (1996) to state: “Disturbance of one sort or another is so much the norm in natural communities, that it is an open question whether truly equilibrium situations ever occur in nature”. However, the need for non-equilibrium concepts already arose 30 years before Begon et al. posed their question. Mechanisms other than competitive interactions were focussed in order to interpret patterns in biodiversity and to explain the maintenance of species coexistence. Processes that violate the first two conditions of the CEP prevent communities from reaching equilibrium and are in the broadest sense termed “disturbances”. Krebs (2001) gives the following definition: “A whole range of factors can prevent equilibrium, including predation, herbivory, fluctuations in physical factors and catastrophes such as fires, and we lump these together as ‘disturbance’”. Disturbance was recognized by ecologists since the beginning of the 20th century (Cooper 1913, Clements 1916, Aubréville 1938, Jones 1945, Eggeling 1947, Watt 1947, Tansley 1949). But it did not gain attention as an ecologically significant phenomenon until the 1970s. Since this time, disturbance has been repeatedly suggested to counteract the CEP (Dayton 1971, Grime 1973, Horn 1975, Connell 1978, Sousa 1979).

The relationship between the strength of a disturbance and diversity was already indicated by Tansley (1949) as he stated, “diversity of plants in grassland may be related to grazing; e.g. intensively grazed or undergrazed areas”. Odum (1963) observed, “the greatest diversity occurs in the moderate or middle range of a physical gradient”. These observations were brought into a concept by Grime in 1973, and he provided for the first time a graph linking species richness and disturbance. He called it later the "hump-backed model" (Grime 1979). This concept was then picked up by Horn (1975) and finally by Connell (1978) who coined the term "**intermediate disturbance hypothesis (IDH)**". Although Grime formulated the concept for the first time and provided the graph, which stands synonymously for the concept itself, Connell is most often cited as its inventor (see Wilkinson 1999 for further discussion).

The IDH states that species richness is highest at intermediate frequencies or intensities of disturbance while too intense or too frequent disturbances exclude all but some pioneer species. Too weak or too rare disturbances are not capable of preventing competitive exclusion. At intermediate levels of frequencies and/or intensities of disturbance, pioneer species are able to re-establish and coexist with the dominant competitors while the latter are suppressed in their abundances but not fully removed from the system (Grime 1973, Connell 1978, Huston 1979, Petraitis et al. 1989, Fig. 1). Species richness is the dependent variable in Connell's IDH while Grime (1973) produced his unimodal graph for species density, which is species richness per unit area. Later, evenness and a number of composed diversity indices (e.g. Shannon index, Simpson's D) were incorporated into the concept. It became a central paradigm in community ecology and Hoopes & Harrison (1998) stated, "Intermediate disturbance has become perhaps one of the best-accepted principles in ecology". Non-equilibrium concepts and the IDH are portrayed in almost every ecological textbook (Ricklefs 1990, Colinvaux 1993, Brewer 1994, Begon et al. 1996, Krebs 2001).

1.2 Characteristics of disturbance

Even after 30 years of discussion no consensus on the definition of disturbance has emerged. Furthermore, it remains particularly difficult to distinguish between stress and disturbance (see Rykiel 1985 for further discussion). Former publications provided a multitude of criteria to characterize disturbance, and some of the most influencial are cited here in chronological order:

Odum (1963) regarded disturbance as a physical gradient. Grime (1973, 1979) distinguished between stress and disturbance. He defined stress as a resource shortage (e.g. of water, space or nutrients) as well as a physical-chemical limitation (e.g. temperature or salinity conditions) that results in a restriction of productivity: "Stress will be defined simply as the external constraints which limit the rate of dry-matter production of all or part of the vegetation" (Grime 1979).

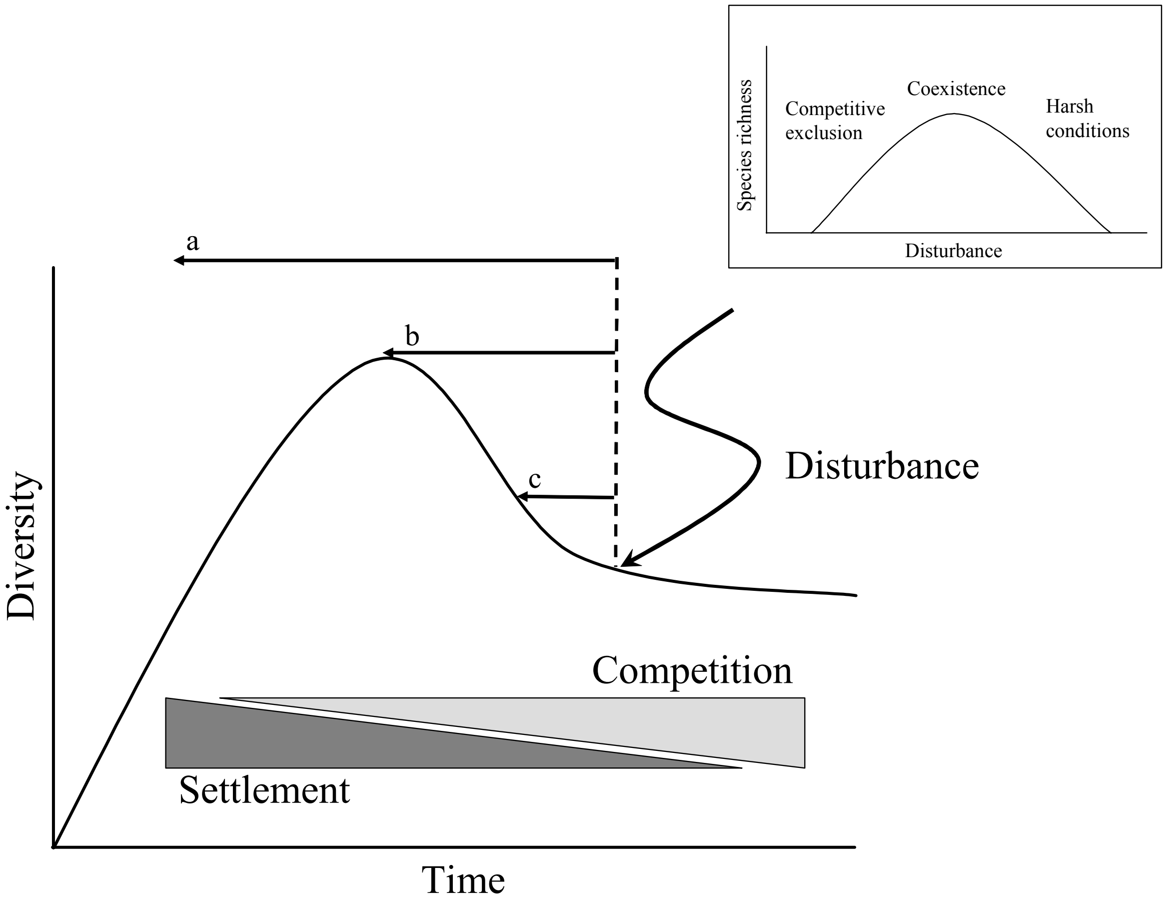


Fig. 1: The role of disturbance in setting back the successional process. Intermediate disturbance maintains maximal diversity (b), while too harsh disturbances suppress diversity (a), and too weak disturbances are not capable of overriding competitive exclusion (c). The smaller picture shows the unimodal model (sensu Grime 1973, sensu Connell 1978).

In contrast to stress, disturbance is associated with the partial or total destruction of biomass and can be abiotic as well as biotic in its origin. Pickett & White (1985) defined disturbance as: "Any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment". Further, they distinguished between two kinds of disturbances: (1) destructive events (e.g. fires or floods) and (2) environmental fluctuations (e.g. severe frost).

They also discriminated between abiotic (e.g. fire, storms, ice-scouring) and biotic disturbances (predation, grazing) as well as between endogenous and exogenous causes of disturbance. The last mentioned distinction is not always satisfying when it is applied to natural systems, since the inner causality of a disturbance often is not straightforward, e.g. a tree-fall can be induced by a storm, what is a clearly exogenous cause, and by tree senescence, what is an endogenous cause, at the same time. Disturbances are supposed to open space. This enhances the availability of resources and creates patchiness. The authors stressed that disturbance must be viewed in relation to the spatial (organism size) and temporal (organism lifespan) dimensions of the system at hand. They advised strictly, when testing the IDH, to adapt disturbance characteristics to system-specific scales (disturbance patch size/organism size-ratio or disturbance return interval/organism lifespan-ratio).

Connell & Keough (1985) classified the effects of disturbances on ecosystems into three categories: changes in environmental heterogeneity, changes in temporal heterogeneity and changes in the relative abundance of species.

Rykiel (1985) underlined the significance of a known reference state for the proper identification of disturbance, perturbation, or stress. Therefore, it is mandatory to be able to decide properly at which state an ecological process exceeds its normal range and becomes a disturbance. The author provided the following definitions: **(1) Disturbance** is the cause of a perturbation (including stress) in an ecological component or system. It must be regarded relative to a specified reference state, and it mediates specific effects: (a) destruction, i.e. existing biomass is reduced in quantity (see Grime 1979); (b) discomposition, i.e. particular populations are selectively eliminated, reduced, added, or expanded; (c) interference, i.e. matter/energy/information exchange processes are inhibited. **2) Stress** is an effect. It is the physiological response of an individual or the functional response of a system that is induced by disturbance or other ecological processes. Stress must be defined relative to a specified reference condition and it is characterized by its direction, magnitude, and persistence. It is a type of perturbation and can be classified into sublethal stress (survival trauma), i.e. the stress-induced loss of biomass, and lethal stress (lethal trauma) that is stress-induced individual death.

Menge & Sutherland (1987) defined physical disturbance as the lethal effect of physical stress that occurs when environmental conditions are beyond the tolerance range of the organisms concerned.

Pickett et al. (1989) demanded that a universal definition of disturbance should (a) identify the object disturbed, it should (b) distinguish between disturbance-induced and not-disturbance-induced change, and it should (c) discriminate between direct and indirect consequences of disturbance. They stated that any ecological object (e.g. a community) contains interacting lower level entities that allow the object to persist. The “minimal structure” of an entity at a particular level is regarded as “the system of interacting subunits allowing the focal entity to persist”. They defined it as, “the structure revealed at the first lower-level when analyzing an organized entity”. The authors used these aspects of hierarchy theory (Allen & Starr 1982, O`Neill et al. 1986) to differentiate between a disturbance and its consequences. They suggested that disturbance should be defined as the direct impact on the minimal structure of an ecological object caused by an external factor. In contrast to this, they saw stress as a change in the interactions of the minimal structure. These definitions resemble the view of Grime (1973) by stating that disturbance destroys an entity (e.g. biomass) while stress impairs the interactions without a loss of minimal structure (e.g. restricting productivity). Disturbance on one hierarchical level can result in stress at the next higher level by adversely affecting the interactions between its subunits. Following this concept, disturbance and stress can occur simultaneously in a system and they are interrelated.

Mackey & Currie (2001) defined disturbance as: “A temporally discrete event that abruptly kills or displaces individuals or that directly results in the loss of biomass”. Additionally, they distinguished between chronic (e.g. grazing) and episodic (e.g. landslides) disturbances.

Krebs‘ (2001) definition, cited above, summarized the statements of Pickett & White and emphasized the equilibrium preventing character of disturbance.

To summarize the listed definitions, disturbances (1) are discrete events in time, (2) reduce existing biomass and enhance the availability of resources, (3) can occur as destructive events or environmental fluctuations, (4) can be chronic or episodic, (5) can be of abiotic or biotic origin, (6) can be exogenous or endogenous with regard to the system they act on, (7) must be defined in spatial and temporal relation to the system examined, (8) must be defined with regard to a known reference state, (9) can alter the composition of communities by selectively excluding, reducing, adding or expanding particular populations, (10) can create patchiness, (11) can change environmental and temporal heterogeneity, (12) can alter the relative abundance of species, (13) prevent equilibrium conditions by setting back the successional process.

The components of a disturbance are its frequency, intensity and return interval. Pickett & White (1985) gave the following definitions: (1) **Disturbance frequency** is the mean number of events per time period. It is often used as a measure for the probability of a disturbance as well. (2) **Disturbance intensity** is regarded as the physical force of an event per area per time (wind speed of hurricanes, temperature of fires, air temperatures experienced by aquatic organisms during periods of emersion). (3) **Return interval** is the inverse of frequency measured as mean time between disturbance events.

1.3 IDH related studies

Due to its attraction to community ecologists, the IDH was the subject of numerous studies which can be basically classified into two categories: (1) Correlative studies are linking field observations with a naturally occurring disturbance gradient in the system under investigation. These studies are lacking a manipulative control of the independent variable.

Their outcomes give hints on the validity of the IDH but are insufficient to prove any causality. (2) In manipulative studies the independent variable, disturbance frequency or intensity, is under the experimenter's control. These investigations are suitable to test for the causality between disturbance and observed patterns in diversity.

Experimental studies that consider less than three disturbance levels, but include at least one treatment and an undisturbed control, are sufficient to test for the hypothesis that disturbance is enhancing diversity (e.g. Barbiero et al. 1999, Schnitzer & Carson 2001), but they can not provide information about the unimodal model. Furthermore, experimental studies can be classified into two categories, both providing assets and drawbacks: *in situ* studies do not allow the control of environmental parameters, which leads to a higher variance of the dependent variable, while in-vitro studies mostly fail to resemble natural conditions. Mesocosm experiments combine characteristics of both: they provide natural abiotic environmental parameters but allow the control of biotic factors.

Mackey & Currie (2001) recently reviewed 85 IDH-studies published between1985 and 1996 and references therein. They differentiated between the dependent variables: species richness, diversity, and evenness and grouped them according to the shape of the observed relationship. The authors subdivided the relationships described into five groups: nonsignificant (flat), unimodal, monotonic decreasing, monotonic increasing, and U-shaped (inverse unimodal). A total number of 116 richness-, 53 diversity-, and 28 evenness-disturbance relationships were identified and from those only 16 % of the richness-, 19 % of diversity-, and 11 % of the evenness- disturbance relationships were unimodal, i.e. matched the IDH.

The IDH originally considered species of one trophic level competing for a non-dynamical resource (e.g. Grime 1973, Connell 1978). Grime (1973) developed his unimodal model for herbaceous vegetation, consisting of sessile producers primarily competing for space and light, while Connell (1978) applied the concept to tropical rain forests and coral reefs. A large number of diversity-disturbance studies, mostly observational, that were conducted since this time took place in systems with similar properties. With regard to the community type investigated, the 89 mentioned studies can be grouped into five categories: (1) **Terrestrial plant communities** including tropical rain forests (e.g. Uhl 1987, Phillips et al. 1994, Cohen et al. 1995), temperate broad-leaved deciduous forests (Elliott & Schwank 1994, Hiura 1995, Meier et al. 1995), grassland systems (Martinsen et al. 1990, Collins 1992), old-field plant communities (Armesto & Pickett 1985, Inouye 1987), herbaceous flora (Keeley et al. 1981, McIntyre et al. 1995), desert vegetation (Gutterman et al. 1990), alpine plant communities (Fox 1985, Roxburgh et al. 1988), and salt marsh vegetation (Valiela & Rietsma 1995).

(2) **Marine benthic communities** including shallow water hard- and softbottom assemblages (e.g. Ayling 1981, Mook 1981, Sousa 1979, Ambrose 1993, Widdicombe & Austen 1998, 1999), deep-sea communities (Kukert & Smith 1992), coral reefs (e.g. Aronson & Precht 1995), and intertidal habitats (e.g. Lubchenco & Menge 1978, Paine & Levin 1981).

(3) **Freshwater communities** were mostly examined in stream ecosystems (e.g. Doeg et al. 1989, Anderson 1992, Death & Winterbourn 1995, Lake & Doeg 1995, Rosser & Pearson 1995, Townsend 1997, McCabe 2000). Studies of freshwater plant assemblages were concerned with lake shoreline vegetation (Keddy 1983, Keddy 1985, Wilson & Keddy 1988), stream-edge vegetation (Nilsson 1987), lotic algal communities (Steinman & Lamberti 1988), and periphyton (Swamikannu & Hoagland 1989, Cohen 1993).

(5) **Marine and freshwater phytoplankton communities** have been investigated in a small number of experimental studies (Gaedeke & Sommer 1986, Sommer 1995, Flöder & Sommer 1999) that approached the “paradox of the plankton” (Hutchinson 1961). The observation of diverse planktonic communities, existing in a homogenous habitat with a small number of resources, was one of the initial observations leading to the development of non-equilibrium concepts.

(4) **Terrestrial animal communities** have been the subject of observational studies concerning ant assemblages (Abensperg-Traun et al. 1996, Jackson & Fox 1996), bird communities (Morgan & Freedman 1986, Raphael et al. 1987) and small mammal communities (Huntly & Inouye 1987, Parker 1989).

All studies listed in Mackey & Currie (2001) were separated into experimental and correlative ones by the use of the appendix available in the Ecological Archives of the Ecological Society of America. Thirty % of the 85 studies were found to be experimental approaches while the remaining ones were based on observational investigations. For the manipulative studies only, the unimodal curve was detected in three experiments and was absent in all other cases.

Three further experimental studies provided confirmation of the IDH: Flöder & Sommer (1999), Widdicombe & Austen (1998, 1999). Nevertheless, the overall picture reveals a mismatch between the unanimous acceptance of species diversity as a peaked function of disturbance in the ecological literature and the weak existing evidence for the concept. This circumstance and the significance of the model as one central paradigm in community ecology demand further experimental investigations of the diversity – disturbance relationship.

1.4 The study system and types of disturbance

In this study effects of two abiotic, naturally occurring disturbance types, emersion and exposure to UVB radiation, on 3 and 12 mo old fouling communities of the Western Baltic are investigated. Referring to the criteria listed above, the disturbances applied in this study are (1) abiotic, (2) natural, (3) chronic, (4) environmental fluctuations according to the definition of Pickett & White (1985), (5) damaging biomass and restricting productivity, (6) exogenous with regard to the system they are applied to, (7) defined with regard to a known reference state (undisturbed controls), and (8) spatially defined with regard to the system they act on since entire communities were affected.

Due to the brackish character of the Baltic Sea and its young geological age, the focal communities are poor in species. Furthermore, the system is eutrophic and shows a high productivity during the summer months. Fouling communities of Kiel Fjord mainly consist of 10 to 12 macroinvertebrate species and 5 common algae (personal observation). Therefore, they are easy to survey and consequently suitable for experimental studies on biodiversity. Fouling organisms in temperate, eutrophic waters are commonly fast growing forms that quickly respond to external influences. The latter fact allows the temporal replication of experiments in manageable time spans. Organisms are relatively small in size, and experimental units are not space-consuming, which allows an appropriate number of replicates within one study site.

Generally, fouling assemblages consist of species with generation times encompassing several temporal magnitudes. These reach from days, in the case of diatoms and ciliates, up to years in the case of mussels or barnacles. When disturbing a community as a whole, it is almost impossible to choose disturbance intervals related to these generation times as it is requested by Pickett & White (1985). Therefore in this study, disturbance intervals were chosen which were feasible and mostly lay in the temporal range of naturally occurring disturbance events.

It was impossible to define all emersion-/UVB exposure-treatment levels as a disturbance (removal of biomass, sensu Grime 1973) or as stress (restriction of productivity, sensu Grime 1973) for each individual species, since treatments were applied to complex communities and encompassed a wide range of frequency or intensity levels. When regarding the community as a whole, they rather represented a mixture of both. This restriction in methodical stringency is unavoidable in an experimental field study concerning natural and complex communities. In the following, all treatments will be termed disturbances.

With regard to the intermediate disturbance hypothesis this study was designed to address the following questions: (1) Are dominant competitors detectable in the fouling community under investigation? (2) Are these organisms susceptible to the disturbance types applied? (3) Is the CEP overridden by the forcing of disturbances? (4) Are the predictions of the IDH valid in this hardbottom ecosystem, i.e. is an intermediate range of emersion intensities that produces maximum diversities detectable? (5) Are disturbance components, disturbance frequency and intensity, comparable in their effects? (5) Do disturbance effects change with successional stage, i.e. are older communities less susceptible to the disturbance regimes applied? (6) Are processes consistent between study years?

2. Emersion: effects and adaptations

Emersion, i.e. exposure to the air, confronts aquatic organisms with a multitude of environmental strains. These often occur simultaneously and burden species' physiological tolerance in various ways. Studies on the effects of emersion on marine benthic organisms were almost exclusively concerned with intertidal species (but see Dromgoole 1980, Adams & Bate 1994). For these species emersion is a periodically occurring stress, and intertidal organisms have evolved numerous physiological and behavioural strategies to deal with restricted photosynthetic activity or nutritional intake, temporal dehydration, osmotic stress, freezing, overheating and increased UV radiation.The different adaptations of species to various levels of emersion are one of the essential factors determining the zonation of intertidal habitats (e.g. Foster 1971, Norton 1986).

Although the detrimental nature of emersion for aquatic organisms seems to be self-evident, the physiological challenges of exposure to the air, and adaptations to it, will be considered here in order to elucidate emersion-mediated effects on individuals, populations, and communities.

2.1 Emersion effects and adaptations in seaweeds

Stress tolerance in macroalgae depends, because of their incapability of active movements and the frequent absence of protective morphological structures, to the largest extent on the tolerance of cellular stress (Davison & Pearson 1996). An obvious effect of emersion on intertidal algae is the, intraspecific, decrease in size with increasing tidal elevation. It is suggested that this is due to higher metabolic costs, which are associated with the maintenance of stress tolerance, that reduces algae scope for growth (Madsen & Maberly 1990, Davison & Pearson 1996). Though extensive literature exists, which concern stress tolerance mechanisms and their energy expenses in higher plants, relatively little is known about similar processes in seaweeds (Davison & Pearson 1996).

(1) Restriction of photosynthetic ability. Exposure to the air, experienced by seaweeds, does by no means stand for the cessation of photosynthesis. Intertidal species are known to perform high rates of photosynthesis in air (Madsen & Maberly 1990). It has been shown that low shore species exhibit lower rates of photosynthesis in air than in water, but the opposite was found to be the case for high shore species (reviewed in Davison & Pearson 1996). A number of studies demonstrated that photosynthesis increases, compared to the fully hydrated emersed status, during a moderate degree of dehydration (Quadir 1979, Johnston & Raven 1986, Madsen & Maberly 1990). This is presumably due to the reduction of the aqueous diffusion barrier for CO_2. Brinkhuis et al. 1976 reported an increase in photosynthesis under conditions of 0 - 25 % thallus dehydration for *Ascophyllum nodosum* and *Fucus vesiculosus*, but beyond this point the rate levels off and decreases sharply at 50 % water loss. Maberly & Madsen (1990) calculated, by the use of a model for *Fucus spiralis*, that under conditions of mild desiccation photosynthesis in air contributes 50 - 75 % to the total productivity of the alga while under conditions of high dehydration it decreases to an extent of 20 - 40 %. Increasing thallus temperature is primarily associated with an increase in photosynthetic rate and dark respiration. Beyond an optimal range, which varies over latitudinal and seasonal gradients, both physiological parameters decline rapidly (Beach & Smith 1997). High insolation causes high photosynthetic rates until inorganic carbon becomes a limiting factor while a further increase in irradiance leads to photoinhibition due to photoprotection and/or photodamage of the photosystem II (Davison & Pearson 1996). Low-light adapted algae should be most severely affected by high-light conditions during emersion.

A high affinity for CO_2 in air is a further adaptation to periodical emersion. Algae adapted in this way are able to achieve higher photosynthetic rates during periods of emersion than under submersed conditions (Einav & Beer 1993).

(2) Nutrient limitation. Seaweeds experience nutrient shortage during emersion. This was demonstrated for *Pelvetia canaliculata* and *Fucus spiralis* by the artificial compensation of growth deficits through nutrient addition within a fertilization experiment (Schonbeck & Norton 1979). Consistent with this, the tissue nitrogen content of the red alga *Gracilaria pacifica* was found to drop down after transplantation to higher tidal levels (Thomas et al. 1987).

(3) Thermal stress. Emersion is very often associated with thermal stress, since ambient temperature frequently differs widely between water and air. In warm weather hydrated algal thalli are cooled by evaporative water loss when emersed, and they are therefore commonly below air temperature. In contrast, tissue temperature of fully dehydrated thalli can easily exceed air temperature by far, leading to heat damage (e.g. denaturing of proteins, disintegration of cell membranes) (Bell 1995). The temperature of the thallus is also critical for the rate of photosynthesis recovery after re-immersion: high thallus temperature, experienced during emersion, is associated with a prolonged time of photosynthesis recovery. Because of this, thallus heating, which is influenced by the thallus morphology, affects growth rates (Bell 1995). A limited number of studies provided records of the stress-induced expression of proteins in seaweeds, e.g. for the expression of 70 kDa heat shock proteins in the antarctic red alga *Plocamium cartilagineum* (Vayda & Yuan 1994). Dehydrin proteins promote desiccation tolerance in higher plants, and dehydrin-like proteins were also found in fucoid algae (Li et al. 1998, Brawley et al. 1999). These findings suggest that mechanisms of heat-stress-tolerance in seaweeds might be similar to those performed by higher plants and presumably are associated with comparable metabolic costs. Freezing, which is common in intertidal areas of higher latitudes, can lead to severe mechanical tissue damage, cellular dehydration, and it impairs photosynthetic activity (Davison et al. 1989, Dudgeon et al. 1989, Pearson & Davison 1993). Macroalgae from arctic tundra streams form resistant vegetative cells that contain large amounts of reserves and low molecular weight solutes in order to lower the freezing point (Sheath et al. 1996).

(4) Dehydration. Dehydration interrupts photosynthetic activity by disturbing the transfer of energy from antenna pigments to the photosystem II (Fork & Oequist 1981, Smith 1984, Dudgeon et al. 1989). It damages cell membranes, leading to an insufficient re-hydration after re-immersion and a loss in low molecular weight solutes (Schonbeck & Norton 1980). In contrast, dehydration has also been reported to confer protection against photoinhibition and thermal damage presumably by ceasing photochemical activity and stabilizing macromolecules (Smith 1984, Havaux 1992, Muslin & Homann 1992).

(5) Active oxygen species. Active oxygen species and hydroxyl radicals are generated by all aerobic organisms. They are highly reactive and have the potential to denature proteins, membrane lipids, and nucleic acids. It has been shown that a disruption of respiratory or photosynthetic metabolism caused by physical stress initiates the production of active oxygen in seaweeds (Collen & Davison 1997). Thus, all environmental fluctuations mediated by emersion can raise the quantity of active oxygen in algal tissue. Two mechanisms are described for plants that disarm these products: firstly, antioxidants like carotenoids, ascorbates, tocopherols, and anthocyanins. They are found in a great variety of marine organisms (reviewed by Winston & Di Guilio 1991). They are able to disarm reactive species by scavenging free radicals before they react with cell components. Secondly, enzymes like the superoxide dismutase and catalases that convert harmful active oxygen species into harmless agents (reviewed by Davison & Pearson 1996).

(6) Osmotic stress. Fluctuations in ambient salt concentrations during periods of emersion can, on the one hand, be due to evaporation, which increases the salinity of a small tide pool, a puddle, or even of the water adherent to the thallus surface, or, on the other hand, can be caused by rainfall that leads to hypoosmotic conditions. Because of their phototrophic mode of life, plants generally exhibit a higher surface/volume ratio than animals, and under stressful ambient salinity conditions their osmotically charged surface area per unit body volume is higher. This is associated with an enhanced loss of tissue water during periods of emersion. Mostaert et al. (1995) reported active ion-transport systems, like the accumulation of K^+ and Cl^-, and extrusion of Na^+, to be responsible for the largest proportion of internal osmotic pressure (67 - 94 %) in the red alga *Caloglossa leprieurii*. Furthermore, the significance of low molecular body weight carbohydrates like mannitol, dulcitol, sorbitol, and sucrose as osmoprotectors has been outlined in a number of studies (Jacob et al. 1991, Mostaert et al. 1995, Karsten et al. 1997, Zhao et al. 2000). Free amino acids like proline are acting as osmotically active agents as well, and examples of increasing proline concentration with increasing ambient salinity have been provided for the green alga *Ulva sp*. (Liu et al. 2000, Zhao et al. 2000). All these mechanisms are presumably associated with metabolic costs.

Conflicting observations have been made on the influence of rainfall on intertidal seaweeds: Schonbeck & Norton (1980) simulated rainfall in the laboratory and observed no significant impact on the physiological performance of *Pelvetia canaliculata* and *Fucus spiralis*. Jacob et al. (1991) tested the influence of different salinity regimes on the green alga *Prasiola crispa ssp. antarctica* and found growth rates, photosynthesis, and dark respiration reduced at salinity levels that exceeded the normal seawater range while hypoosmotic conditions were not harmful. Detrimental effects of desalination were described for Californian *Porphyra sp.* intertidal specimens by Arasaki (1981) who reported enhanced algal mortality due to rainfall. Ohno & Miyanoue (1980) found yields of the food alga *Enteromorpha prolifera* reduced because of rainfall, and Wiencke & Davenport (1987) recorded severe damage of the photosynthetic apparatus of the intertidal alga *Cladophora rupestris* after an abruptly induced drop in ambient salinity in the laboratory.

(7) UVB radiation. Ultraviolet-B radiation (UVBR) is the fraction of the UV radiation naturally reaching the earth’s surface that is most harmful to lifeforms. Its detrimental potential roots mainly in two general processes: photo-oxidative stress and the absorption of UVBR by organic molecules. Productivity of unicellular and multicelluar algae, as well as of higher plants, is reduced under high doses of UVBR (e.g. Calkins & Thordardottir 1980, Ekelund 1990). In marine systems the effects of UVBR are best studied in planktonic microalgae while less information is available for macroalgae.

Carbon fixation rates are diminished by UVBR as a result of photoinhibition of the photosystem I and II (Jokiel & York 1984). Adverse effects on the primary electron transport, the coupled ATP-synthase, and the reduction of carbon dioxide have also been reported (reviewed in Nordic Council of Ministers 1996). Furthermore, for higher plant cells it has been shown that enzymes of the photosynthetic metabolism are inactivated by UVBR, and that their amount decreases under enhanced irradiance levels. This presumably goes back to changes in gene expression (Strid et al. 1994). The restriction of algae photosynthesis rates is a result of the breakdown of photosynthetic pigments induced by UVBR (reviewed in Nordic Council of the Ministers 1996). Additionally, Häder et al. (1995) found photosynthesis rates suppressed by UVBR in many red, brown, and green macroalgae. DNA lesions, induced by UVBR, are altering the molecular structure of nucleic acids and this impairs DNA expression, resulting in reduced protein synthesis (Mitchell & Karentz 1993). This process disequilibrates metabolic pathways (Vincent & Neale 2000). Nucleic acids and proteins absorb in the UVB range, and because of this, the entire metabolic apparatus of the cell is affected by UVB radiation (Vincent & Neale 2000). Consistent with this, adverse effects of UVBR on the nitrogen accumulation of microalgae have been described (Döhler & Biermann 1987, Döhler et al. 1991, Döhler 1997). The authors found several enzymes involved in the nitrogen metabolism inactivated under conditions of enhanced UVBR. High UVBR can also cause the disintegration of membrane structures what is accompanied by a decrease in the lipid content (Häder & Worrest 1991). This is supposed to be an effect of radiation on the membrane component synthesis mechanisms (Döhler & Biermann 1987), mediated through the generation of reactive species that cause damage to organic molecules like the membrane lipids (Karentz & Bosch 2001).

Additionally, UVR seems to have the potential to alter carbon allocation within organisms. Arts & Rai 1997 found the relative allocation of fixed carbon to lipids, proteins, polysaccacharides, and low molecular compounds modified by UVR in a phytoflagellate, a cyanobacterium, and a diatom species. Further hints for UV-modification of lipid and fatty acid composition were found in phytoplankton cultures by various authors (reviewed in Vincent & Neale 2000). Hessen et al. (1995, 1997) showed that phosphorus uptake in phytoplankton can be impaired by UVR, and that UVR-modified N- and P-uptake, accompanied by carbon allocation, leads to significant changes in the C:N:P stoichiometry of the cell.

External morphological structures like cuticles and hairs are able to absorb more than 95 % of incoming UVBR and represent an effective irradiance protection (Karentz 1994, Rawlings 1996). The silicate cell wall of diatoms has been found to reduce incoming UVBR by 30 % (Davidson et al. 1994). Effective screening from direct or indirect solar radiation is provided by secondary metabolites that absorb in the UV-wavelength range. Mycosporine-like amino acids (MAAs) are very widespread among marine organisms (Karentz 2001). They absorb effectively in the UVB and UVA range, showing an absorption maxima from 309 -

360 nm. MAAs are supposed to be synthesized through the shikimate pathway. This metabolic pathway can be performed by bacteria, fungi, algae, and higher plants, and its products are involved in the synthesis of the aromatic amino acids tyrosine, phenylalanine, and tryptophan. So, the production of MAAs in the marine environment is almost exclusively restricted to bacteria and algae, whereby the Rhodophyta exhibit the highest levels of MAAs (Karsten et al. 1998).

It has been shown for microalgae that the production of MAAs can be triggered by an increase in ambient UV-irradiance intensity, but the results are equivocal (reviewed by Karentz 2001). A wavelength-specific activation of gene expression, as it is observed in higher plants, is not known from algae (Karentz 2001). MAAs and antioxidants (see above) can function as optical filters as well (Karentz & Bosch 2001).

UV radiation induced DNA lesions, like cyclobutane-type pyrimidine dimers, pyrimidine-pyrimidone photoproducts, thymine glycols, cytosine damage, DNA strand breaks, and DNA protein cross-links, impair the molecular functioning of the metabolism and, at least the first two lesions, are supposed to be cytotoxic and mutagenic (Kumar & Häder 1999). Photoreactivation, excision repair, and postreplication repair are the known cellular mechanisms that are capable of removing detrimental UVBR-induced effects on DNA molecules (Mitchell & Karentz 1993).

2.2 Emersion effects and adaptations in marine invertebrates

Different from algae, sessile animals are frequently able to reduce the amount of air-exposed body surface or can even shut themselves off entirely from the environment. These behavioural strategies diminish detrimental impacts on cells and tissues, but they are associated with a restriction of nutritional uptake and the respiratory metabolism.

(1) Restrictions of food supply. Sessile or hemisessile suspension feeders that experience emersion are cut off from food capture. Reduced nutritional supply adversely affects overall organismal fitness: it delays larval development (Qiu et al. 1997), restricts scope for growth (Shick et al. 1988), alters reproduction rates (Bayne et al. 1988), and enhances mortality (Incze et al. 1980). Presumably, all sessile intertidal animals are capacity adapted to compensate for an intermitted food intake. This can be achieved by increasing the energy input during immersion or by decreasing energy expenditures during emersion. The first strategy, termed energy-supplementation, has been shown for the barnacle *Balanus balanoides*. Individuals of this species compensate for the elevated tidal levels they live in by an increase in cirral feeding activity during submersion (Ritz & Crisp 1970). Furthermore, a rapid resumption of feeding activity after re-immersion shortens the intermission of nutritional uptake. This behavioural adaptation has been reported for intertidally acclimatized individuals of *Cardium edule* (Widdows & Shick 1985) and barnacles (Barnes & Barnes 1958). Physiological adaptations that allow the optimization of energy absorption, e.g. the prolonging of the digestive process during emersion, come under the energy-supplementation strategies as well.

In contrast, energy-conserving strategies depend on the deceleration of metabolic processes and mechanical activities during periods of emersion.

(2) Restrictions of the respiratory activity: Gill breathing animals experience significantly reduced or even completely ceased oxygen uptake during emersion. Many species maintain a minimal gaseous exchange via their body surface. Nevertheless, this process can normally not compensate for oxygen shortcoming during long periods of emersion. Animals that possess a solid exoskeleton, like bivalves, bryozoans, and barnacles, can close their valves in order to minimise desiccation rates. Attributable to the complete cessation of gaseous exchange caused by this behaviour, these species are often effectively anaerobic organisms (de Zwaan 1977). Oxygen consumption rates of intertidal bivalves during emersion lie invariable below rates measured under submerged conditions (Sadok et al. 1999). Widdows et al. (1979) reported the oxygen uptake rate of *Mytilus edulis* during emersion to be 4 - 17 % of the rate during submersion. This reduced aerial gas exchange is conducted via diffusion through the epithelial lining of the mantle cavity while the shell is gaping. Shell-gaping is associated with an increase of mantle cavity fluid loss by evaporation and dripping. Blue mussels often close their valves during emersion and shift their metabolism towards anaerobic respiration (Shick et al. 1988). Widdows et al. (1979) found anaerobic end-products to be accumulating in mussel tissue during exposure. The use of anaerobiose, which is supposed to set in shortly after valve closure (Sadok et al. 1999), is associated with a loss of energy because of the insufficient degree of energy utilisation and metabolic costs caused by the need for excretion or conversion of the toxic end-products. Similar to mussels, the barnacle *Balanus nubilis* opens its tergal plates and moves its cirri in order to oxygenate the mantle cavity fluid, but it is not able to reach oxygen levels comparable to immersed conditions (Burnett et al. 1991). *Balanus balanoides* is reported to posses a micropylar opening that allows aerobic respiration to continue during emersion. Grainger & Newell (1965) found the degree of utilisation of this micropylus positively correlated to the ambient relative humidity: a behaviour that minimizes desiccation rates.

(3) Thermal stress. Fluctuations in the ambient temperature that induce an in- or decrease in animal body temperature impact all physiological processes. A rise in body temperature accelerates all metabolic rates. This enhances, e.g., the oxygen demand. A substantial temperature increase can bring the animal to the upper end of its thermal tolerance range; i.e. it causes the thermal inactivation or denaturation of enzymes, damages the structure of cell membranes, and perturbs the biochemical balance of the organism by differentially influencing enzymes of various thermal sensitivities (Schmidt-Nielsen 1997). The body temperature of emersed sessile organisms is determined by air temperature, ground temperature, wind-speed, air humidity, solar radiation, evaporation rate, and body size (Elvin 1979, Helmuth 1998). It can significantly exceed the thermal regime experienced during immersion. Helmuth (1999) found a daily fluctuation in body temperature of 10 - 20° C in intertidal *Mytilus californianus* individuals during the summer months to be common. However, even sessile animals are able to regulate their body temperature to a small extent in order to keep it below the ambient temperature. Cooling can be achieved by evaporation of the mantle cavity fluid in bivalves and barnacles, but this is associated with an increase in body water loss. Behavioural strategies, like aggregation, can lead to the generation of microclimates within clusters of e.g. bivalves (Moulton 1962).

Induced thermotolerance in invertebrates is observed to be associated with the synthesis of heat shock proteins (hsps). Bradley et al. (1998) found the level of hsp-70 stress proteins elevated in Baltic *Mytilus edulis* specimens exposed to 20 ° C water temperature when compared to individuals kept at 4° C. Chapple et al. (1998) recorded a positive correlation of hsp-70 levels in *Mytilus edulis* with the increase in ambient temperature during the annual course. With regard to the metabolic costs for the synthesis of these proteins, evidence has been found for *Drosophila* and *Saccharomyces* that the production of stress proteins reduces their overall organismal fitness (Feder et al. 1992, Sanchez et al. 1992, Krebs & Loeschke 1994). Hofmann (1999) provides an overview on the expression of heat shock proteins in intertidal animals.

On the opposite end of the thermal gradient, which is usually experienced by temperate intertidal organisms, lurks the risk of freezing. Physiological adaptations to low thermal regimes, or even frost, have been reported for a vast number of intertidal animals (Loomis 1995). They include the synthesis of antifreeze glycoproteins, proteinnaceous ice nucleators, cryoprotectants, reductions of metabolic rates, and changes in the composition of membrane phospholipids (Loomis 1995). These adaptations are presumably associated with metabolic costs.

(4) Dehydration. Desiccation means the loss of body water and the dehydration of tissues. This induces changes in osmotic conditions of the inner- and extracellular fluids and results in the impairment of metabolic processes. Rates of body water loss during emersion have been measured in intertidal gastropods (e.g. McMahon 1990, Britton 1993), bivalves (Coleman 1973, Kennedy 1976, Mingoa-Licuanan 1993), and crustaceans (Foster 1971, Jones & Greenwood 1982, Marsden 1991, Thurman 1998). For the blue mussel *Mytilus edulis,* Coleman (1973) reported that the amount of water loss during a three day emersion was smaller than the quantity of water retained in the mantle cavity. This indicates that mussel tissue is not subjected to dehydration within naturally occurring periods of emersion. A similar picture was found for *Tridacna gigas* that lost less than 5 % of body water within a 27 h period of emersion (Mingoa-Licuanan 1993).

(5) Osmotic stress. Invertebrates are able to perform different physiological mechanisms to overcome salinity fluctuations (Schmidt-Nielsen 1997). The four most important are: (a) active uptake or extrusion of ions or other osmotically active substances, (b) regulation of body water volume, (c) conservation of water or salts by the excretory organs, (d) regulation of cellular osmotic concentrations, e.g. by the quantity of free amino acids present.

Sadok et al. (1997) demonstrated that all of these processes are associated with energy costs. The authors reported that haemolymph hypoglycaemia accompanies all physiological adjustments to changing ambient salinity in *Mytilus edulis*. This indicates that glucose is utilised in the osmoregulatory processes in this bivalve. Nery & Santos (1993) provided similar information for the crustacean *Chasmagnathus granulata.*

Further extensive research work concerning the osmoregulatory abilities of crustaceans are reviewed in Pequeux (1995).

(6) UVB radiation. In general, animals face the same threats as plants when exposed to UVBR (see above): DNA molecules and proteins are submitted to modification. Oxidative stress, mediated by peroxides and free radicals, increases the need for anitoxidative substances, burdens the immune system and modifies cell membranes. Growth and fecundity are reduced and mortality is enhanced. Early life stages are more sensitive to UVB radiation due to their high developmental activity, their small size (optical radius), their low morphological complexity and their lack of protective structures (Adams & Shick 1996, Adams & Shick 2001).

Motile, UVBR sensing animals can actively avoid exposure by moving away from direct or indirect irradiance. Avoidance of intense solar radiation is observable in many organisms, and UV radiation has been shown to change the motility and photo-orientation of protists and metazoans (e.g. Karentz 2001). Sessile animals with an opaque exoskeleton or cuticle are well protected against intense insolation and can additionally shut themselves off against the ambient light regime. This behaviour is associated with a transient intermittence of respiration and nutrient uptake.

Sunscreening secondary metabolites in invertebrates are the pigment melanin and mycosporine-like amino acids, but probably more, yet unknown, substances have evolved. The role of melanin in the UV-protection of the mammalian skin is well investigated, and the compound is reported to be widespread and important in aquatic invertebrates as well (Karentz 2001). However, pigmental UV-protection seems to be effective but costible, since melanic morphs of the freshwater crustacean *Daphnia pulex* are more resistant to UV radiation, but they are slow growing and competitively inferior to non-melanic morphs (Hessen 1996). Invertebrates and chordates are unable to synthesize MAAs and depend on the uptake of these compounds by their food. It is assumed that ingested MAA can be interconverted into other MAAs in animal metabolism. MAAs are presumably bioaccumulating through trophic levels, since highest MAA concentrations have been found in consumer organisms. Animal regulation of the MAA content depends on the available food and the kinetics of MAA translocation between the ingested material and tissues (Karentz 2001).

The role of antioxidants and the modes of DNA repair have been exemplified for seaweeds (see chapter 2.1) and are similar in invertebrates.

2.3 Intertidal organisms in a non-tidal environment

The Baltic Sea is a geological young and brackish sea; organisms have invaded this area from the fully marine systems of the Atlantic or the North-Sea and from freshwater habitats of the adjacent landmasses. Salinity declines steadily from the west to the east: reaching from fully marine (Kattegat) to almost freshwater (Bothnian Bay) conditions. The Western Baltic exhibits an intermediate salinity of 15 - 20 PSU and supports an impoverished marine fauna and flora that is supplemented by a few freshwater species.

Tides in the Baltic are very small (< 15 cm) and are mostly super-imposed by wind-induced fluctuations in water-level, which lasts from hours to days (personal observation). Hence, periods of emersion range within those of intertidal coasts but can occasionally exceed them by one dimension. For this reason, upper subtidal organisms experience unpredictable, aperiodical time spans of emersion.

Most sessile species that invaded from fully marine habitats colonize intertidal areas there, but the majority of their Baltic descendants exist under conditions of permanent submergence. Because of this, the selective pressure for the maintenance of emersion tolerance is presumably lapsed in the Baltic. This fact and the costs of dealing with conditions of low salinity as a new stress factor very likely lead to the loss of emersion-related stress traits. An evolutionary divergence of Baltic species from their fully marine progenitors has been discussed for seaweeds. Russel (1988) found the salinity tolerance of Atlantic *Fucus vesiculosus* broader than that of their Baltic conspecifics. For the latter, the optimal salinity was 6 PSU while Atlantic *Fucus* exhibited an optimum of 34 PSU at 4° C. Pearson et al. (2000) found the ability of Baltic *Fucus* to recover from freezing or desiccation reduced in comparison to individuals from intertidal populations of the North Sea.

3. Material and Methods: emersion treatments

3.1 Study site and fouling communities

Experiments were conducted from May 1999 to December 2000 within the Kiel Fjord at the mouth of the Kiel Canal (54° 22‘N, 10° 09‘E) in a small sheltered bay (Fig. 2 + 5).

Kiel Fjord is an extension of the Kiel Bight; the latter is a shallow water area with an average water depth of 18 - 20 m. It is located between the fully marine Kattegat region (30 - 35 PSU) and the low-saline Central Baltic Sea (7 PSU). Salinity at the study site was measured from July 2000 to February 2001 at least 3 x a week and ranged from 15 to 21 PSU with an average of 17.5 PSU. The climate of the Western Baltic is temperate and humid. Surface water temperature in the two study years was highest at 22° C in July and August 1999 and lowest at 0.8° C in December 1999. Air temperature was maximal at 31° C in the June of 2000 and minimal at –4° C in February 2001 (Climatic data were acquired from the meteorological station of the Institute for Marine Research, Kiel).

The predominant wind direction in this region is south-west while the Kiel Fjord extents in north-south direction. For this reason, wave height seldom exceeds 0.5 m. The study site itself is surrounded by land in three directions and opens to the south-east, therefore wave action in the bay is mostly due to shipping traffic. The Baltic Sea exhibits, due to its small size, almost no tides. The tide-related diurnal water-level amplitude lies below 15 cm (Lass & Magaard 1995). This amplitude can be exceeded 15 x (≈ 2 – 2.5 m) by wind-driven changes in water-level (personal observation).

Kiel Fjord is a eutrophic coastal area. Stienen (1986) found the phosphate level 4 x increased in comparison to the Kiel Bight (up to 4µM/l) and detected 10 x as much nitrate as in off-shore areas (up to 60 µM/l). This is mainly caused by the agricultural input that is brought to the Fjord by the Kiel Canal and the river Schwentine. Due to this elevated nutrient supply, the phytoplankton productivity within the Fjord is significantly higher than in offshore areas.

Fouling communities in Kiel Fjord, older than 1 yr, are generally dominated by the blue mussel *Mytilus edulis* (Dürr & Wahl in review). The mussel is one of the dominant competitors for space in the Western Baltic. The second local species that is able to dominate solid substrata is the barnacle *Balanus improvisus*. Other important faunal components beside the two main competitors are the hydroid *Laomedea flexuosa*, the spionid polychaete *Polydora ciliata,* and the bryozoan *Membranipora membranacea*.

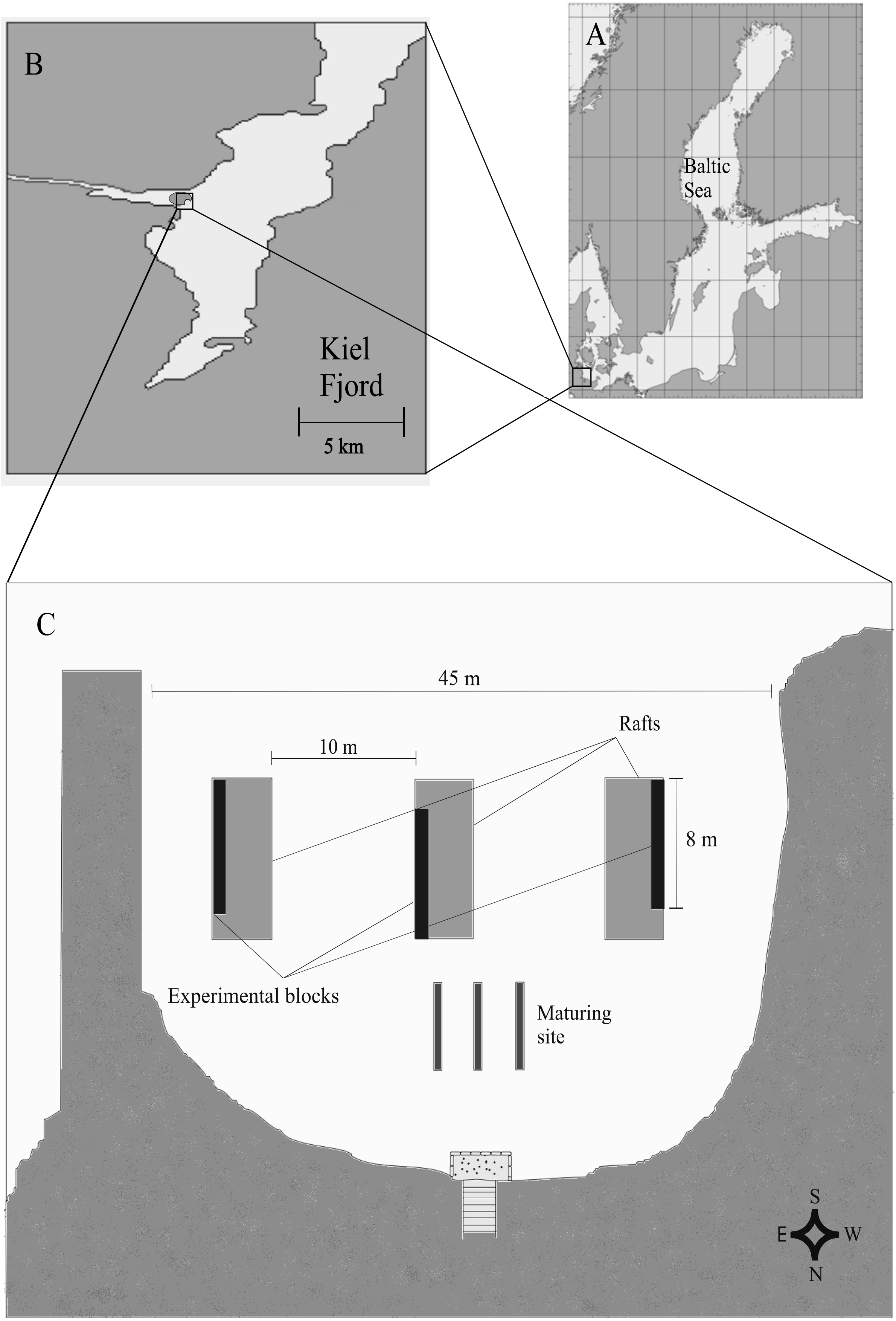


Fig. 2. (A) The Baltic Sea. (B) Kiel Fjord with the Kiel Canal. (C) The bay, rafts, maturing site, and the distribution of experimental blocks in 2000. In 1999 all experiments were conducted on one raft.

Floral components of the communities are the green algae *Enteromorpha* sp., the sea lettuce *Ulva sp.*, the filamentous *Chaetomorpha tortuosa,* and the brushy *Bryopsis plumosa*. The predominant red alga is *Ceramium strictum*. Present but less common are *Polysiphonia elongata*, *Rhodomela sp*., and the genus *Porphyra*. The brown alga *Fucus* spp. (mostly *Fucus vesiculosus*) is abundant and forms dense stands in the bay. Specimens of the genus *Laminaria* never occur in high abundances while the ephemerals *Pilayella littoralis* and *Ectocarpus* sp. are temporarily abundant.

Benthic diatoms are omnipresent as pioneer forms on newly opened space or exposed artificial substrate. However, they can also persist for longer times as dense mats or even re-invade a community and overgrow other settlers (personal observation).

The main motile benthic predators in this system are the shore crab *Carcinus maenas* and the starfish *Asterias rubens*. The most important grazers are the periwinkle *Littorina littorea,* the isopod *Idotea spp.,* and amphipods of the genus *Gammarus spp.* All but the amphipods and isopods were excluded from the settlement panels by the experimental set-up.

3.2 Settlement panels and maturing of communities

PVC-panels of 7 x 7 cm served as settlement substrata for the fouling communities. To produce communities at various stages of succession, 150 bare panels were vertically exposed to colonization in a water depth of 20-30 cm in May 1999, and 64 of them were brought into the experiments 3 mo later. Communities on the remaining panels continued maturing for another 9 mo and were used for the first experiment in May 2000. They were subsequently replaced by bare panels on which fouling communities developed for another 3 mo; these were used for the second experiment in the late summer of 2000 (Fig. 3).

In both years time of maturing encompassed the months June and July when the blue mussels spawn and heavy settlement and recruitment occurs. For this reason, all panels used in the study were dominated by blue mussels of different sizes at the beginning of the experiments.

When an experiment was started, start values for t_0-reference were obtained from 6 or 8 randomly chosen panels.

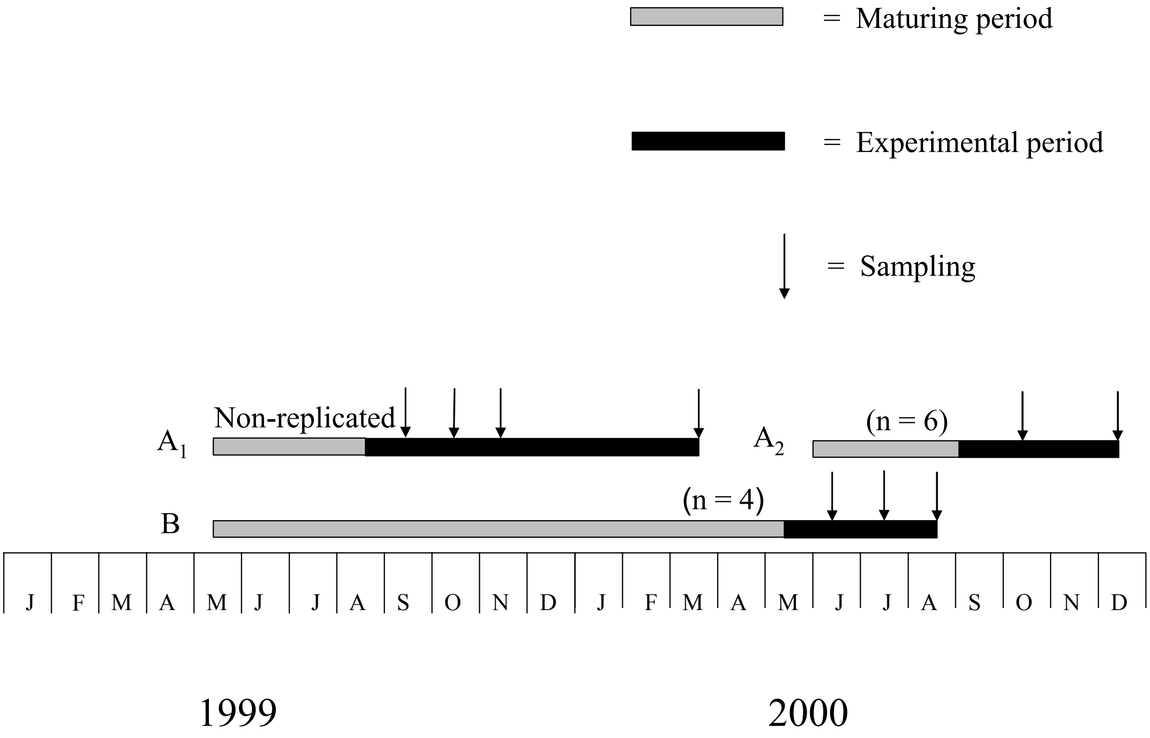


Fig. 3. Time schedule of the maturing periods and the emersion experiments in the two study years. A_1 = study on 3 mo old communities in 1999. A_2 = study on 3 mo old communities in 2000. B = study on 12 mo old communities. Their maturing started in 1999 while the experiment was conducted in 2000. N = number of replicates.

3.3 Experimental set-up

The experimental set-up was mounted on wooden rafts 3 x 10 m in size (Fig. 4 + 5). Emersion of settlement panels was realized by an automatically controlled seesaw-system. Settlement panels were fixed to PVC-rings (in 1999) or carrier plates (in 2000), hanging at the end of a thin rope that was attached to the tip of the seesaws (Fig. 4). Fixation of the panels on rings or carrier plates was done either by Velcro® or by cable ties.

In the submersed state (Fig. 4) seesaws were toppled towards the water, and settlement panels were kept in a water-depth of 20 cm; the water-depth where they had matured.

At the end of the seesaws shorter extension, a small container was fixed that could be filled with seawater by an immersed pump. The weight of the inflowing water toppled the seesaw and lifted the settlement panels 20 cm above the water level. The seesaw remained in this position as long as the pump was running, i.e. the disturbance treatment was applied (Fig. 4).

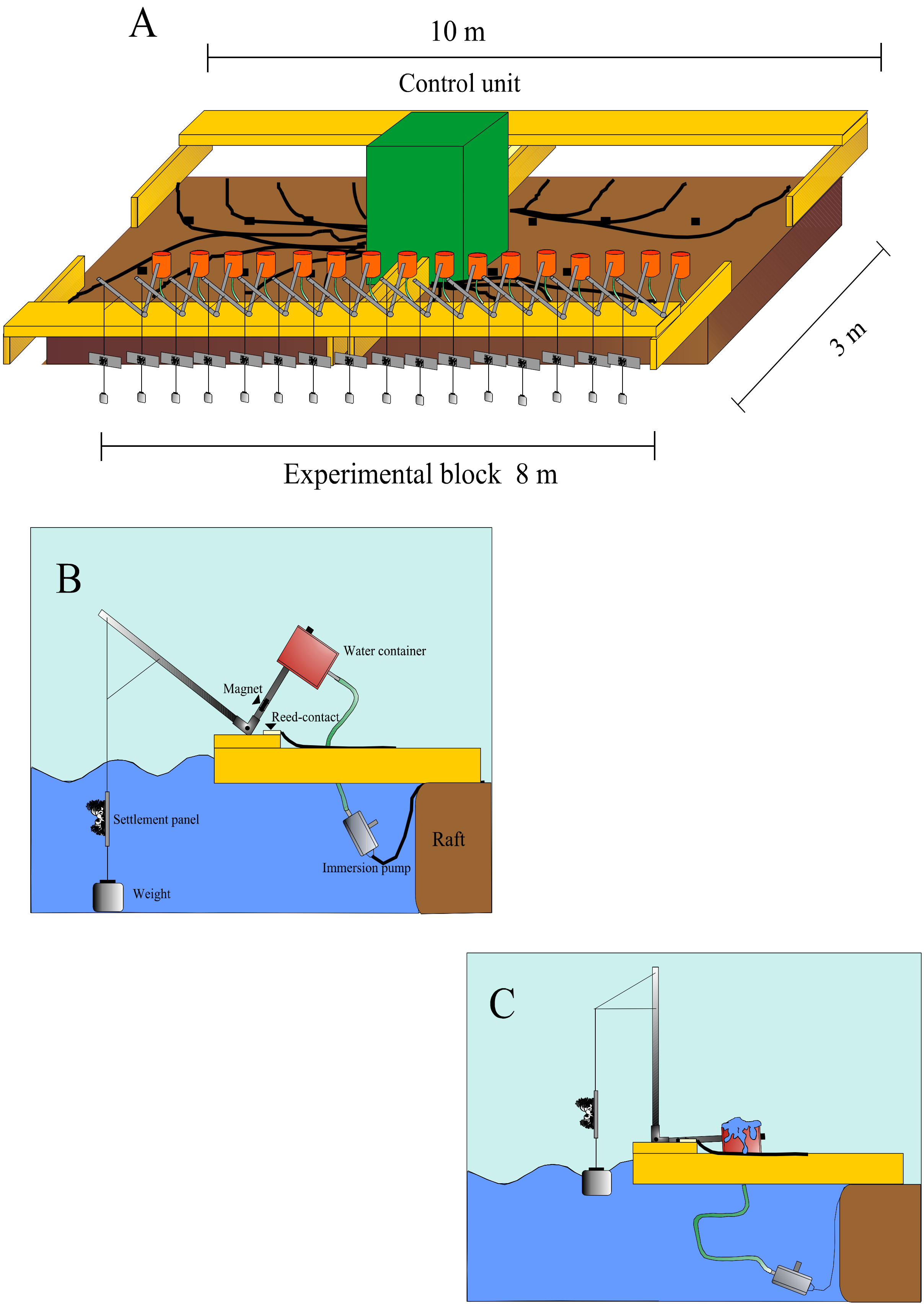


Fig. 4. Experimental set-up of 2000: (A) Raft with experimental block. The lower pictures show the settlement panels in (B) submerged and (C) emerged positions.

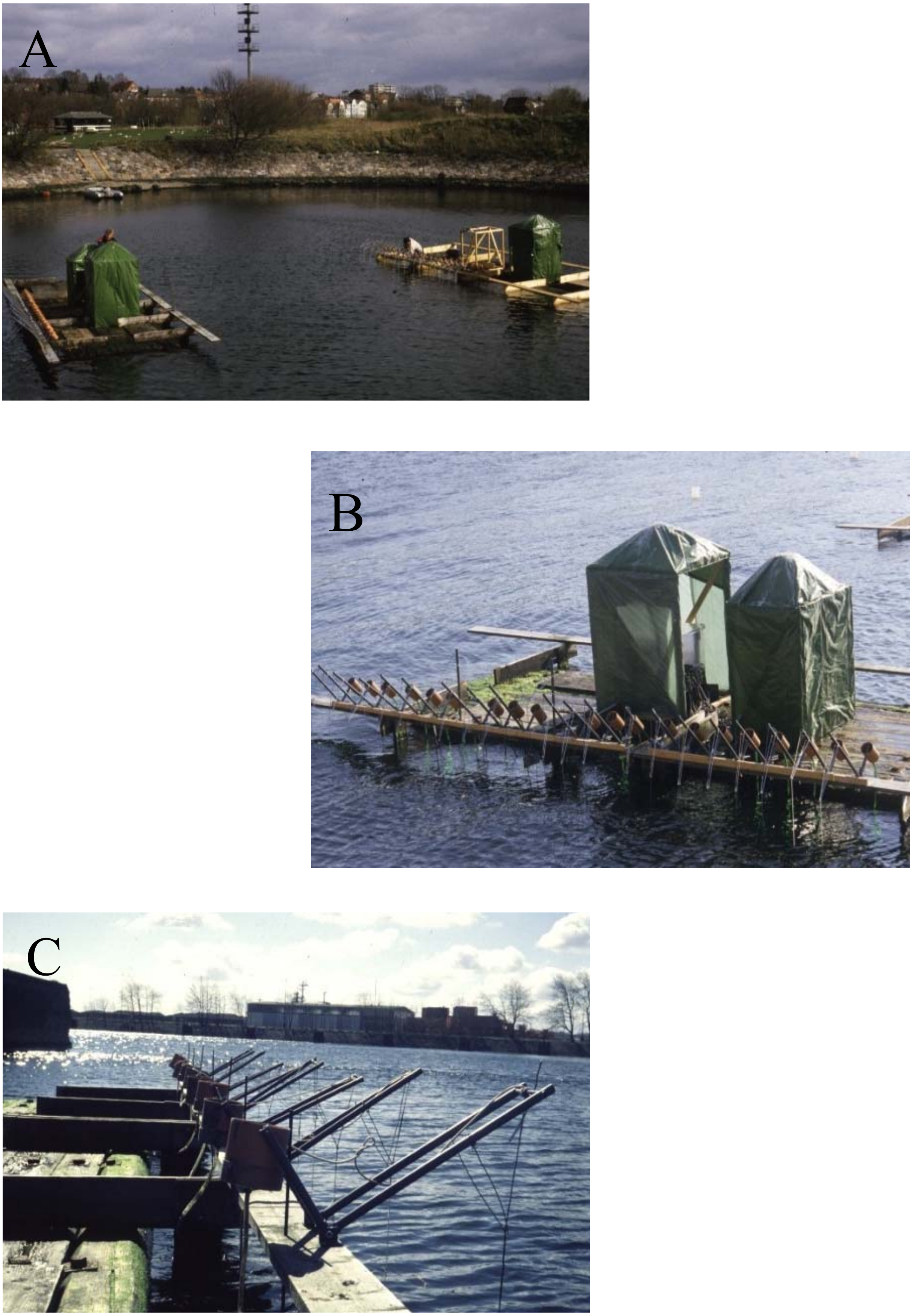


Fig. 5. (A) The experimental set-up under construction in the spring of 2000. (B) One experimental block in 2000, the green ‘huts’ contain the control units for the emersion and the UVBR exposure treatments (see chapter 7). (C) The experimental set-up in 1999.

Each pump was individually controlled by an electric timer. The correct function of pumps and seesaws was independently controlled by a magnet, switching a Reed contact when the seesaw toppled towards the raft. A working hour meter (one for each seesaw) registered the length of time the panel was emersed. Working hour meters were read by the investigators 5 x a week during summer and autumn and 3 x a week in the winter months.

During the second experiment in 2000, procedural controls were conducted to test whether the process of breaking through the water surface had a mechanical impact on the communities. A fact that would have confounded treatment effects. Procedural control seesaws were manually lifted out of the water and dropped back immediately 10 x quickly after another. This was done by the investigators each time the working hour meters were read.

3.4 Experimental design

All experimental units in the first year were located on one raft. Settlement panels were fixed to PVC-rings, 31.5 cm in diameter, and each ring carried four equidistant panels. Nine different emersion intensity treatments and eight different emersion frequency treatments were randomly distributed among seesaws. Four undisturbed panels, positioned on the raft front sides, served as controls. Statistical evaluation of these results is restricted due to pseudo-replication.

A complete randomized block design was realized in 2000 (Fig. 2). Sixty-eight seesaws were evenly distributed among three experimental blocks and each block was located on another raft. The three rafts were positioned in the bay with a distance of 10 m between them, and this resulted, due to the position of the blocks, in a distance of approximately 15 m between blocks. Blocks were 8 m in length. Each seesaw carried one settlement panel that represented one replicate of the respective treatment. Six seesaws were inactive and their settlement panels served as controls for both experimental series (emersion frequency + intensity). Each treatment was replicated twice within each block in the study on 3 mo old communities in 2000 (n = 6). Four replicates were used in the study on 12 mo old communities. Treatments, treatment controls, and undisturbed controls were allocated randomly among seesaws.

3.5 Treatment levels

During the frequency experiment in 1999, panels were exposed for 1 x, 2 x, 3 x, 4 x, 6 x, 8 x, 16 x, and 32 x 15 min per day. In 2000 1 x, 4 x, 8 x, 24 x, and 48 x 15 min per day were the applied frequency treatments. Emersion frequency treatments of both study years are shown in Fig. 6.

In 1999 periods of 0.25, 0.5, 0.75, 1, 1.5, and 2 h per day were chosen for the lower intensity range while the higher range was wider spread by applying 4, 6, and 8 h of daily emersion.

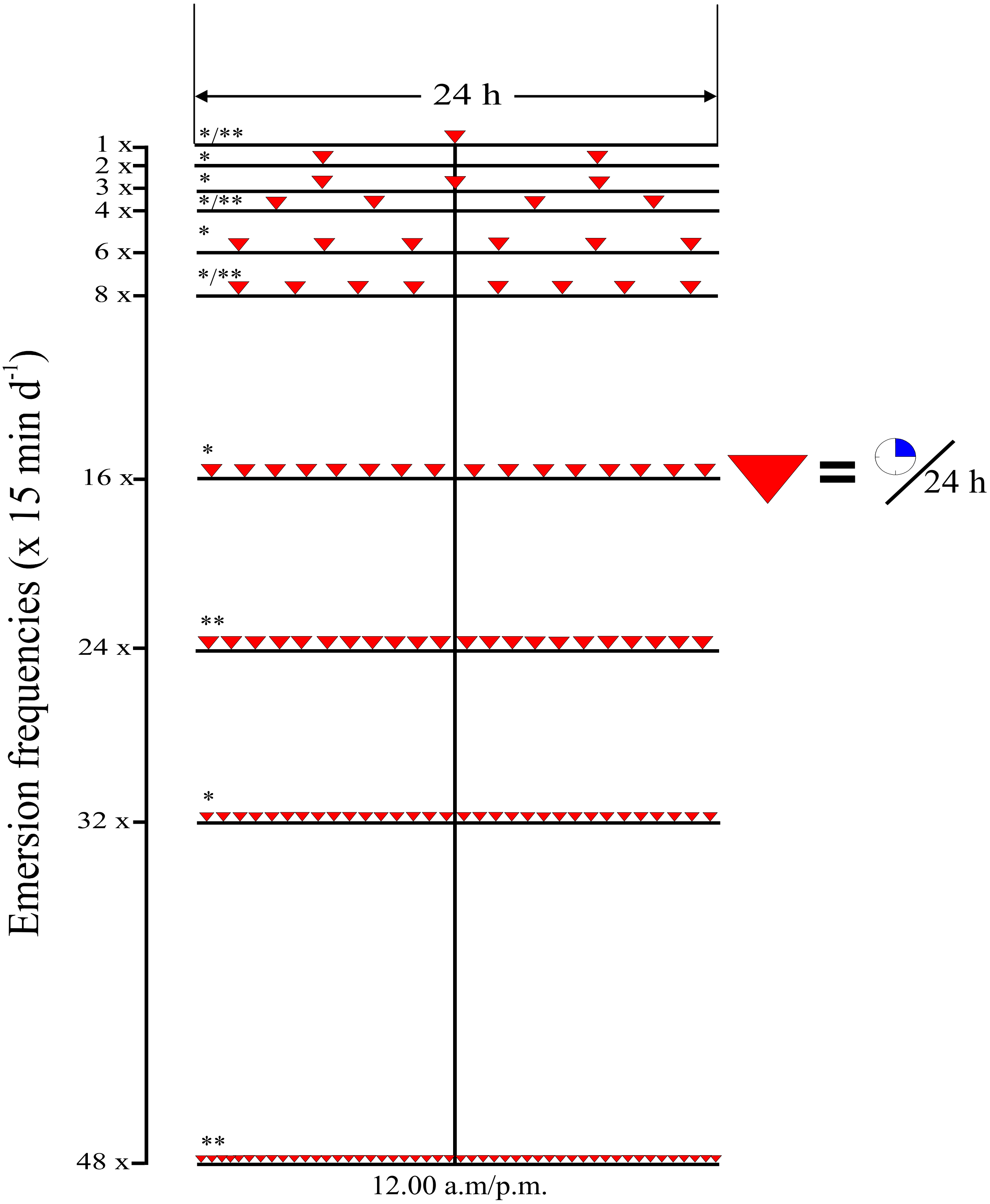


Fig. 6. Frequency treatments applied in the two study years. Emersion frequencies are shown on the left hand axis; asterisks indicate the year of application * = 1999, ** = 2000.

The temporal centre of the frequency and intensity treatments was switched from 12 a.m. to local midnight and vice versa once a week. This was done to achieve more natural emersion regimes.

As a consequence of the improved experimental design in 2000, which was associated with an increased number of replicates per treatment, total number of treatments was reduced. Applied intensity levels were 0.25, 1, 2, 6, and 12 h of emersion per day (Fig. 7).

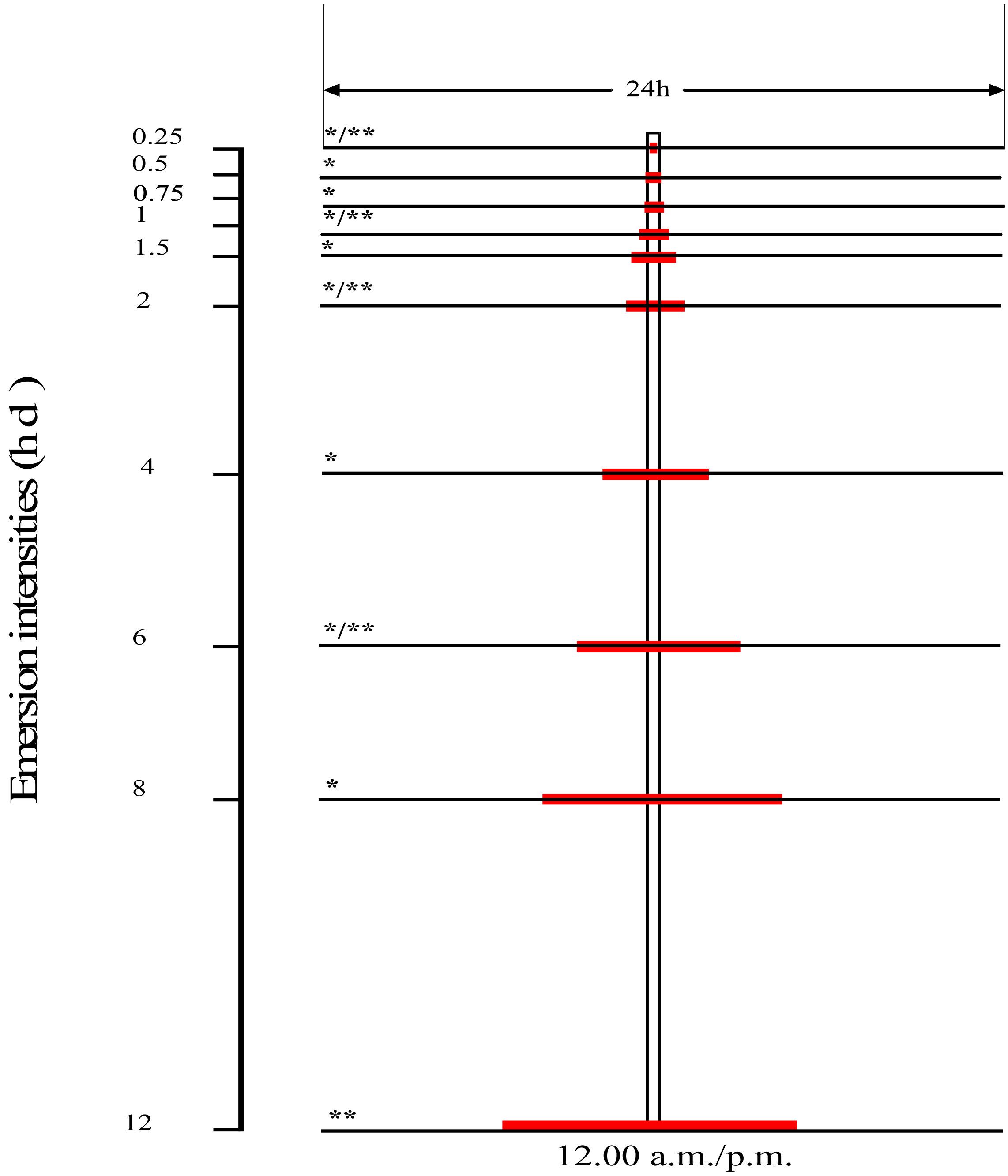


Fig. 7. Intensity treatments applied in the two study years. Emersion intensities are shown on the left hand axis; asterisks indicate the year of application * = 1999, ** = 2000.

3.6 Larval supply and the course of natural succession

Larval supply was monitored on recruitment panels, which were exposed every month and retrieved 4 wk later, in both study years. The course of undisturbed succession at the study site was followed on 8 control panels, which were equally distributed in the bay, during the whole experimental phase of 2000.

For the comparison of climatic conditions in both study years, meteorological data were acquired from the Institute for Marine Research, Kiel.

3.7 Sampling procedure

Settlement panels were sampled monthly, except during the last experiment in the fall of 2000 when sampling took place after 6 and 14 wk (Fig. 3). Sampling was non-destructive: panels were retrieved from the carrier plates, placed in water filled containers, examined in a nearby field laboratory, and were brought back to their respective position afterwards. Within 15 min percent cover of all settlers was estimated and blue mussels were counted and divided into size classes on three fields of vision (covering 40 % of the whole panel surface) within the upper half of the panel under a Wild binocular with 12x magnification. The lower half of the panels was omitted because their bottom ends were more humid. This led to an erratic pattern of colonisation. Two reasons are presumably responsible for the constitution of this gradient: the down running water from the panels itself kept their lower ends wet, at least for a certain time, and splash water that sprayed the bottom ends of the panels more intensively than their upper parts.

To avoid edge effects, the outer 1 cm of the panels was disregarded. Total percent cover exceeded 100 % in the case of multi-strata growth.

3.8 Diversity indices

The measures of diversity used in this study stem from information theory. The Shannon index (also termed Shannon-Wiener index) was calculated from the equitation:

$$H' = -\sum p_i \ln p_i$$

where p_i = the proportion of individuals of the ith species.

Log_e was used in calculating the Shannon index. The value of the index normally falls between 1.5 and 3.5 and rarely exceeds 4.5 (Margalef 1972).

Evenness, defined as the ratio of observed diversity to maximum diversity (Pielou 1969), was calculated from:

$$E = H' / H_{\max} = H' / \ln S$$

where S = total number of species

E ranges from 0 to 1.0, while the latter value is reached when all species are equally abundant (Magurran 1988).

3.9 Statistical analyses

Similarities between communities were assessed on untransformed data by a multivariate 1-way Analysis of Similarity (ANOSIM) based on the Bray-Curtis Similarity index (Clarke 1993). If there were significant main effects on the 0.05 probability level, pairwise comparisons were used to determine which treatment levels differed. Subsequent SIMPER analyses quantified the contribution of each species to dissimilarities between communities (Clarke 1993). The Primer software package from the Plymouth Marine Laboratory was used for both analytical methods. For the calculations of the Bray-Curtis index and the ANOSIM and SIMPER analyses, benthic diatoms were treated as one taxon. They were excluded from the calculations of diversity parameters. The IDH prediction of a unimodal response curve was tested by a 2nd degree polynomial regression (pr) while the fit of the data to the proposed extended model was checked by a 3rd degree polynomial regression. Linear regression analyses (lr) were used to test for significant interactions between the disturbance gradient and response variables other than the diversity parameters. Correlations were analysed by Spearman’s Rank Correlation (src).

Differences in blue mussel percent cover between treatments and controls, and among treatments were tested for significance by ANOVA. Due to the non-replicated experimental design of the 1999 study, only mean values, calculated from the four treatment panels, were used for the plottings of these data and no ANOSIM and SIMPER analyses were done. A 2-tailed t-test and the nonparametric Kruskal-Wallis ANOVA were used for analyses of meteorological data.

4. Results: emersion treatments

4.1 Course of natural succession

Species richness, diversity (Shannon index), and evenness peaked in the 10th wk of undisturbed succession and declined afterwards while abundances of blue mussels increased dramatically between the 10th and 12th wk as a consequence of a massive spat fall in mid July (Fig. 8, raw data of all analyses presented in this chapter are provided on a CD-ROM enclosed at the end of this thesis). Mussel abundance and diversity parameters were inversely correlated (species richness: srcR = -0.69, $p < 0.001$; Shannon index: srcR = -0.81, $p < 0.001$; evenness: srcR = -0.70, $p < 0.001$).

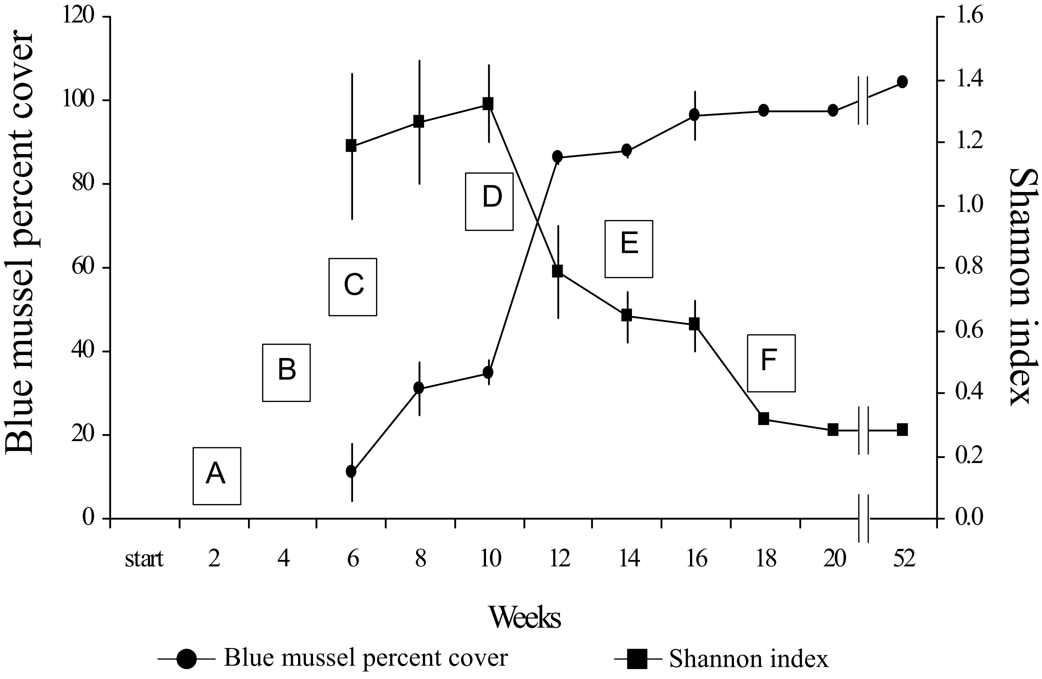


Fig. 8. Mean (± SE) Shannon index and blue mussel percent cover on undisturbed settlement panels sampled biweekly from May to October 2000 and again in May 2001. Rectangles correspond to the pictures shown in Fig. 9.

4.2 Procedural controls

No significant differences in community composition as well as in diversity parameters between controls and procedural controls were present at any sampling date. Thus, the mechanical process of breaking through the water surface can be ignored.

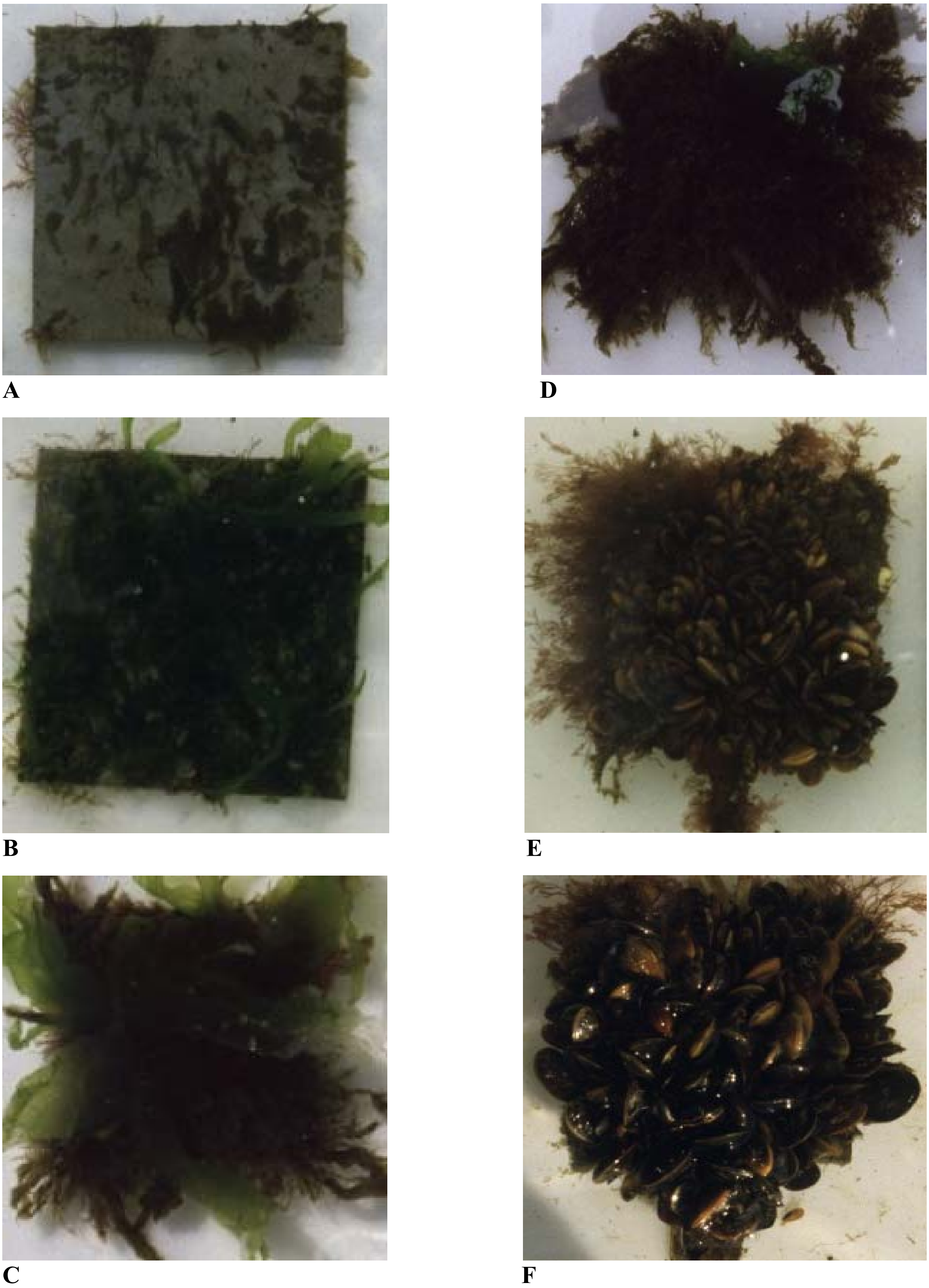


Fig. 9. Settlement panels of the succession monitoring. (A) 2nd wk, (B) 4th wk, (C) 6th wk, (D) 10th wk, (E) 14th wk, (F) 18th wk.

4.3 Larval supply and mussel growth rates

Monthly overall recruitment, recorded as total percent cover on separate panels, were significantly higher in September 1999 than in September 2000 (Kruskal-Wallis ANOVA: H = 6.54, $p < 0.05$). Differences were non-significant in October. Juvenile blue mussels exhibited higher growth rates during the experimental phase in 1999 (Fig. 10).

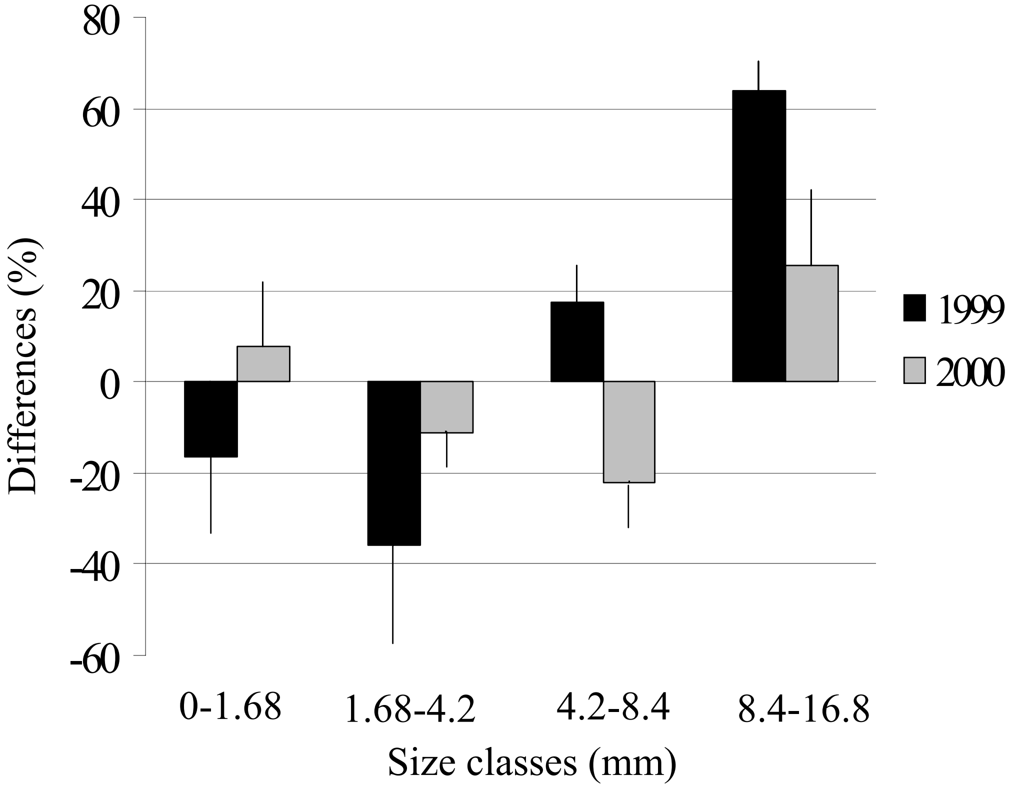


Fig. 10. Relative increase and decrease in the proportions of juvenile blue mussels in four size classes between the beginning of the experiment and the last sampling date (1999 and 2000 respectively). Size class limits were defined by an ocular scale. Randomly chosen panels, which were examined at the beginning of the study, were compared to the undisturbed controls (n = 3 in 1999, n = 6 in 2000) with regard to mussel abundance and size distribution. Bars are mean values (± SE).

4.4 Climatic data

The two subsequent study years were markedly different with regard to the prevailing weather conditions in September and October. Monthly mean water temperatures were significantly higher, by 2.5 °C on average, in September 1999 than in the same month of the following year (Kruskal-Wallis ANOVA: H = 33.41, $p < 0.001$). Monthly mean air temperature in September 1999 was significantly higher than in September 2000 (t-test: $t_{58} = 6.05$, $p < 0.001$). The difference was 5.6° C on average while 11° C was the largest difference between equivalent days. Mean solar radiation was significantly higher, by 87 W m^{-2} on average, in October 1999 than in October 2000 (Kruskal-Wallis ANOVA: H = 5.97, $p < 0.05$)

while monthly average rainfall did not differ significantly between years in both months. Air temperature, insolation, and rainfall did not differ significantly between years in November. The water temperature was significantly higher, by 1° C on average, in November 2000 (Kruskall-Wallis ANOVA: $H = 4.23$, $p < 0.05$).

4.5 Frequency treatments

4.5.1 Three month old communities

4.5.1.1 *1999*

At the end of the undisturbed maturing period, communities were dominated by blue mussel spat (72 %, percent cover values are means of four panels) and by the barnacle *B. improvisus* (22 %). Five other species: the algae *Enteromorpha sp.* and *Ceramium strictum,* as well as the invertebrates *Polydora ciliata*, *Membranipora membranacea,* and *Laomedea flexuosa* were present but their respective proportions did not exceed 5 %. The grouped benthic diatoms covered 7 % of the panel surfaces.

No significant disturbance-diversity relationships were detected after 4 and 8 wk while the picture obtained after 12 wk persisted until the end of the experiment after 7 mo.

After 12 wk of experimental duration, species number on the controls has dropped from 5.5 on average, at the beginning of the experiment, to 2.5 while it reached a maximum of 7 species in the 32 x 15 min frequency treatment. Even low disturbance frequencies enhanced community diversity markedly in comparison to the undisturbed controls: Shannon index- ($prR^2 = 0.35$, $p < 0.001$) and evenness- ($prR^2 = 0.49$, $p < 0.001$) diversity relationships were significantly unimodal. Species richness-disturbance relationship was non-significant (Fig. 11). Differences in the shape of the response curves of the combined diversity measures and species richness were presumably due to four species that were present on the most frequently disturbed panels: the algae *Enteromorpha sp.* and *C. strictum*, the bryozoan *M. membranacea,* and the spionid polychaete *P. ciliata.* They contributed to species richness, but, because of their low abundances, they did not enhance Shannon index and evenness.

Mussel cover declined in all emersion treatments while it increased on the control panels during the course of the experiment. Mussels were mostly impaired within the intermediate range. They exhibited a minimum of 7 % cover in the 4 x 15 min treatment but increased towards the most frequent emersion treatment (68 %, Fig. 12).

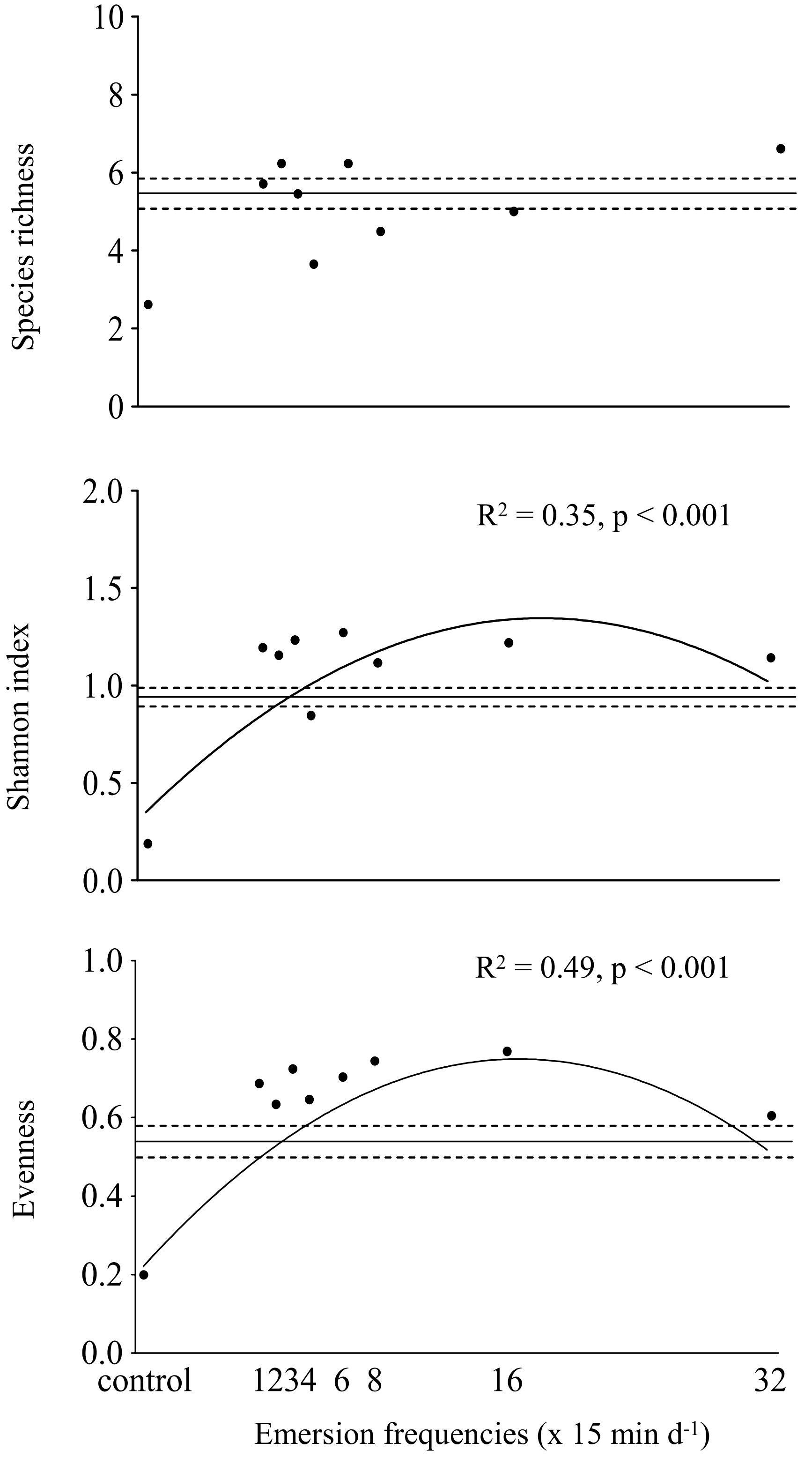


Fig. 11. Diversity parameters of the 3 mo old communities in 1999 after 12 wk of experimental duration. Dots are values from replicated settlement panels ($n = 4$) and represent parameter means as a function of the emersion frequency treatments. The solid horizontal line is the respective start parameter value and the dashed lines its SE. Regression lines are shown only for significant relationships ($p < 0.05$).

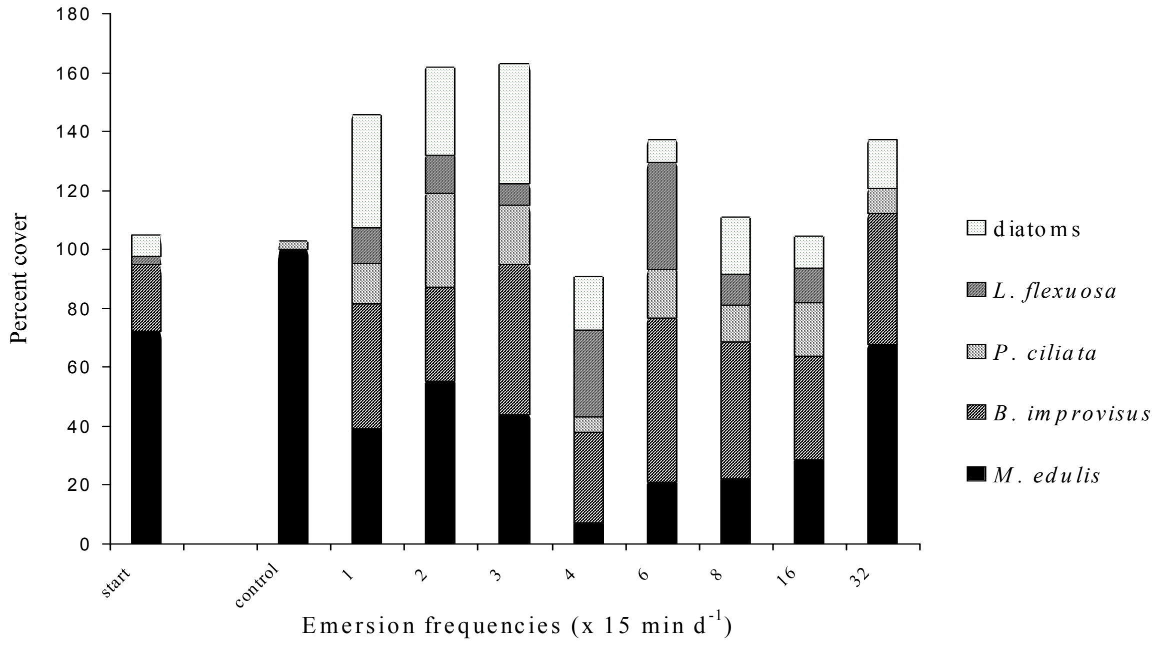


Fig. 12. Mean percent cover values of the predominant settlers (presented species accounted for 88 % of total cover on average) after 12 wk across the 8 frequency levels and controls in 1999. Their proportions in the 3 mo old start communities are shown in the very left column.

At the last sampling date in the early spring of 2000, Shannon index- ($prR^2 = 0.34$, $p < 0.01$) and evenness- ($prR^2 = 0.49$, $p < 0.001$) disturbance relationships were significantly unimodal. Species richness-disturbance relationship remained non-significant.

4.5.1.2 *2000*

After 3 mo of undisturbed maturing, blue mussels covered 84 % of the panel surfaces while *Balanus improvisus* contributed 16 %. Three epibiotic algal species and the polychaete *P. ciliata* constituted the remaining community. Compositions of the start communities differed significantly between the two subsequent study years (ANOSIM: R = 0.135, p < 0. 05) due to different proportions of blue mussels (40 *, all following numerical values marked with asterisks indicate contributions of the mentioned species to observed dissimilarities in percent) and barnacles (17 *). Nevertheless, start values for the three diversity parameters were almost identical in both years.

Weak U-shaped (i.e. inverse unimodal) relationships between disturbance and diversity were detected after 6 wk (species richness: $prR^2 = 0.08$, $p = 0.10$, Shannon index: $prR^2 = 0.14$, $p < 0.05$; evenness: $prR^2 = 0.11$, $p = 0.055$). Community composition changed significantly during the first 1.5 mo (ANOSIM: $p < 0.01$, Appendix Table 4) due to a decrease in mussel cover (22 *) that coincided with an increase in *P. ciliata* (21 *), *B. improvisus* (13 *), and benthic diatom abundances (19 *).

After 14 wk of treatment, controls and the most frequently emersed communities exhibited the highest values for species richness and Shannon index while parameters of the low and intermediate disturbance range remained close to their initial values. Diversity-disturbance relationships for both parameters were significantly U-shaped (species richness: $prR^2 = 0.18$, $p < 0.05$; Shannon index: $prR^2 = 0.24$, $p < 0.05$) while the evenness-diversity relationship was non-significant (Fig. 13). Multiple comparisons among all treatments and controls revealed that the 48 x 15 min level exhibited significantly lower blue mussel percent cover values than the majority of the remaining treatments (Table 1 A+B). A slight tendency for the mussel to decrease with increasing frequency level was found but was not significant (Fig. 14).

Tab. 1 A) One-factor ANOVA for the effect of emersion frequencies on *Mytilus edulis* abundances (estimated as percent cover, arcsine-transformed) on the panels of the 3 mo old communities in 2000 after 14 wk.

	df Effect	*MS Effect*	*df Error*	*MS Error*	*F*	*p*
Emersion frequencies	5	0.68	30	0.17	3.89	< 0.01

B) Tukey's HSD multiple comparisons. All other treatments differed not in their effect on blue mussel abundance.

	controls	*1 x 15*	*4 x 15*	*8 x 15*	*24 x 15*
48 x 15	p = 0.06	p < 0.01	p < 0.05	p < 0.05	n.s.

Although variations of mussel cover across the disturbance gradient were vague, Shannon index was inversely correlated with blue mussel abundances (srcR = -0.61, $p < 0.001$). Barnacle cover did not vary significantly among treatments but was inversely correlated with proportions of the blue mussel (srcR = -0.71, $p < 0.001$), indicating that *B. improvisus* was not restricted by the applied disturbances but by the competitively superior mussel.

The spionid polychaete *P. ciliata* also was an important competitor for space. Its abundances were lowest at both ends of the disturbance gradient while they peaked in the intermediate disturbance range. The polychaete, which was nearly absent at the beginning of the study but was abundant by its end, contributed mainly to community change over time (29 *). Blue mussels (22 *) and benthic diatoms (18 *) did as well.

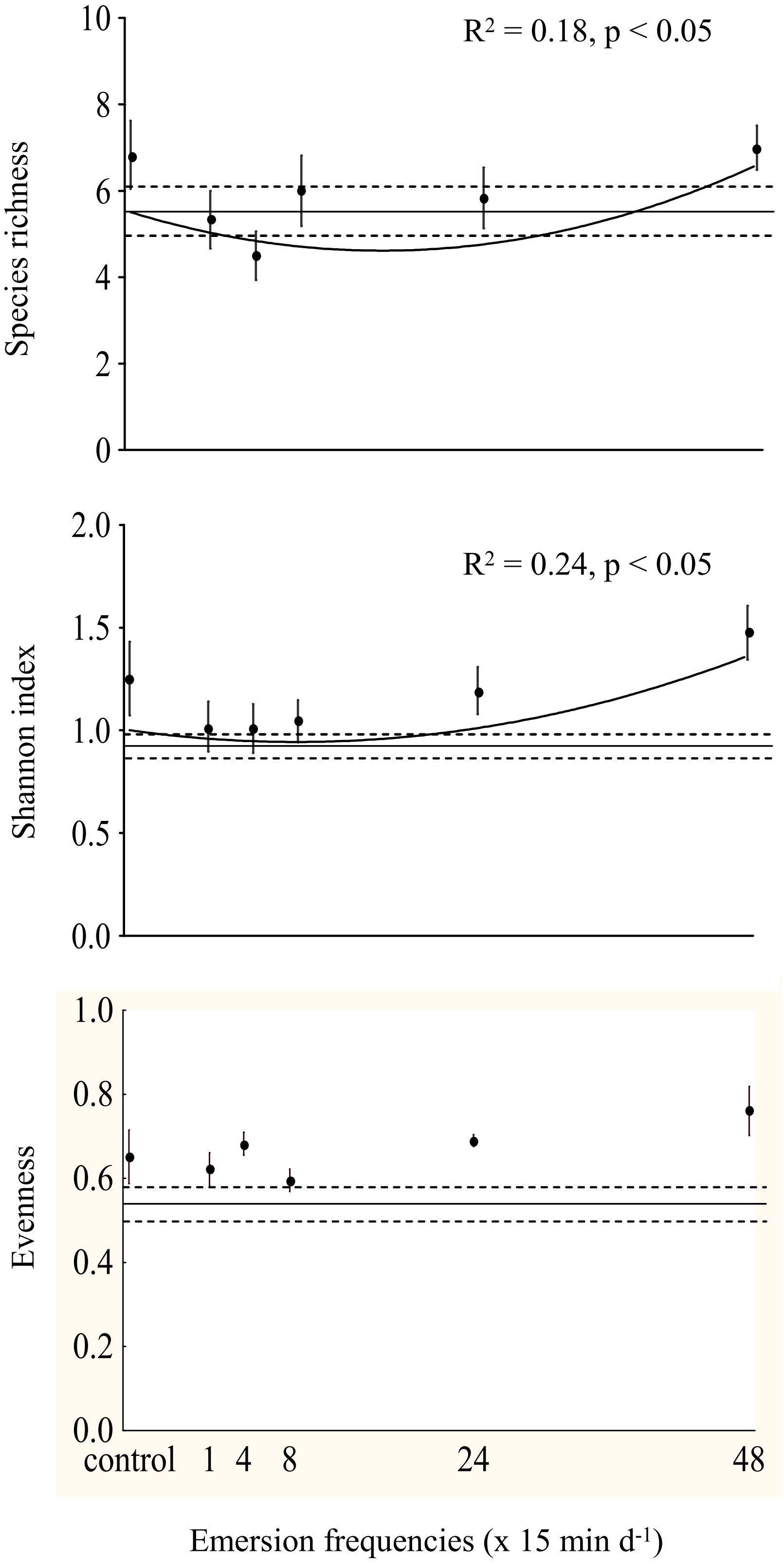


Fig. 13. Diversity parameters of the 3 mo old communities in 2000 after 14 wk of experimental duration. Dots are values from replicate panels (n = 6), representing parameter means (± SE) as a function of the emersion frequency treatments. The solid horizontal line is the respective start parameter value and the dashed lines its SE. Regression lines are shown only for significant relationships ($p < 0.05$).

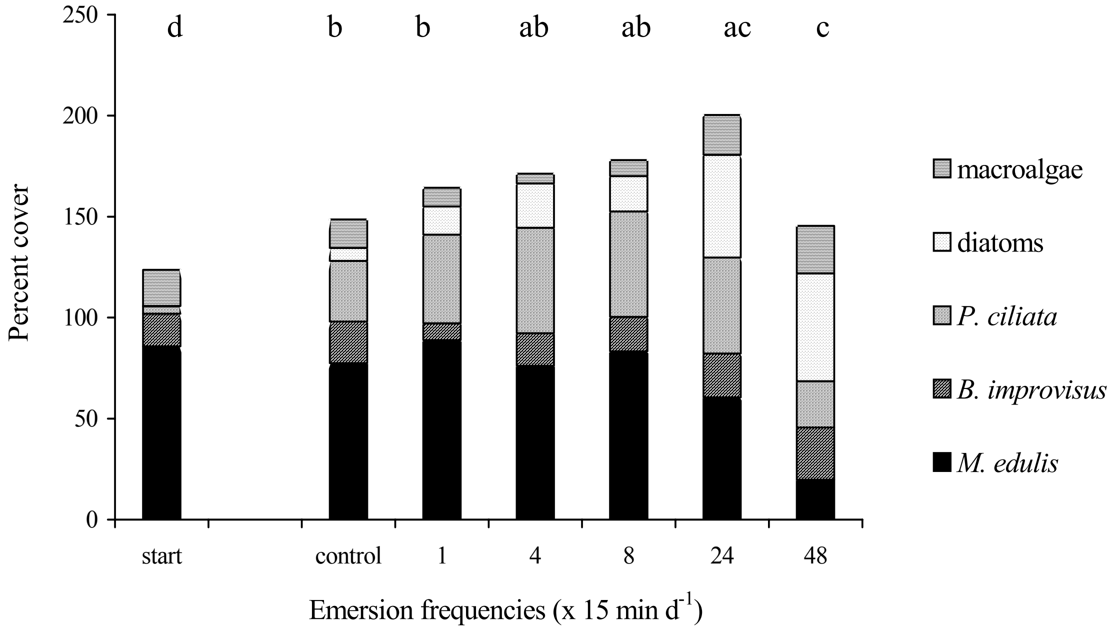


Fig 14. Mean percent cover values of the predominant settlers (presented species accounted for 99 % of total cover on average) after 14 wk across the 5 frequency disturbance levels and controls in 2000. Their proportions in the 3 mo old start communities are shown in the very left column. Different letters indicate significant differences in community composition (ANOSIM: $p < 0.05$).

Communities of the two severest disturbance levels were significantly different from the controls (ANOSIM: $p < 0.01$, Appendix Table 5). This was due to the suppression of blue mussel abundances (30 *) and enhanced proportions of benthic diatoms (26 *) on frequently emersed panels. The 48 x 15 min treatment differed from all other treated communities, except from those of the 24 x 15 min level (ANOSIM: $p < 0.05$; *M. edulis*: 34 *, diatoms: 22 *, Appendix Table 5, Fig. 14), for the same reasons.

Diatoms seemed to have benefited from the high frequent disturbances because their abundances were maximal in the 24 x 15 and the 48 x 15 min treatments. They were lowest in the controls at the same time. Total proportions of algae (diatoms + macroalgae) increased significantly with increasing disturbance level and were highest at the most severe treatment level ($lrR^2 = 0.46$, $p < 0.001$).

4.5.2 Twelve month old communities

After 1 yr of undisturbed succession, blue mussels dominated all panels to 100 %. Seven other species were associated with *Mytilus*: *Ectocarpus sp.*, *C. strictum*, the peritrich ciliate *Vorticella sp.*, *L. flexuosa*, *M. membranacea*, *P. ciliata*, and *B. improvisus*.

After 4 wk evenness declined monotonously across the disturbance gradient ($prR^2 = 0.36$, $p < 0.01$) while other disturbance-diversity relationships were non-significant. Diversity parameters of almost all communities dropped below their respective start level during the first month.

After 8 wk this was still the case for Shannon index and evenness while species richness values of the low and intermediate disturbance range equalled their start values. Disturbance-diversity relationships were non-significant for Shannon index and species richness, but evenness exhibited a significant U-shaped pattern ($prR^2 = 0.29$, $p < 0.01$).

Controls were different from all treated communities after 8 wk (ANOSIM: $p < 0.05$, Appendix Table 6). These differences were due to a decrease in the abundance of *L. flexuosa* (23 *) and *C. strictum* (19 *) on all treated panels and to fluctuations in blue mussel cover across the disturbance gradient (17 *). The most frequently disturbed assemblages were different from all communities but not from those of the 24 x 15 min level (ANOSIM: $p < 0.05$, Appendix Table 6). Reduced abundances of blue mussels (38 *) and increased proportions of *Enteromorpha sp.* (17 *) were responsible for these dissimilarities.

Response curves of species richness ($prR^2 = 0.34$, $p = 0.51$), Shannon index ($prR^2 = 0.29$, $p < 0.05$), and evenness ($prR^2 = 0.22$, $p < 0.05$) were U-shaped after 3 mo (Fig. 15). No conspicuous disturbance impact on adult mussels was detected after 3 mo of emersion disturbance. *Mytilus* persisted on all panels, and total mussel cover exceeded 100 % in all cases due to settlement of mussel spat on their adult conspecifics. No significant differences in community composition were generated by the four intermediate emersion treatments.

The most frequently disturbed communities differed significantly from all other treated assemblages (ANOSIM: $p < 0.05$, Appendix Table 7). They contained the smallest proportions of blue mussels (34 *), which was still 108 % cover on average. This indicates that 1 yr old adults were not impaired by the disturbances while mussel spat recruitment was restricted. High proportions of *Enteromorpha sp.* (21 *) and diatoms (13 *), which were present on these panels, accounted for further dissimilarities. Total algae proportions (diatoms + macroalgae) were positively correlated with disturbance severity ($lrR^2 = 0.22$, $p < 0.05$).

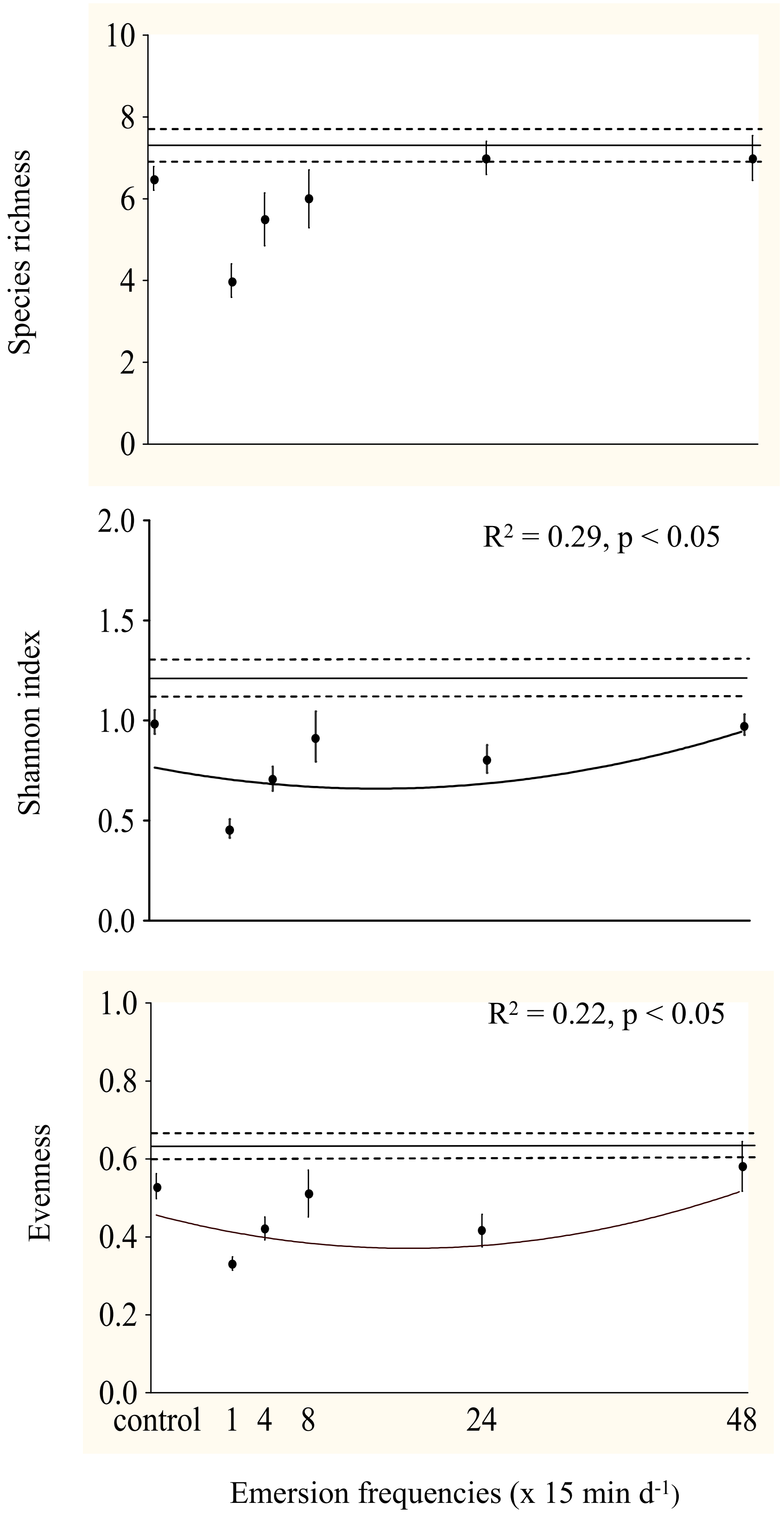


Fig. 15. Diversity parameters of the 12 mo old communities in 2000 after 12 wk of experimental duration. Dots are values from replicate panels ($n = 4$), representing parameter means (± SE) as a function of emersion frequency treatments. The solid horizontal line is the respective start parameter value and the dashed lines its SE. Regression lines are shown only for significant relationships ($p < 0.05$).

Control communities were different from the assemblages of the 1 x, 24 x, and 48 x 15 min level (ANOSIM: $p < 0.05$, Appendix Table 7). Predominantly, this was due to fluctuations in blue mussel abundances (31 *) and low abundances of *C. strictum* (20 *) on all treated panels. Of further significance was a decrease in barnacle cover (10 *) and the retreat of *P. ciliata* (10 *) under harsher disturbance conditions (Fig. 16).

Due to an incisive change in species composition during the experimental period, no treatment community corresponded to the start assemblages (ANOSIM: $p < 0.05$, Appendix Table 7). The following species were essentially responsible: *M. edulis* (26 *) was more abundant on all panels after 12 wk.; *C. strictum* (15 *) was present at the beginning of the experiment and persisted on the undisturbed controls but was rare or absent on all others; benthic diatoms (10 *) were more abundant on treated panels by the end of the experiment (Fig. 16).

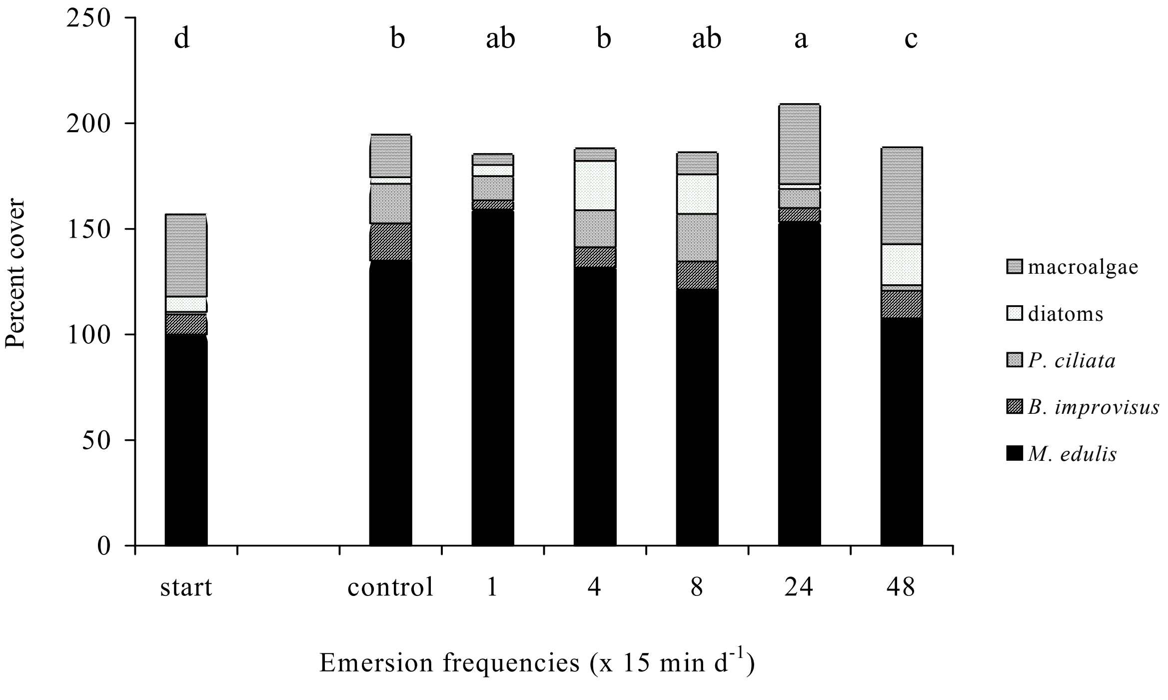


Fig. 16. Mean percent cover values of the predominant settlers (presented species accounted for 98 % of total cover on average) after 12 wk across the 5 frequency disturbance levels and controls in 2000. Their proportions in the 12 mo old start communities are shown in the very left column. Different letters indicate significant differences in community composition ($p < 0.05$).

4.6 Intensity treatments

4.6.1 Three month old communities

4.6.1.1 *1999*

See chapter 4.5.1.1 for a detailed description of the communities at the beginning of the experiment.

In the 4th wk, all diversity parameters showed the unimodal pattern (species richness: $prR^2 = 0.59$, $p < 0.001$; Shannon index: $prR^2 = 0.43$, $p < 0.001$; evenness $prR^2 = 0.20$, $p < 0.01$). During the second month, the unimodal diversity-disturbance relationships became less pronounced in the case of Shannon index ($prR^2 = 0.16$, $p < 0.05$) and evenness ($prR^2 = 0.19$, $p < 0.05$) but was not significant for species richness after 8 wk.

After 12 wk most of the species that were present in the start communities (see chapter 4.5.1.1) had disappeared from the undisturbed controls, despite the blue mussels which covered 100 % of the panels. The few remaining species were epibiotic forms. Species numbers on control panels dropped from 5.5 on average, at the beginning of the experiment, to 2.5 after 3 mo. Species richness was highest at intermediate disturbance levels: panels exposed for 1.5 h per day carried six species on average while the controls and panels exposed for 6 h daily exhibited less than three species (Fig. 17). The most severely disturbed communities, however, did not differ significantly from the start communities in this respect. Shannon index and evenness showed the same pattern. Regression analyses revealed significant unimodal disturbance-diversity relationships (species richness: $prR^2 = 0.26$, $p < 0.01$; Shannon index: $prR^2 = 0.32$, $p < 0.01$; evenness: $prR^2 = 0.24$, $p < 0.01$; Fig. 17).

After 12 wk blue mussel cover was reduced in all treated assemblages. Forty percent of *Mytilus* cover remained on the least disturbed panels while it dropped below 20 % in the intermediate disturbance range. Panels exposed to air for 6 or more h d^{-1} showed ≤ 5 % of *Mytilus* cover (Fig. 18). Community structure was incisively affected by all treatments: *Balanus improvisus* dominated on panels emerged for 1.5, 4, 6, and 8 h d^{-1}. Apparently, it benefited from the absence of blue mussels. Algae abundance increased at higher intensity levels while the invertebrates *L. flexuosa* and *P. ciliata* were more abundant on the less severe treated panels. Proportions of algae, including macroalgae and diatoms, significantly increased with increasing disturbance level ($lrR^2 = 0.15$, $p < 0.05$). The increase in diatom cover was correlated with a decrease in blue mussel abundance ($srcR = -0.33$, $p = 0.06$). The relationship between mussel abundance and diversity was not significant.

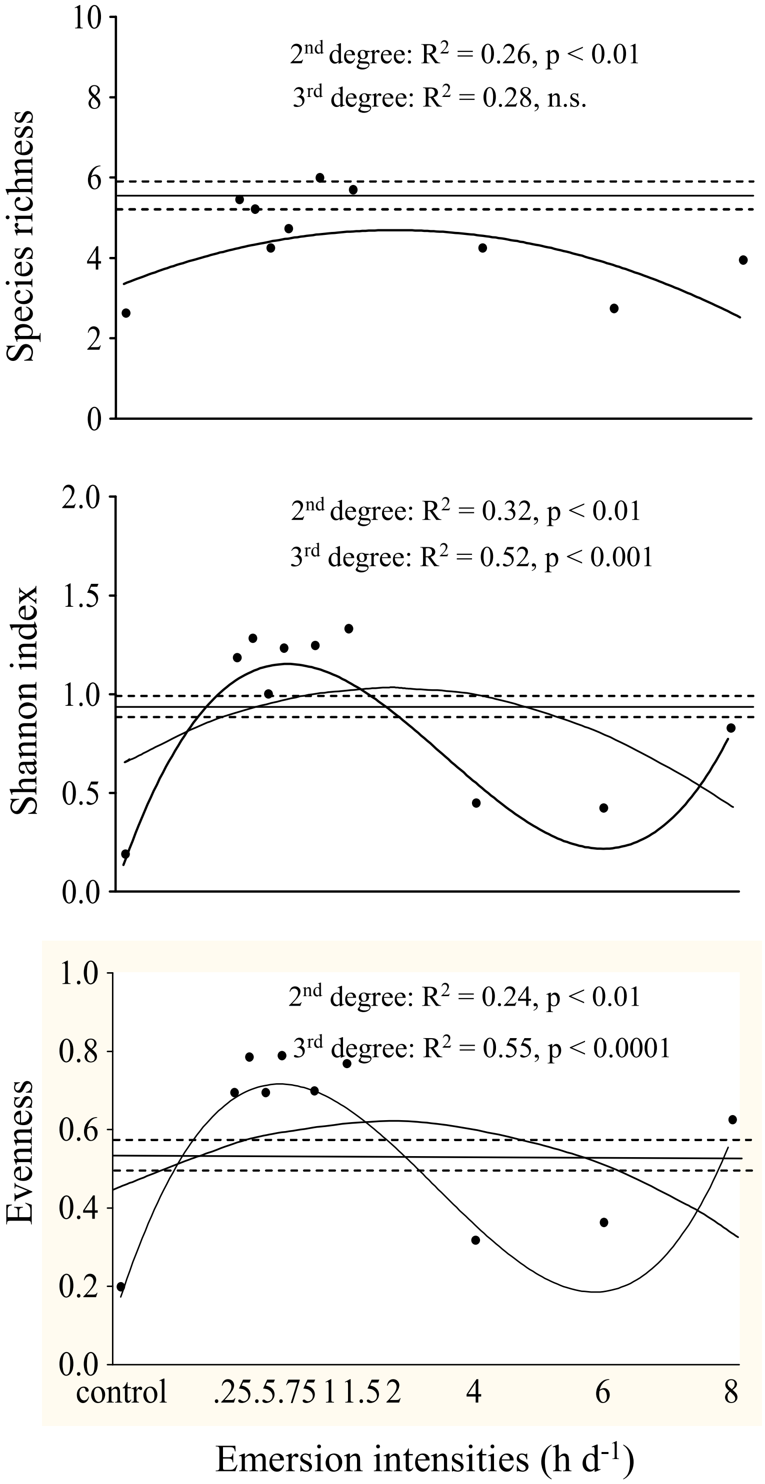


Fig. 17. Diversity parameters of 3 mo old communities in 1999 after 12 wk of experimental duration. Dots are mean values from the four settlement panels of each treatment. The solid horizontal line is the respective start parameter value and the dashed lines its SE. The solid regression line indicates the 2nd degree polynomial function and the dashed one the 3rd degree polynomial function. Regression lines are shown only for significant relationships ($p < 0.05$).

After 28 wk of emersion treatment, the unimodal pattern was even more conspicuous than after 12 wk. Diversity parameters were clearly reduced in the controls and in the 6 and 8 h treatments while they were elevated, partly above their start value, in the low and intermediate treatments (species richness: $prR^2 = 0.59$, $p < 0.001$; Shannon index: $prR^2 = 0.53$, $p < 0.001$; evenness: $prR^2 = 0.20$, $p < 0.05$).

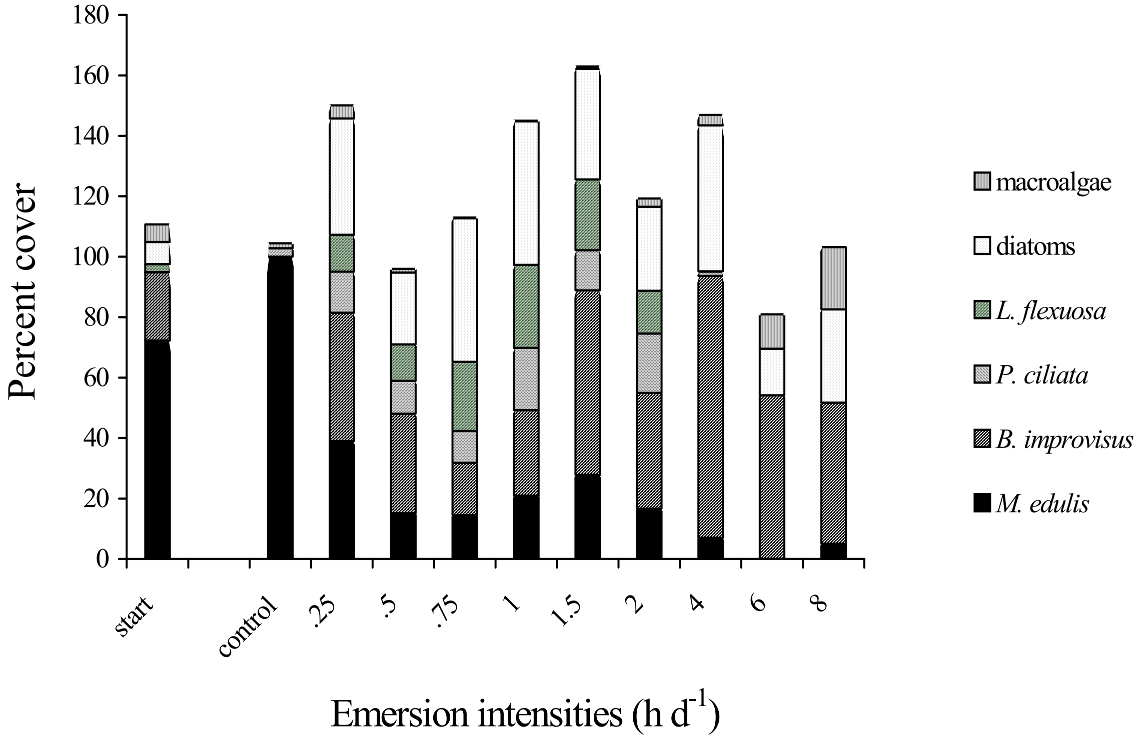


Fig. 18. Mean percent cover of the predominant settlers (presented species accounted for 99 % of total cover on average) in the 3 mo old communities after 12 wk of experimental duration across the 9 intensity disturbance levels and controls in 1999. Their proportions in the 3 mo old start communities are shown in the very left column.

4.6.1.2 *2000*

For a comparison of start communities in the two subsequent study years see chapter 4.5.1.2.

After 6 wk of experimental duration, species richness and Shannon index declined monotonous with increasing disturbance level (species richness: $lrR^2 = 0.12$, $p < 0.05$; Shannon index: $lrR^2 = 0.12$, $p < 0.05$) while the evenness-disturbance relationship was non-significant. A decrease in mussel cover (25 *) on most of the panels, the spread of *P. ciliata* (19 *) and benthic diatoms (10 *), and fluctuations in barnacle cover (16 *) changed community composition during the first 1.5 mo. Communities of the 12 h treatment were significantly dissimilar to the controls and all treated communities (ANOSIM: $p < 0.05$, Appendix Table 8) but not to those of the 6 h level. Dissimilarities were mainly due to a decrease in mussel cover (25 *), and an increase in diatom cover (12 *), as well as green alga cover (14 *).

After 14 wk of emersion treatments, regression analyses demonstrated a significant U-shaped pattern across the five disturbance intensity levels and controls for species richness ($prR^2 = -0.18$, $p < 0.05$) and Shannon index ($prR^2 = 0.20$, $p < 0.01$). The relationship between evenness and disturbance was non-significant (Fig. 19). During the entire experiment, mussel cover was not significantly affected by the emersion intensity levels applied. It was suppressed below 50 % on average only on the panels of the 12 h treatment level (Fig. 20).

Species richness and Shannon index were inversely correlated with the presence of *Mytilus* (species richness: $srcR = -0.49$, $p < 0.01$; Shannon index: $srcR = -0.82$, $p < 0.001$).

Changes in community composition during the course of the study were small and mainly due to the polychaete *P. ciliata* (34 *), which was rare at the beginning of the study but abundant by its end. This was a seasonal effect because the worms spawn and recruit during late summer and autumn (personal observation). Twelve h of emergence per day suppressed the polychaete and blue mussels but increased diatom proportions. Cover of macroalgae was positively correlated with disturbance intensity ($lrR^2 = 0.18$, $p < 0.01$). For these reasons, communities of the 12 h disturbance level differed from all other treatments (ANOSIM: $p < 0.05$, Appendix Table 9, Fig. 20).

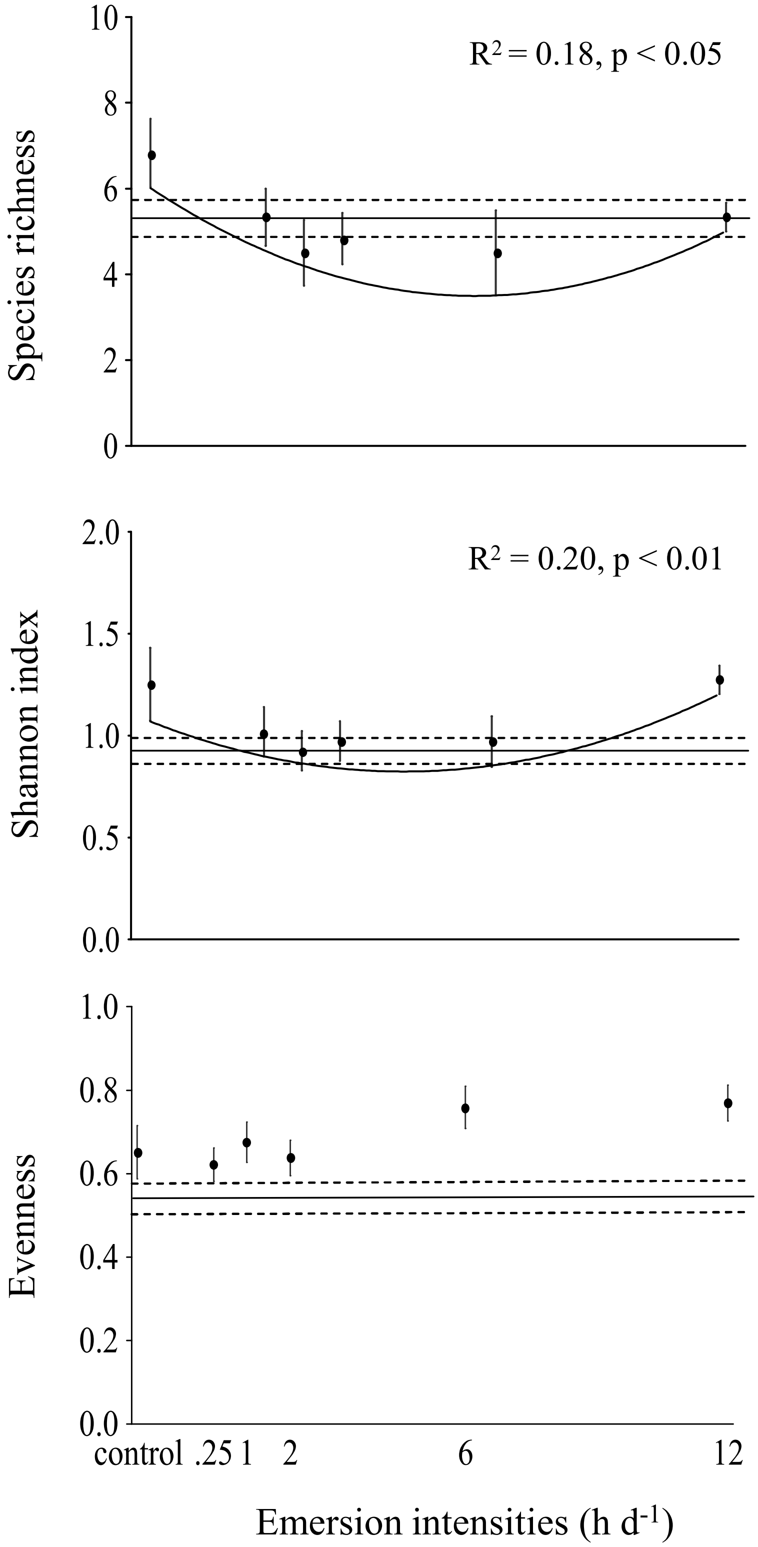


Fig. 19. Diversity parameters of 3 mo old communities in 2000 after 14 wk of experimental duration. Dots are mean values (± SE) from replicate panels (n = 6). The solid horizontal line is the respective start parameter value and the dashed lines its SE. Regression lines are shown only for significant relationships ($p < 0.05$).

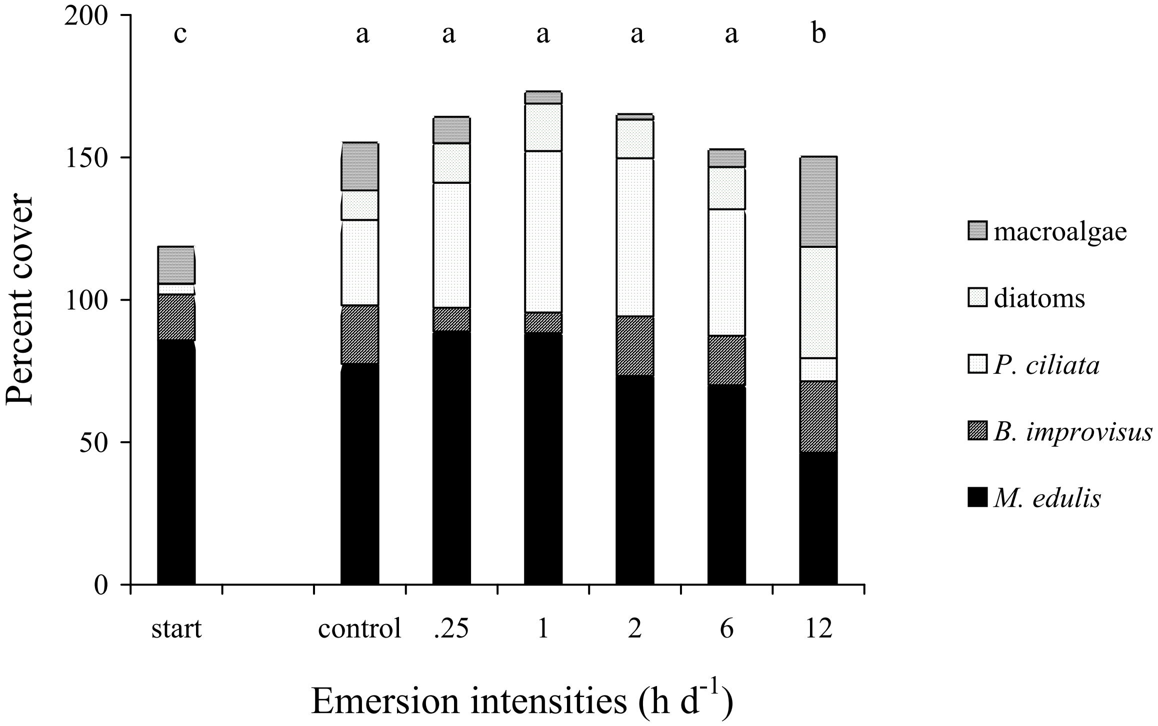


Fig. 20. Mean percent cover of the predominant settlers (presented species accounted for 98 % of total cover on average) in the 3 mo old communities after 14 wk of experimental duration across the five intensity disturbance levels and controls in 2000. Their proportions in the 3 mo old start communities are shown in the very left column. Different letters indicate significant differences in community composition (ANOSIM: $p < 0.05$).

4.6.2 Twelve month old communities

After 1 yr of undisturbed succession, blue mussels dominated all panels to 100 %. Seven more species were associated with *Mytilus*: *Ectocarpus sp.*, *C. strictum*, the peritrich ciliate *Vorticella sp.*, *L. flexuosa*, *M. membranacea*, *P. ciliata*, and *B. improvisus*.

The U-shaped diversity-disturbance relationship emerged already after 1 mo. Regression analyses confirmed a significant relationship for Shannon index ($prR^2 = 0.42$, $p < 0.05$) and evenness ($prR^2 = 0.53$, $p < 0.001$) while the disturbance-species richness relationship was non-significant. The picture was the same 4 wk later (Shannon index: $prR^2 = 0.31$, $p < 0.01$; evenness: $prR^2 = 0.26$, $p < 0.05$).

After 1 mo already all communities were dissimilar to the start assemblages. Control communities were significantly dissimilar to all treated communities after 4 wk, despite those of the 0.25 h level (ANOSIM: $p < 0.05$, Appendix Table 10). After 8 wk they were dissimilar to all of them (ANOSIM: $p < 0.05$, Appendix Table 11).

In the 12th wk, diversity parameters were suppressed at intermediate disturbance intensities. All diversity-disturbance relationships were significantly U-shaped (species richness $prR^2 = 0.49$, $p < 0.001$; Shannon index $prR^2 = 0.67$, $p < 0.001$; evenness: $prR^2 = 0.53$, $p < 0.001$; Fig. 21). On all but the 12 h treatment panels, blue mussels occurred in several layers and exceeded 100 %. Only the highest disturbance level impaired the 1 yr old bivalves. Mussel cover was significantly lower on these panels than on those of the 0.5 (Tukey's HSD: $p < 0.05$) and 1 h level (Tukey's HSD: $p < 0.01$, Table 2).

Assemblage composition changed significantly during the experiment (ANOSIM: $p < 0.05$, Appendix Table 12) due to the following species: *M. edulis* (30 *) contributed mostly to the observed dissimilarities between the start communities and all assemblages after 3 mo; *C. strictum* (16 *) disappeared from all disturbed panels; benthic diatoms (11 *) increased in percent cover on the panels of the 1 and 12 h treatments. Controls differed from almost all treated communities (ANOSIM: $p < 0.05$, Appendix Table 12) but not from those of the 0.5 h level. This was due to the same species: *M. edulis* (29 *), *C. strictum* (18 *), *B. improvisus* (12 *), *P. ciliata* (12 *), and diatoms (13 *).

Communities that experienced the severest treatment level were significantly dissimilar to all other (ANOSIM: $p < 0.05$, Appendix Table 12). Reduced proportions of blue mussels (33 *) as well as enhanced abundances of diatoms (28 *) and of the green alga *Ulva sp.* (12 *), present on the most severely disturbed panels, were mainly responsible for the observed differences.

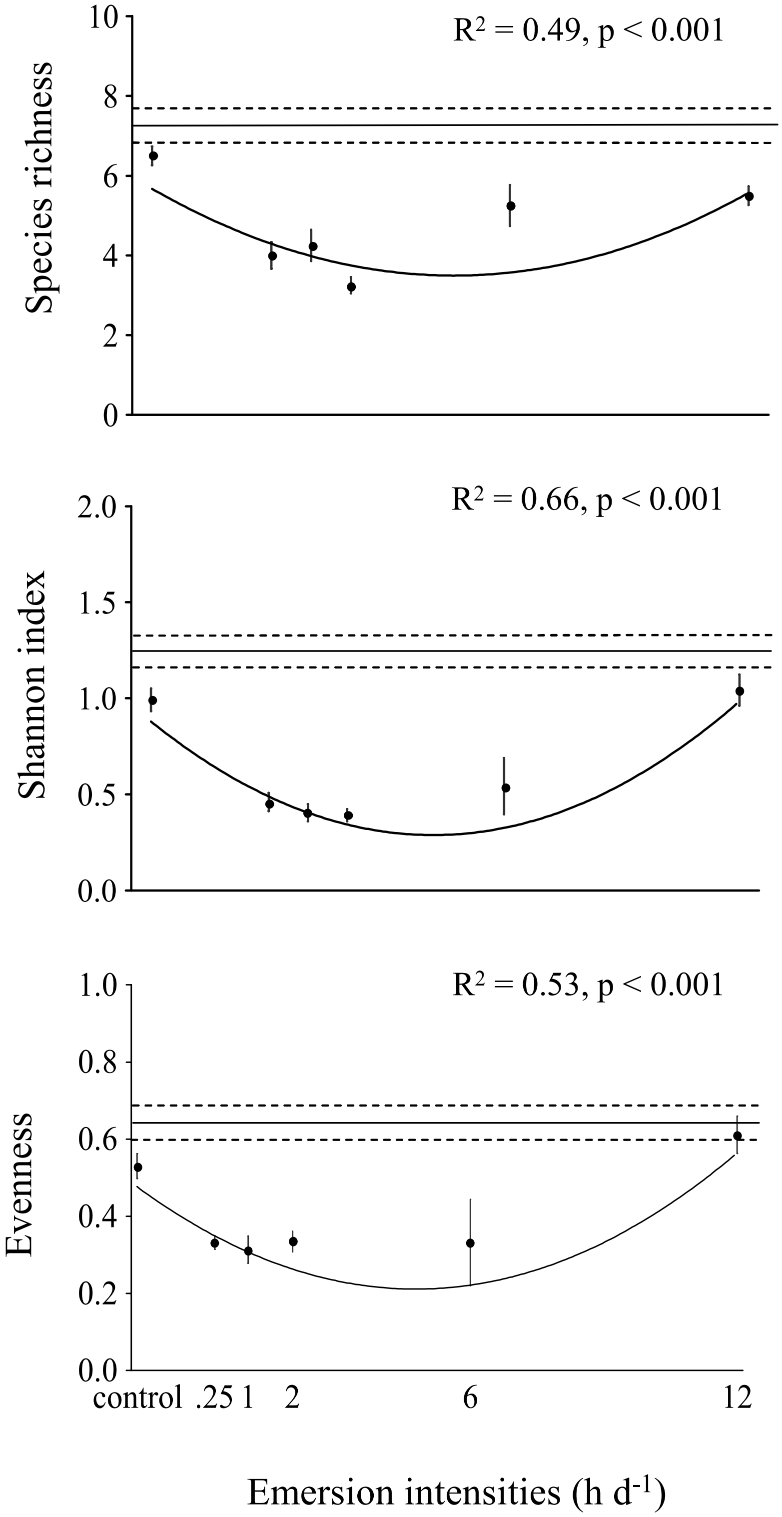


Fig. 21. Diversity parameters of 12 mo old communities in 2000 after 12 wk of experimental duration. Dots are mean values (± SE) from replicate panels (n = 4). The solid horizontal line is the respective start parameter value and the dashed lines its SE. Regression lines are shown only for significant relationships ($p < 0.05$).

Communities of the 1 h level were dissimilar to assemblages of the 2 and 6 h treatment (ANOSIM: $p < 0.01$). These dissimilarities were due to differences in the proportions of *M. edulis* (50 *) and diatoms (23 *) in both cases. Proportions of algae (macroalgae + diatoms) were positively correlated with disturbance intensity and were highest under the severest emersion conditions (srcR = 0.44, $p < 0.05$; Fig. 22).

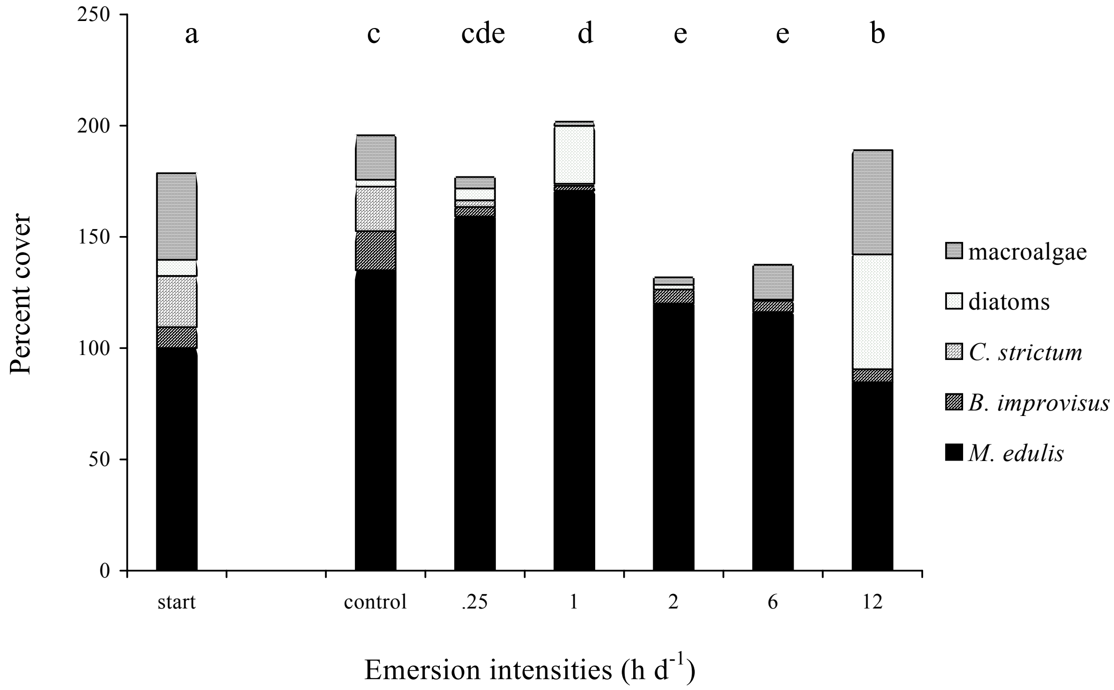


Fig. 22. Mean percent cover of the predominant settlers (presented species accounted for 94 % of total cover on average) in the 12 mo old communities after 12 wk of experimental duration across the five intensity disturbance levels and controls in 2000. Their proportions in the 12 mo old start communities are shown in the very left column. Different letters indicate significant differences in community composition (ANOSIM: $p < 0.05$).

Table 2: One-factor ANOVA for the effect of emersion intensities on *M. edulis* abundances (estimated as percent cover, divided by two, and arcsine-transformed) on the panels of the 12 mo old communities in 2000 after 12 wk.

	df Effect	MS Effect	df Error	MS Error	F	p
Emersion intensities	5	0.13	18	0.029	4.66	< 0.01

5. Discussion: emersion treatments

5.1 General aspects

Blue mussels dominated all undisturbed communities in both study years, and their abundances were frequently inversely correlated to diversity parameters. In 1999 blue mussel cover was suppressed by frequency as well as intensity emersion treatments, and the unimodal relationship between disturbance and diversity, as predicted by the IDH, was found in both experimental series. In 2000, however, disturbance-diversity relationships were non-significant, monotonously increasing or U-shaped. Three environmental factors were identified that differed markedly between the two study years and presumably contributed to the development of contrasting patterns in disturbance-diversity relationships.

(1) Absence of recruits on undisturbed panels in 1999. In 2000 diversity in the controls of the 3 mo old communities increased during the experiment through recruitment of new species while no new recruitment occurred on the control panels in 1999. Together with species exclusion by the dominant blue mussel (see below), this probably led to low diversity in the controls during the first study year. No conclusive explanation was found for the absence of recruits in 1999. It was not due to an insufficient larval supply, since monthly overall settlement rates were even higher in September 1999 than in September 2000 and did not differ between years in October.

(2) Mussel growth rates. Competitive exclusion of nearly all other species by the blue mussels took place in the controls in 1999. In 2000 mussels occupied less than 100 % of the control surfaces at the end of the study on 3 mo old communities. This reduction of dominance could have been caused by lower mussel growth rates in 2000; what was possibly due to lower water temperatures.

(3) Disturbance impact on mussel survival. In 1999, in contrast to 2000, the dominant competitor was negatively influenced by the disturbances applied. In 1999 space was opened to different degrees on all treated panels. This led to an increase in diversity in the intermediate disturbance range because species like the barnacle *Balanus improvisus*, the polychaete *Polydora ciliata*, the hydrozoan *Laomedea flexuosa*, and benthic diatoms had the opportunity to settle in communities or spread from their refuges. In 2000 the absence of disturbance effects on the dominant mussels concurred with the impairment of desiccation-sensitive species and resulted in a stagnation (3 mo old communities) or even reduction (12 mo old communities) of diversity in the intermediate disturbance range.

Higher air temperatures and higher insolation in 1999 should have amplified the detrimental impact of a given emersion treatment (frequencies as well as intensities) by causing higher tissue temperatures, higher rates of tissue water loss due to evaporation, and severer tissue damage due to UV radiation in organisms lacking morphological protection. Thus, the absence of a disturbance impact on blue mussel cover in 2000 is very likely attributable to colder and cloudier weather conditions in this year. This observation underlines that experimentally applied disturbances can be modified by environmental parameters, and that the diversity enhancing intermediate disturbance range can shift along the disturbance gradient. This observation was true for emersion frequency and intensity disturbances.

5.2 Emersion frequency

The predicted unimodal response curve was observed for Shannon index and evenness of the 3 mo old communities in 1999. In 2000, for communities of the same successional stage, relationships between Shannon index as well as species richness and disturbance were U-shaped while evenness exhibited a monotonic increase across the disturbance gradient. Different from the first study year, when all treatments impaired the dominant competitor, in 2000 only the two severest levels reduced mussel cover in comparison to the undisturbed controls. Significantly U-shaped relationships were also found for Shannon index and evenness of the 1 yr old assemblages in 2000. Adult blue mussels were not impaired by any emersion treatment, and total *Mytilus* cover increased on treated panels during the study due to mussel spat recruitment. Only the severest treatment level restricted recruitment rates of the mussel. Because of these processes, diversity parameters in 1999 remained close to their initial levels or were elevated above them in the intermediate range. This was due to the use of open space by already present, but subdominant, species or new colonizers. Additionally, diversity parameters were decreased towards both ends of the disturbance gradient due to competitive exclusion or species impairment. These observations are consistent with the IDH. The severest treatment suppressed Shannon index and evenness but unexpectedly enhanced species richness. This was due to the exclusion of the otherwise abundant hydrozoan *L. flexuosa* and the facilitation of a number of low abundant algal species. In 2000 diversity stagnated (3 mo old communities) or was even reduced (12 mo old communities) in the intermediate disturbance range due to the persistence of the blue mussel concurrent with the impairment of emersion-sensitive species. These two effects reversed the forces of disturbance in this year. In contrast to the pattern suggested by the IDH, diversity increased again towards the severe end of the gradient due to mussel suppression and increased proportions of algae. The latter fact is interpreted as a change in community composition that took place when the assemblage drifted from mussel towards algal dominance. An extended disturbance-diversity pattern that includes this diversity-enhancing change in community composition is suggested in Fig. 23. Further, the observed disturbance-diversity patterns of the two study years are allocated to different sections of the extended curve.

Most of the experimental studies that approached the impact of disturbance frequencies on community structure have been conducted in terrestrial systems. In most cases fire frequency was the factor applied (Tester 1989; Wilson 1990; Collins 1992, 1995; Mehlman 1992). None of these studies reported a unimodal diversity-disturbance relationship. Reice (1985) and Lake & Doeg (1989) worked on the effects of frequencies of physical disturbance on lotic communities but could neither support the concept. Sommer (1995) and Flöder & Sommer (1999) modulated phytoplankton communities by various frequencies of mixing and breaking up the thermocline. Sommer (1995) found no significant relationship between disturbance frequencies and diversity while the IDH was confirmed by Flöder & Sommer (1999).

With regard to our observations concerning variable community responses, we conclude that even observations that are incongruent with the unimodal pattern are not invalidating the IDH. It is possible that experimenters observed different sections of the curve given in Fig. 23 as a response to the disturbance regimes they applied. A widespread disturbance range is therefore mandatory when the IDH is tested. Furthermore, two premises must be fulfilled: (1) the dominant competitor must be affected by the disturbances applied and (2) competitive exclusion must take place (both not the case in this study in 2000). This latter point has already been stressed in former IDH-related experimental studies: contrasting disturbance-diversity patterns in the studies of Carpenter (1981) and Sammarco (1982) on grazer effects on algal communities were explained by the absence of a dominant competitor in the second case (Sammarco 1982). These studies are discussed in detail in chapter 5.3. Reice (1985), who investigated the validity of the IDH for stream benthic macroinvertebrate communities, reasoned that the absence of a unimodal pattern in his study was due to an indistinct competitive hierarchy in the focal system. Fluctuations in these influencing variables generally restrict the testability of the concept.

Concerning the relationship between community age and disturbance resistance, an unexpected observation was made: older communities were not more resistant to the applied emersion frequency disturbances than younger assemblages. Though 1 yr old assemblages were richer in species than younger communities at the beginning of the experiment, they experienced a greater loss in diversity in the intermediate disturbance range during the experimental period due to the extinction of emersion-sensitive species. The most abundant among these species, which constituted an associated community within the blue mussel matrix during the 1 yr long maturing period, were the hydrozoan *L. flexuosa*, the bryozoan *Membranipora membranacea*, brown algae of the genus *Ectocarpus* and the two delicate protozoans *Zoothamnion sp.* and *Vorticella sp.* The conclusion that species loss was due to species sensitivity towards emersion conditions is confirmed by the fact that the mentioned algae, as well as *M. membranacea*, and *L. flexuosa*, in North Sea intertidal areas, are restricted to the lower intertidal or the subtidal. Presumably, they are not well adapted to emersion conditions (Kornmann & Sahling 1983, Hayward & Ryland 1995). Adult mussels were less sensitive towards various frequencies of emersion than subadult individuals. The latter were effectively harmed by all treatments in 1999 and at least by the two most frequent emersion treatments in 2000. This was probably a size effect because larger individuals exhibit a smaller surface/volume ratio. This fact decelerates the process of tissue temperature change during emersion. Additionally, adult mussels presumably possess a greater portion of storage tissue, making them less susceptible to periods of alimentary deficiency. Finally, aggregates of older individuals are more voluminous, leading to an improved buffering of detrimental conditions by shading and retention of water. The latter circumstance provides a humid microclimate and cooling through evaporation.

5.3 Emersion intensity

Observed effects of emersion intensity treatments were similar to those that are described above for frequency treatments: the unimodal pattern was found in 1999 while in 2000 all disturbance-diversity relationships were non-significant or U-shaped. The reasons for these contrasting patterns are presumably identical with those that have already been discussed in chapter 5.1 and 5.2. Due to the assumed environmental modification of the applied disturbances in the second study year, the dominant blue mussel was not significantly affected by the majority of disturbance levels. Again, an insufficient suppression of competitive exclusion concurred with the impairment of emersion-sensitive species in the intermediate range of the disturbance gradient. This resulted in a U-shaped disturbance-diversity pattern. Species that showed reduced cover proportions under intermediate emersion intensity levels were the red algae *Ceramium strictum* and *Polysiphonia elongata*; the athecate hydrozoan *Clava multicornis* and the thecate hydrozoan *L. flexuosa*. These forms are, similar to the emersion-sensitive species mentioned in chapter 5.2, adapted to conditions of the lower intertidal and subtidal (Kornmann & Sahling 1983, Hayward & Ryland 1995). Therefore, they are presumably susceptible to prolonged conditions of exposure to the air.

A number of experimental IDH-related studies that dealt with disturbance intensities have been conducted in marine benthic systems, but, with regard to the observed disturbance-diversity relationships, the picture remains inconsistent. Some of the contradictory findings have been explained by the presence or absence of a dominant competitor: Carpenter (1981) and Sammarco (1982) worked on the effects of different grazing intensities of the sea urchin *Diadema antillarum* on reef algae communities. Carpenter (1981) used three density levels (0, 8, 16 urchins m^{-2}) and found a maximum of algal species richness at intermediate *Diadema* densities. Sammarco (1982) conducted an experiment with four density levels (0, 4, 16, 64 urchins m^{-2}) at the same study site, and he detected a monotonous decline of species richness with increasing number of urchins per cage. Unexpectedly, these very similar experiments yielded an ambiguous picture, and Sammarco (1982) argued that in his study the unimodal pattern did not emerge because dominant algae were absent. Hixon & Brostoff (1983) generated three different intensity levels of fish grazing on reef algae, and they found highest algal species richness at the intermediate level, since dominant algae were present and were effectively harmed by this disturbance. This is consistent with our observation that impairment of the dominant competitor is essential for the appearance of the unimodal pattern.

Mook (1981) simulated predation pressure on fouling communities by mechanically removing coverage from settlement panels to different degrees (four intensity levels). He found no unimodal species richness-disturbance relationship. Ambrose (1993) worked with four different densities of ophiuroids that affected a soft-bottom infauna community. He found no effect of brittle star density on species richness and evenness but a slight decrease in diversity (Shannon index) with increasing predator density. Austen et al. (1998) investigated the influence of different bioturbator species on meiobenthic nematode assemblages. They generated an intensity gradient for two burrowing bivalves (*Nuculoma tenuis*: 612, 1469, and 3059 individuals m^{-2}; *Abra alba*: 612, 1836, and 3304 individuals m^{-2}) and found a maximum of nematode species richness at intermediate intensities in one case and a decline with increasing density in the other. Widdicombe & Austen (1999) showed that treatment effects on macrofauna assemblages in the same experiment were identical to those on meiobenthic nematode communities. Widdicombe & Austen (1998) extended the experiment and demonstrated maximum infaunal species richness in the presence of intermediate densities of the hearturchin *Brissopsis lyrifera* (0, 28, and 71 individuals m^{-2}).

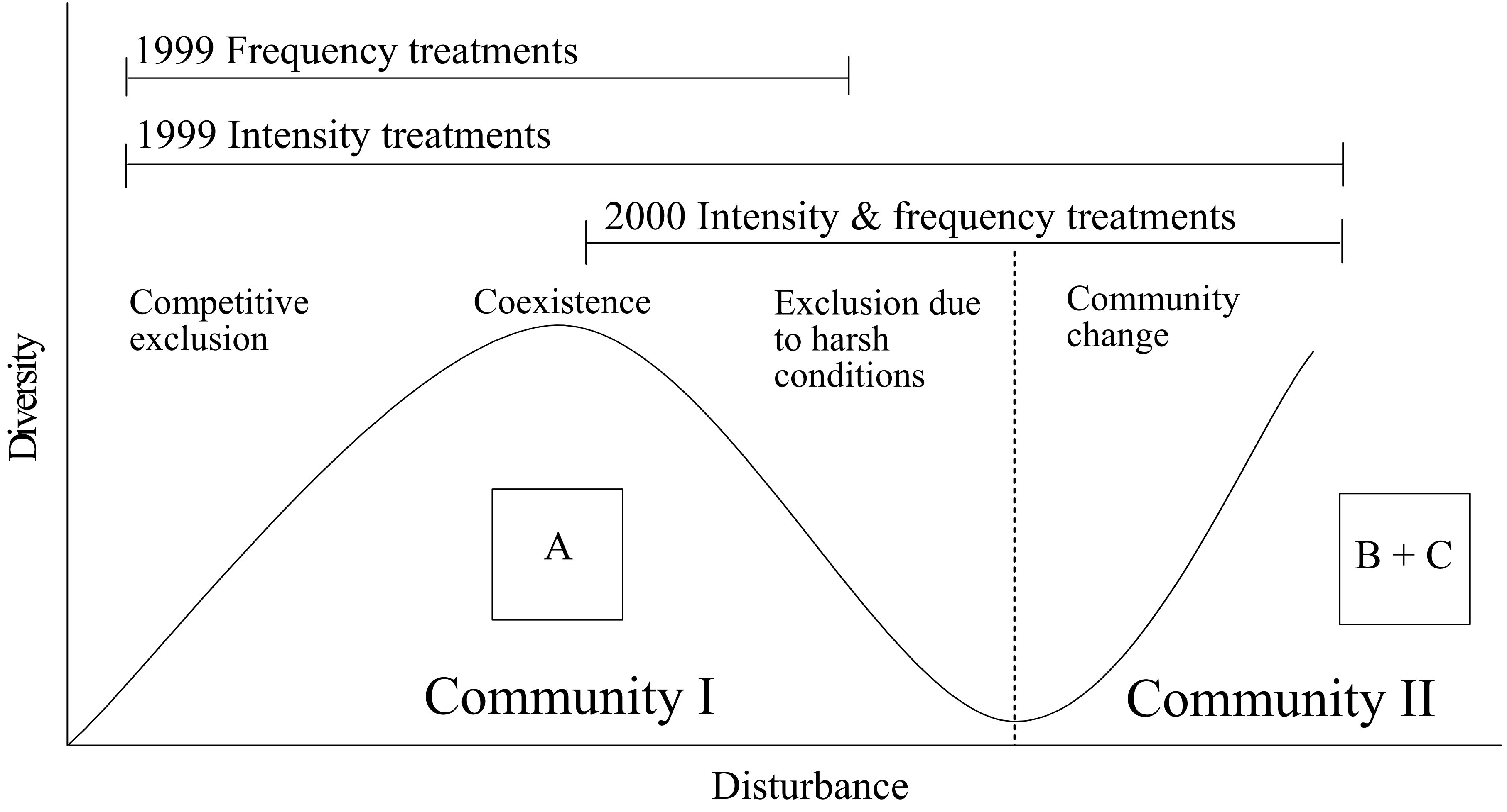


Fig. 23. The extended IDH. Different sections of the model have been observed in the two study years while the widest range was detected by the intensity treatments in 1999. Rectangles correspond to the pictures presented in Fig. 24.

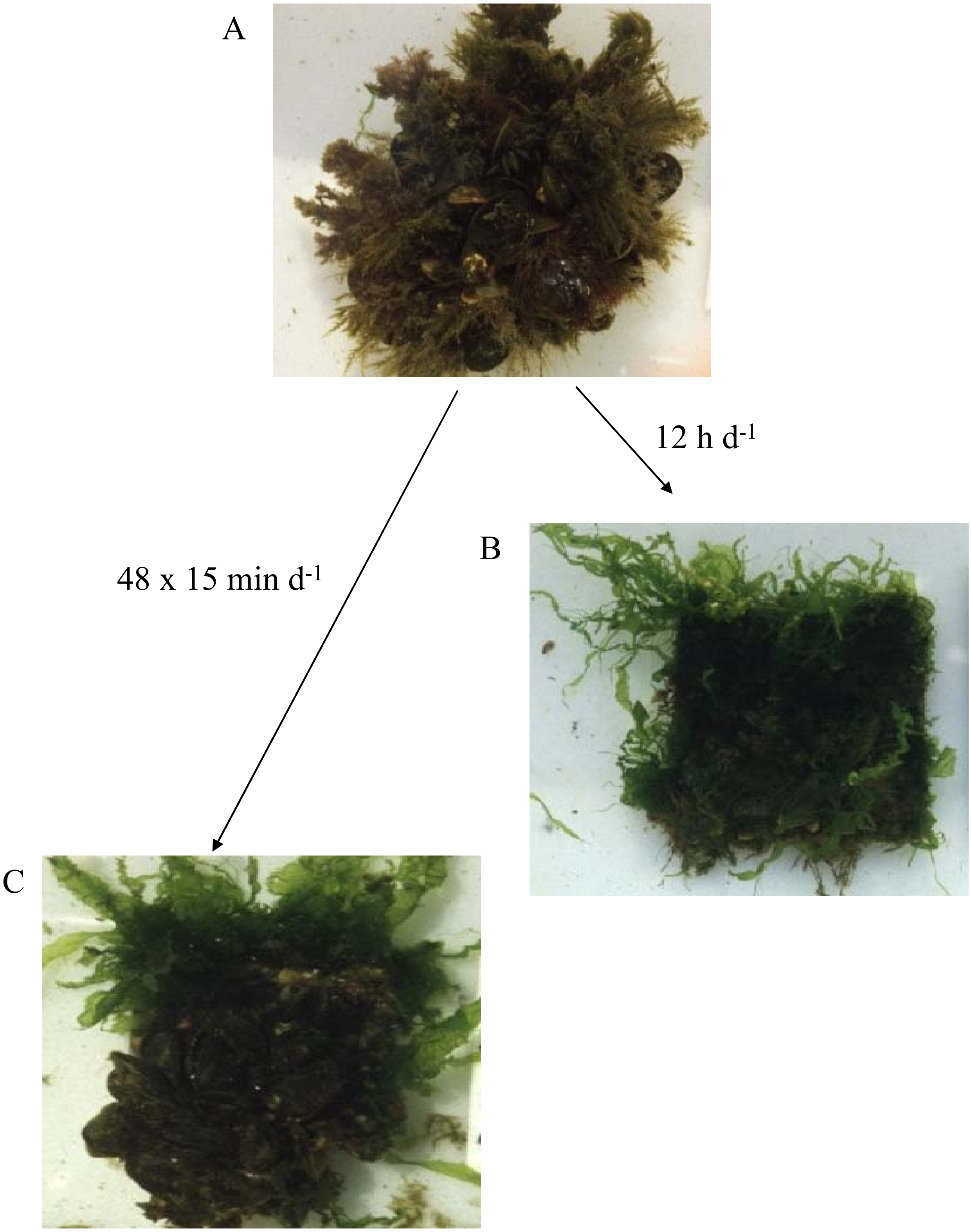


Fig. 24. Disturbance-induced community change. Twelve mo old communities after 8 wk of experimental duration. (A) Undisturbed control panel. (B) Intensity modulated community. (C) Frequency modulated community.

Similar to the studies on emersion frequencies, an unexpected picture was observed with regard to disturbance sensitivity as a function of community age: under similar disturbance regimes, the initially more diverse 1 yr old assemblages experienced a greater decline in diversity in the intermediate disturbance range than younger communities. This was due to the suppression of a number of emersion-sensitive species that had established during the long maturing period within the blue mussel matrix. Species like the hydrozoan *L. flexuosa* and the red alga *C. strictum*, that were suppressed by the applied emersion treatments, are no typical inhabitants of the intertidal and therefore presumably not well adapted to conditions of emersion (see above).

Consistent with the results obtained in the studies on frequency treatments the severest intensity levels induced a change in community composition towards algal dominated assemblages. This was true in all three experimental series. This observation raises the question whether the predictions of the IDH are only valid within a given community. Such a limitation, however, may increase the danger of a tautology, since unimodal relationships are more easily encountered when alternative communities are ignored. Diversity may not only be suppressed under severe disturbance regimes but may increase again under even harsher conditions when a severely disturbed community is replaced by a more resistant one. A community change at the extreme end of a disturbance gradient requires an extension of the model, which is suggested in Fig. 23. Diversity enhancing community change has not yet been considered in the IDH-related literature.

5.4 Frequency vs intensity modulation

For both disturbance qualities, at any given treatment levels, daily cumulated emersion time was identical. Disturbance frequencies and intensities differed in their effects in 1999 and in the summer of 2000 but not in the fall of 2000. In 1999 intensity treatments generated a conspicuous unimodal curve. Simultaneously, frequency treatments elevated all diversity parameters above the level of the controls but did not decrease them again towards the extreme end of the disturbance gradient. In the first study of 2000, both disturbance components generated a U-shaped response curve that was more flattened in the case of the frequency modulated communities. This indicates that repeated emergence is not as detrimental in its effects as single long emergence of the same total daily duration. Long-term continuous emergence is more likely to cause irreversible tissue damages from water loss, UV radiation, overheating during periods of sunshine, osmotic stress during rainfall, or the development of anoxic conditions. Emersion intensities and emersion frequencies differed not in their effects in the study on 3 mo old communities in the fall of 2000. Presumably, this was again due to climatic differences between study years. In the fall of 1999 and the summer of 2000, higher air temperatures and higher insolation probably disproportionately amplified the effects of emersion intensities. Such an asymmetrical amplification was absent in the colder fall of 2000.

5.5 Summary and outlook

The results of this study emphasize the importance of repeated experiments in the *in situ* investigation of ecological models. With regard to the IDH, it emerged that fluctuations in environmental factors must be considered in the conception of the experimental design. In this case different climatic conditions in two subsequent study years very likely shifted the range of maximum diversity along the applied disturbance gradient. This led to contrasting observations that allow contradictory conclusions concerning the validity of the concept. This observation is not only relevant for future *in situ* studies on the IDH but also for the management of diversity conservation projects that base on the assumptions of the concept. A general explanation, which allocates the observations of the two study years to different sections of the extended version of the unimodal pattern, is suggested in Fig. 23.

Furthermore, it was pointed out that the predicted unimodal pattern can only be detected by an experimental approach when two crucial premises of the IDH are fulfilled: (1) the dominant competitor must be affected by the disturbances applied, (2) competitive exclusion must take place. The second point was already stressed in other studies. Environmental fluctuations that modify the effects of disturbance regimes and the necessity for the fulfillment of the mentioned premises restrict the testability of the concept.

A yet unreported, diversity-enhancing change in community composition was observed at the extreme end of the applied gradient of both disturbance components, and an extended version of the unimodal model that takes this change into account is proposed (Fig.23). Future research work on the IDH is necessary to investigate whether this disturbance-induced community change, which goes along with an increase in diversity, is also observable in other systems. The concept of disturbance-induced alternative communities is a valuable extension of the classical hypothesis and a useful tool of forecasts in management programs and conservation projects.

6. UV radiation: physical characteristics and ozone depletion

Solar radiation with wavelength shorter than 400 nm, the ultraviolet range, is subdivided into three wavelength bands: UVA (315 - 400 nm), UVB (280 - 315 nm), and UVC (200 - 280 nm, Tevini & Häder 1985). UVB radiation contributes about 1.5 % to total solar irradiance, but its proportion is reduced to 0.5 % at ground level due to attenuation losses during atmosphere passage. Nevertheless, this quantity is still a relevant hazard for terrestrial and shallow-water organisms.

The amount of UVB flux to the earth's surface is closely related to the ozone content of the lower stratosphere. The gas forms a scattered layer at altitudes from 12 to 45 km. Ozone reduces solar radiation of wavelengths < 330 nm effectively. This spectral range is absorbed to the largest extent, and below a threshold of 290 nm no radiation passes the ozone layer (Madronich et al. 1995, Sandmann 2001). Thus, incoming UVB is reduced and UVC is totally eliminated while UVA as well as the Photosynthetic Available Radiation (PAR: 400 - 700 nm) are not or negligibly affected by the stratosphere gaseous layer. The amount of UVBR at ground-level further depends on the elevation of the sun and the abundance of atmospheric matter that absorbs or scatters incoming radiation (Frederick et al. 1989). Scattering and absorbance is influenced by the atmospheric composition, including gases and particles, and the length of the passage of a photon through the atmosphere. The latter is a function of the zenith angle. Clouds play an important role in determining ground-level UVBR regimes (Lubin & Jensen 1995). Elastic scattering, i.e. scattering without a change in wavelength, of incoming irradiance by air molecules, water drops, or atmospheric particles is, in contrast to absorption, the deflection of ligthwaves into other directions and not the conversion into other forms of energy. Atmospheric scattering is inversely proportional to the 4th power of the wavelength λ and is therefore more effective at shorter wavelengths. For example, visible irradiance at 380 nm is scattered 18-fold stronger than long-waved irradiance at 780 nm. This latter instance is causing the sky to be blue. UV radiation is shorter in wave-lengths than blue light, and it is therefore more scattered. Because of this, shading from direct sunlight provides only a limited protection from UVR exposure due to the high level of diffuse radiation.

Penetration of light through water is firstly restricted by reflection at the water surface while light regimes in the water column are determined by absorption and scattering. In the aquatic milieu, light attenuation is dramatically enhanced due to the high density of the medium. Light is absorbed or scattered significantly by dissolved organic matter (DOM), suspended particles, and planktonic organisms. The quantity of the absorbed light, expressed in terms of the vertical attenuation coefficient (K_d), depends upon light wavelength.

Hence, UVR in water is attenuated faster than visible light especially when DOC concentrations are high:

$$K_d = \frac{-1}{I_d(z,\lambda)}\left[\frac{dI_d(z,\lambda)}{dz}\right]$$

where (I_d) = downwelling irradiance, (λ) = wavelength and (z) = water depth

Eutrophic coastal waters, like the Western Baltic, contain high levels of seston and water humus, and the 10 % depth of UVB is usually less than 1 m (Kirk 1994). In oligotrophic tropical ocean waters UVB is still detectable in a depth of several tens of meters: Smith et al. (1992) found UVB in the Southern Ocean to be penetrating to a depth of 60 - 70 m during the springtime ozone depletion.

UVA is not significantly affected by ozone and it is only poorly absorbed in the atmosphere. Attenuation of UVA in water is lower than that of UVB; for this reason the in-water UVA/UVB ratio depends mainly on water depth and thickness of the ozone layer. This ratio is biologically relevant because of the ambivalent effects of UVA: UVA supports the repair of UVB-induced DNA damage but it restricts carbon fixation in algae. This is presumably due to its potential to generate reactive species like peroxides and hydroxyl radicals (Helbling et al. 1992, Vincent & Roy 1993, Karentz & Bosch 2001).

Anthropogenic-induced depletion of stratospheric ozone concentrations has altered global UV regimes. Ozone depletion goes mainly back to the emissions of chlorofluorocarbons (CFCs), which release ozone-destroying reactive chlorine atoms when they become photolysed in the stratosphere. Released chlorine destroys O_3 in the following reaction sequence:

$$\begin{aligned}
&Cl + O_3 \rightarrow ClO + O_2\\
&ClO + ClO \rightarrow Cl_2O_2\\
&Cl_2O_2 + h\nu \rightarrow Cl + ClOO\\
&ClOO + O \rightarrow ClO + O_2\\
&2 \times (Cl + O \rightarrow ClO + O_2)
\end{aligned}$$

this leads to a net destruction of $2\ O_3 \rightarrow 3\ O_2$ (Whitehead et al. 2000) . Ozone loss is greatest over the Polar regions, and here it is most pronounced over Antarctica. Over the South Pole a hole opens up each spring that shows 60 % and more of ozone depletion and has reached the size of Canada (Weiler & Penhale 1994). In 1997 an ozone loss of 45 % was reported from the Arctic (Whitehead et al. 2000). Significant increases in UVBR levels in temperate latitudes have been recorded already 10 yr ago (Kerr & McElroy 1993). A loss of 3 % per decade in total ozone during the summer month has been recorded in Central Europe since 1968 (Wallasch & Beilke 1999).

Very recent observations suggest that the ozone layer is recovering due to effective reductions in CFC emissions (Kerr 2002). However, this process will take decades and it is therefore mandatory to investigate the effects of increased UVBR on terrestrial and aquatic organisms, populations, communities, and ecosystems. While the impact of UVBR on the organismic level is well studied (see chapter 2 for a detailed introduction into UVR effects on marine organisms and their adaptations to biological harmful irradiance), little is known about the influence of enhanced radiation regimes on entire communities, intra- and interspecific interactions, and food webs. UVBR-induced community change has been repeatedly reported from Antarctic phytoplankton assemblages (Helbling et al. 1994, Karentz & Spero 1995, Davidson et al. 1996). Bothwell et al. (1993) described short- and long-term effects of natural UV radiation on lotic periphyton communities. Knowledge about UVBR-induced effects on the structure of marine benthic assemblages, which often show high proportions of macroinvertebrates, is scarce.

7. Material and Methods: UVBR exposure

7.1 Study site and fouling communities

See chapter 3.1 for a detailed description of the study site and fouling communities.

7.2 Settlement panels and maturing of communities

PVC-panels, 7 x 7 cm in size, served as settlement substrata for the fouling communities. Bare panels were fixed on the top side of wooden planks by Velcro® in a water depth of 20 - 30 cm in May 1999 (Fig. 25). After 12 mo of undisturbed community maturing, they were brought into the first experiment and were replaced by a further set of bare panels. The latter were exposed to colonization for another 3 mo and were used in the second experiment that was started in September 2000 (Fig. 25). Start values of all relevant response variables for t_0-reference were obtained from 8 randomly chosen panels each time an experiment was started.

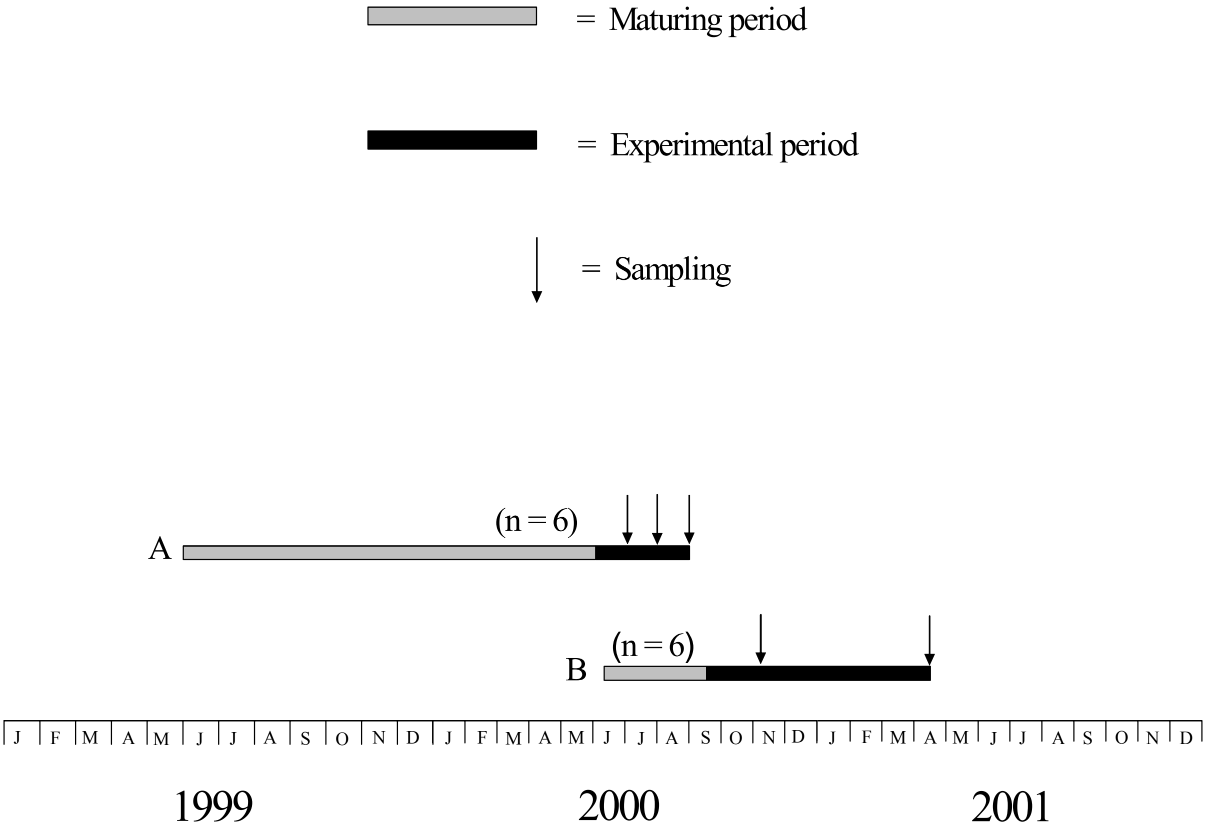


Fig. 25. Time schedule of the maturing periods and the UVBR exposure experiments. A = study on 12 mo old communities in the summer of 2000; maturing started in 1999. B = study on 3 mo old communities in the fall and winter of 2000/2001. N = number of replicates.

7.3 Experimental set-up

Waterproofed, UVBR-transparent Plexiglas pipes (GS 2648; Röhm, Germany; 1500 mm long, Ø 80 mm, 3 mm thick) that contained the UVB fluorescent tubes (UVB-313, Q-panel, USA) were suspended from the bottom side of wooden planks that fringed the alongside of the experimental rafts (Fig. 26 C). Planks were installed 15 cm above the water surface and were subdivided into four compartments at each raft side (Fig. 26 B). Within every compartment two pipes were placed in a semi-overlapping way in order to minimise the use of space. To restrict UVR emission to the respective settlement panels, tube insides were lined with opaque wrapping paper. A square aperture (10 cm x 10 cm), positioned directly above panels, allowed light passage but assured that in the perimeter of the panels UVBR was at ambient level.

To eliminate all UVCR and reduce UVBR longer than 293 nm, which was emitted by the fluorescent tubes, cellulose diacetate foil, cutting out wavelength shorter than 288 nm, served as a filter. Foils were positioned in the tube insides, covering the square aperture, and were exchanged monthly to avoid aging effects that could have confounded the UVBR treatments. After 1 mo of exposure to 8 h of enhanced irradiance, a 5 % loss in foils transparency was detected (Molis, personal communication).

To allow the exchange of cellulose diacetate foils and defective fluorescent tubes, pipes were closed at both ends with removable, O-ring sealed PVC-plugs. Power supply was realized by sea water resistant cables that were led through screwed cable glands within the PVC-plugs.

Settlement panels were fixed on wooden bars by Velcro® in a horizontal position (Fig. 26 C). Bars were suspended from the planks at their both ends and submerged by weights in a water depth of 10 cm, measured from the bar top side. To provide equal shading effects, control panels, that experienced ambient light regimes only, were positioned on the same bars but were outside the light field of any UV lamp (Fig. 3). The plank bottom sides were coated with black paint to avoid the reflection and scattering of light.

Each lamp was controlled individually by an electric timer. The correct function of tubes and timers was checked by working hour meters that registered the length of time the tubes were active. Working hour meters were read by the investigators 5 x a week during summer and autumn, and 3 x a week during winter. All electric devices were stored in waterproofed Zarges®-boxes that were mounted onto the rafts (Fig. 26 B). Plexiglas pipes were cleaned every second day, by using a soft cloth, in order to remove dried salt and dirt particles.

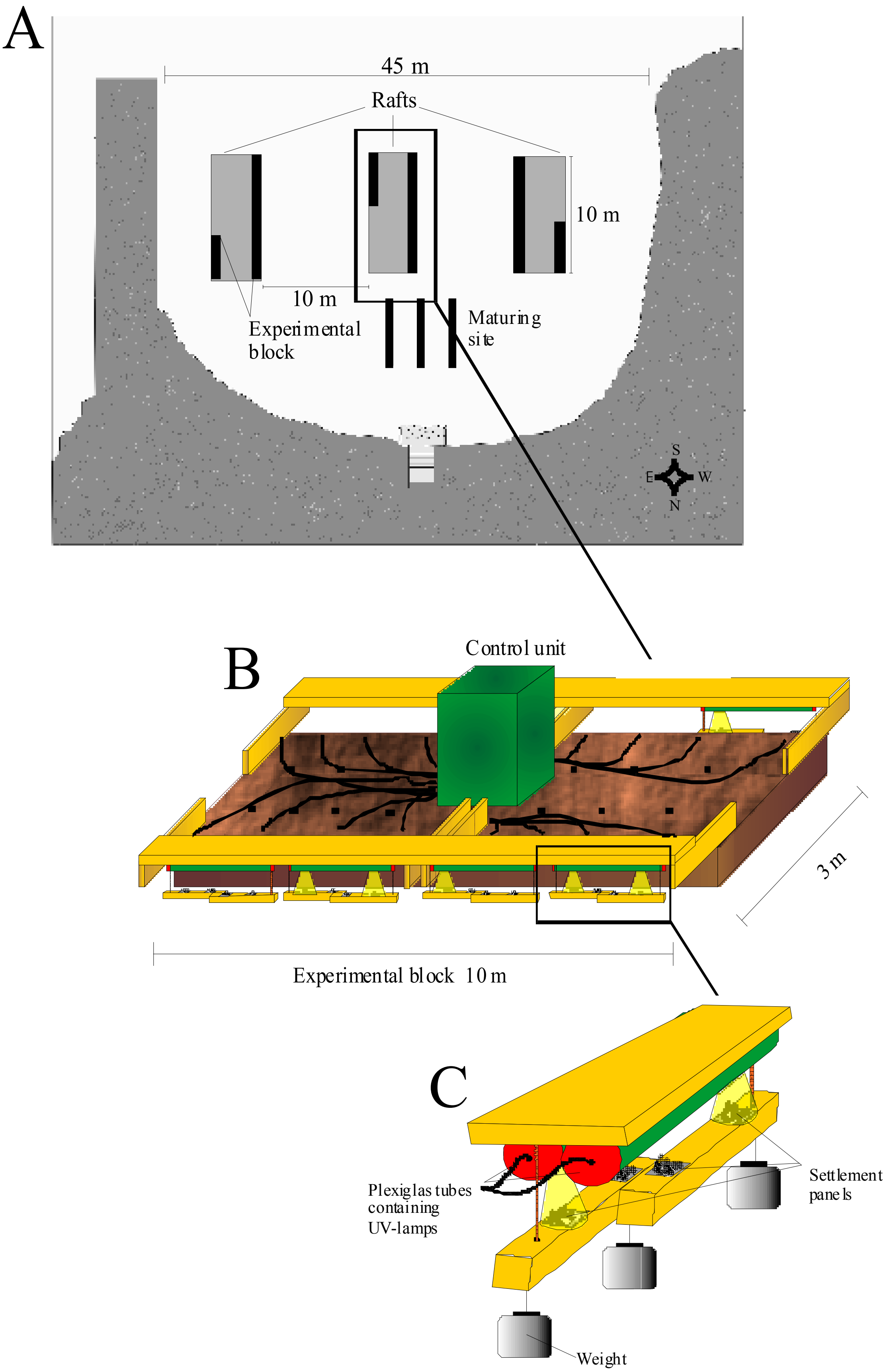


Fig. 26. Experimental set-up of the UV exposure experiments. (A) Distribution of experimental blocks. (B) Raft with one experimental block. (C) Experimental units.

Flux of radiation per unit area of all fluorescent tubes was initially measured by using a Bentham LTD DTM 300 spectralradiometer. Variations between individual tubes were generally marginal (< 5 %). The loss in tubes efficiency due to lamp aging was measured after 5 mo of experimental duration and was < 3 % for all wavelengths between 290 – 400 nm (Molis, personal communication).

Procedural controls were conducted during both experiments to test for any confounding effect of the Plexiglas pipes (e.g. by scattering of ambient light). Therefore, one empty Plexiglas pipe was installed over a settlement panel in each experimental block (total n = 3).

7.4 Experimental design

Treatments were distributed among three experimental blocks, each block was located on one raft, and each treatment was replicated twice within each block (total n = 6). The rafts were equidistantly positioned in the bay with 10 m between them, and this resulted, dependent on the blocks position on the rafts, in a distance of 10 - 15 m between blocks. Blocks are shown in Fig. 26 A. Treatments were distributed randomly within blocks and the minimal distance between settlement panels fixed on the same bar was 40 cm. *In situ* light measurements using a LiCor UW-1800 spectroradiometer proofed that this was sufficient to avoid interference of UVBR treatments (Molis, personal communication).

Intensity treatments were 0.5, 1, 2, 4, and 8 h of continuous exposure to enhanced UVBR per day. Exposure periods were centred around 12 a.m. (Fig. 27).

7.5 Ambient light regimes and enhanced UVBR

Ambient UVBR and cellulose-diacetate-filtered, enhanced UVBR (UV-lamp inactive and active) were measured in various water depths using the LiCor spectroradiometer. This was done with a resolution of 2 nm encompassing the spectral range from 300 - 400 nm on 30.06.99 at local noon (Fig. 28). Lamp output (300 - 320 nm) in 10 cm water depth was measured during nighttime (absence of ambient irradiance) of the very same day and was 0.29 W m^{-2}.

The 10 % depth for UVBR laid between 30 and 40 cm on this day. This is a common value for eutrophic coastal waters (Kirk 1994). The unweighted UVBR enhancement level at 10 cm water depth was ≈ 1.5 x the ambient level. When weighted with a Biological Weighting Function based on generalized DNA damage (Setlow 1974) the enhancement level ≈ 4 x (388 %) the ambient biologically effective midsummer, midday UVB irradiance at Kiel. The stratospheric ozone layer on this day over Central Europe was between 300 and 325 Dobson Units (Total Ozone Mapping Spectrometer (TOMS)-data).

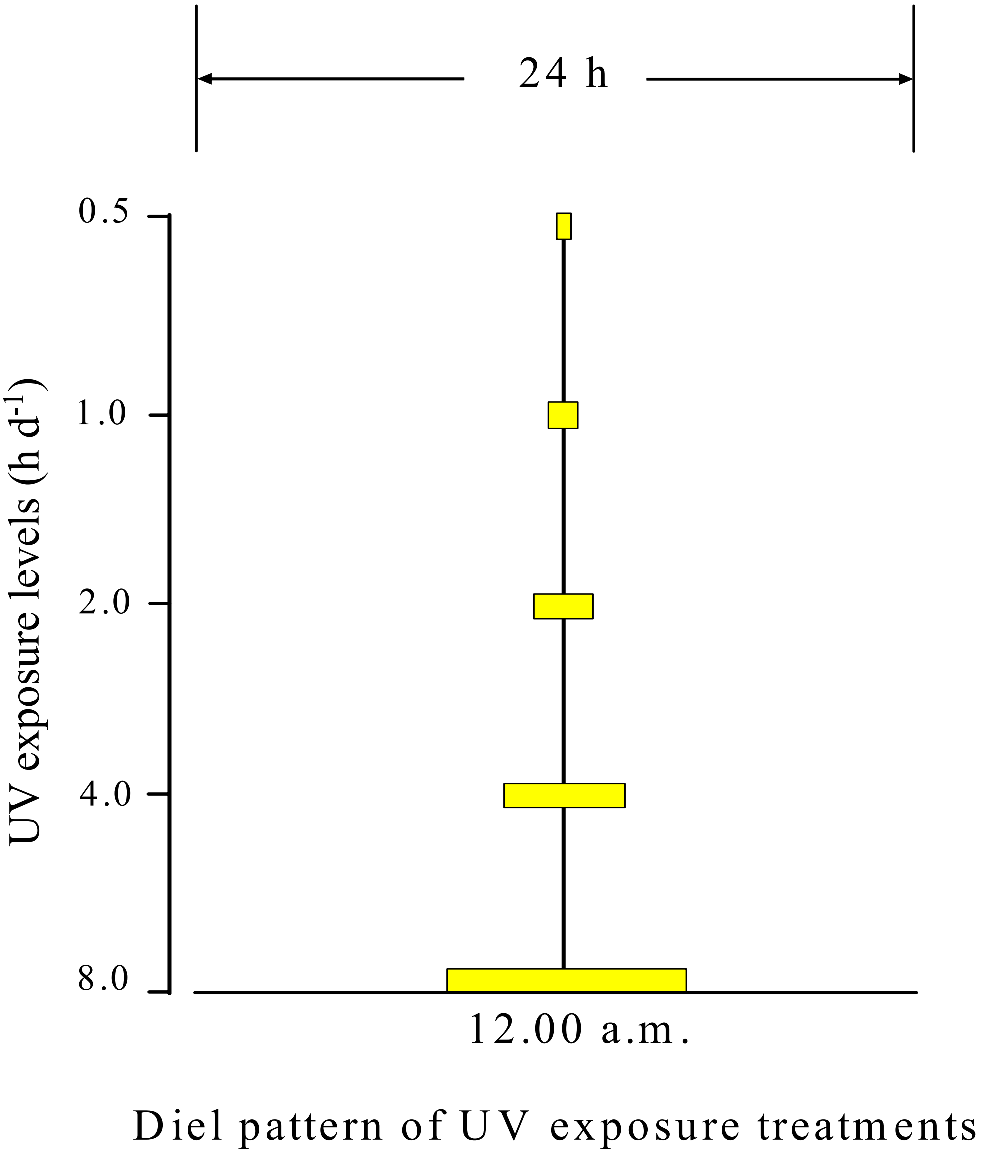


Fig. 27. Levels of exposure to enhanced UVBR applied in the studies on 3 and 12 mo old communities. Daily lengths are shown on the left hand axis. Application times were centred around 12 a.m.

However, UVBR measurements were conducted on a cloudy day and UVBR enhancement rates should have been noticeably lower on sunnier days.

Measurements of ambient UVBR (280 - 315 nm) were conducted at 63 days from the beginning of June 2000 until the mid of October 2000. No measurements took place from the 17.07. until the 08.09. due to technical problems. Ambient UVBR levels were recorded ± 15 min around local noon, every 6th, minute using the pocket radiometer system RM-12 (Dr. Gröbel UV Elektronik GmbH Ettlingen). The UVBR-sensor was installed in a water depth of 10 cm at the front side of one raft. It was cleaned every second day in order to remove dirt particles and biofilms. Recorded data were saved to Excel® data files using a notebook stored in a Zarges®-box. Data were averaged over the 0.5 h daily period and the ambient/enhanced UVBR-ratio (unweighted) was calculated for all days. The mean ratio over all days was 2.02 (SD ± 0.86). Raw data are provided on CD-ROM.

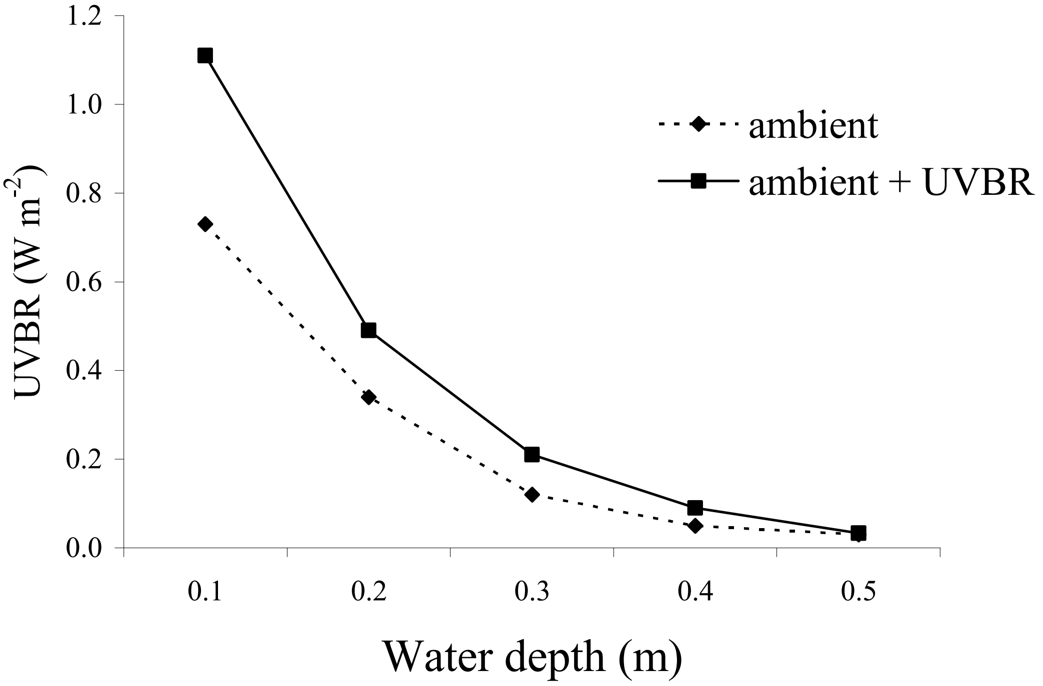


Fig. 28: Ambient and enhanced UVBR (integrated from 300 - 320 nm) over a depth gradient. Measured on 30.06.99 at local noon.

7.6 Larval supply and system productivity

Larval supply was monitored on recruitment panels exposed every month and retrieved 4 wk later.

7.7 Sampling procedure

Twelve mo old communities were sampled monthly during the summer of 2000. The experiment on 3 mo old communities started in September and was sampled once after 7 wk and again after 7 mo of experimental duration in the spring of 2001. For samplings, panels were retrieved from the carrier plates, put into water filled containers, examined in a field laboratory, and brought back to their respective positions.

Percent cover of all colonizers was estimated on three randomly chosen fields of vision under a Wild binocular (12x magnification) within 15 min. To avoid edge effects, the outer 1 cm of the panels was disregarded. Total percent cover exceeded 100 % in the case of multi-strata growth.

7.8 Statistical analyses

See chapter 3.9 for a detailed description of the statistical methods used.

8. Results: UVBR exposure

8.1 Vertical vs horizontal communities

Fouling communities for the emersion experiments (see chapter 3) established and matured in a vertical position while the assemblages used for the UVBR exposure experiments were horizontally orientated during their maturing period. One yr old communities of both spatial orientations differed significantly in their composition (ANOSIM: R = 0.99, p < 0.01; Fig 29). Responsible for these differences were blue mussels (45 *, all numerical values marked with asterisks indicate contributions of the mentioned species to observed dissimilarities in percent) which dominated the vertical communities but were nearly absent on the horizontally orientated ones. Simultaneously, the red alga *Ceramium strictum* (13 *) was dominant on the latter.

Start communities of the vertical and horizontal 3 mo old assemblages differed significantly (ANOSIM: R = 0.49, p < 0.01; Fig. 29, raw data of all analyses presented in this chapter are provided on CD-ROM at the end of this thesis) in their compositions as well. This was again due to blue mussels (31 *) that were more abundant in the vertically matured communities; *C. strictum* (16 *) that was, in contrast, 4 x more abundant on the horizontal panels, and an unidentified green alga (15 *) of the *Enteromorpha*-group that was also more common in the horizontally matured communities. The same was true for the spionid polychaete *Polydora ciliata* (12 *) while *Balanus improvisus* (12 *) was more abundant on vertical panels.

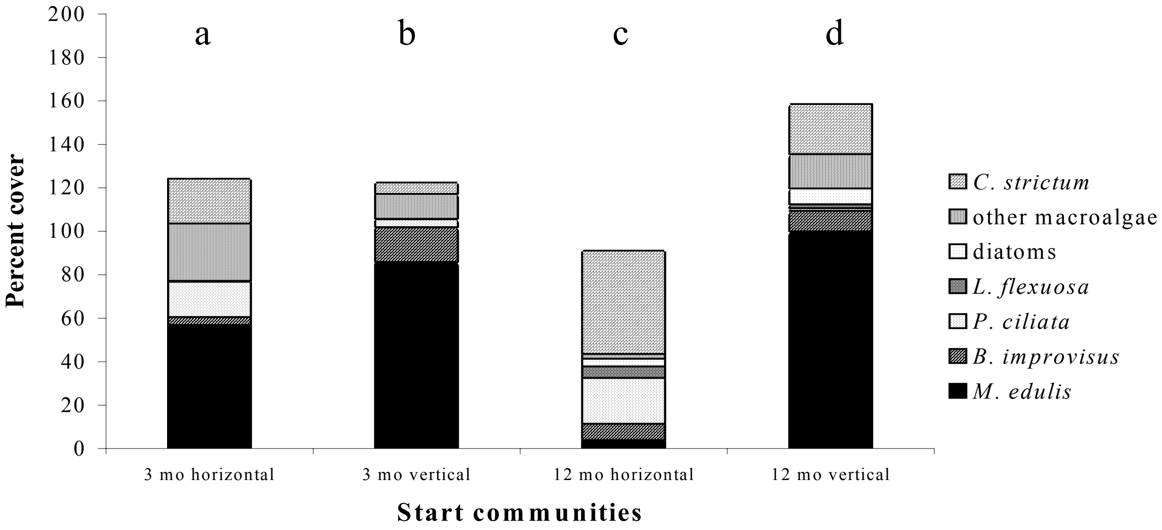


Fig. 29. Compositions of the start communities of the emersion (vertically orientated) and UVBR exposure (horizontally orientated) experiments. Different letters indicate significant differences in community composition (ANOSIM: p < 0.01).

8.2 Procedural controls

No significant differences between controls and procedural controls, concerning community composition and diversity parameters, were found at any sampling date. Thus, the presence of the Plexiglas pipes had no detectable effects.

8.3 Three month old communities

After 3 mo of undisturbed maturing, *Mytilus edulis* dominated all communities by covering 57 % of the panel surfaces on average. Unexpectedly, blue mussel individuals were conspicuously bigger than those that were present in the start assemblages of the 12 mo old communities. *Polydora ciliata*, benthic diatoms, an unidentified green alga of the *Enteromorpha*-group, and *C. strictum* occurred in almost identical proportions: each species occupied 20 % of the substratum on average.

No significant relationships between diversity parameters and the disturbance gradient were found after 7 wk of exposure to enhanced UVBR. All communities were dissimilar to the start assemblages at this sampling date (ANOSIM: $p < 0.05$, Appendix Table 13): *Mytilus* contributed mostly to the observed dissimilarities (29 *). The mussel was abundant at the beginning of the study but decreased heavily in cover on all panels, except on those of the 2 h level, during its course. Benthic diatoms (13 *) and the spionid *P. ciliata* (11 *) were of further importance for the observed dissimilarities: the former were nearly absent in the start communities, but present on all panels after 7 wk while the latter was twice as abundant, on most of the panels, after 7 wk than at the beginning of the study. Concerning *Polydora* this was a seasonal effect, since the polychaete spawns in late summer and fall (personal observation). The green alga *Chaetomorpha tortuosa* (8 *) was highly abundant in the communities of the two severest treatment levels but was absent in the start assemblages.

Almost all treated communities were similar to the control assemblages after 7 wk (Appendix Table 13) while, a non-significant, change in community composition towards the extreme end of the gradient was observable. Red algae decreased and green algae increased in cover with increasing duration of exposure to enhanced UVBR. These correlations were significant for *C. strictum*, *Enteromorpha sp*., and *C. tortuosa* (Table 3, Fig. 30). On panels that experienced the longest exposure to enhanced UVBR, *C. tortuosa* replaced the red algae *C. strictum* and *Polysiphonia elongata* almost completely.

Proportions of *P. ciliata* fluctuated indistinctively across the exposure gradient but were lowest on the panels of the severest treatment level.

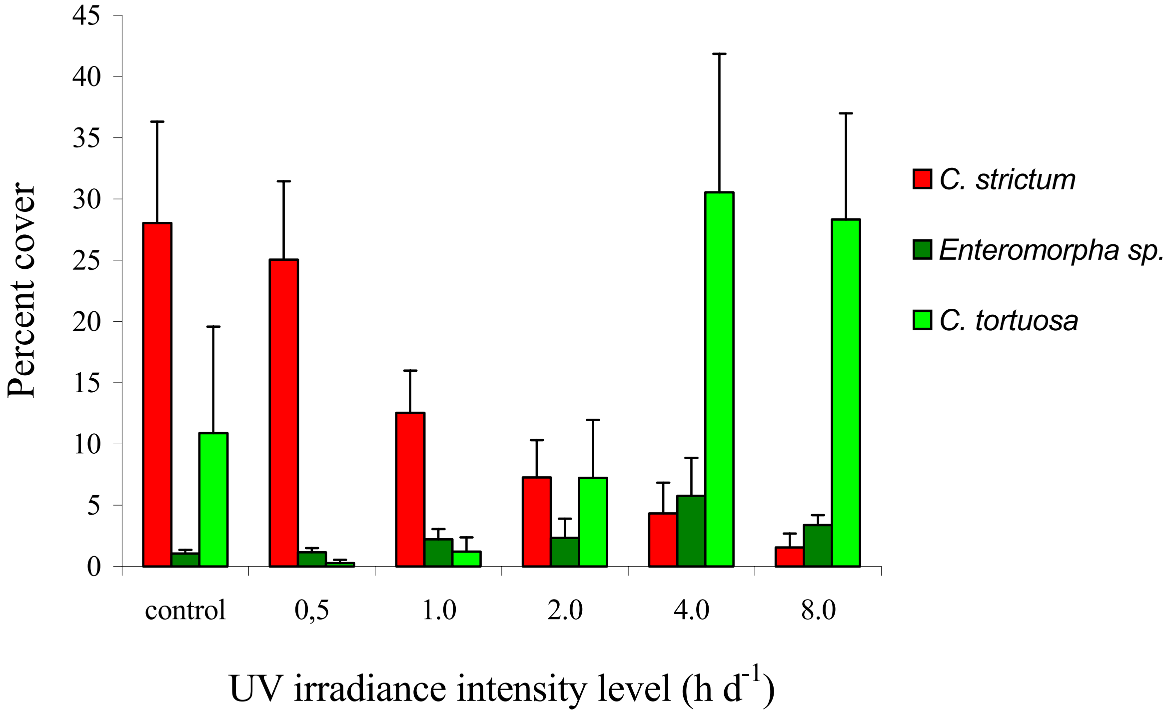


Fig. 30. Proportions of red and green algae across the UV exposure gradient after 7 wk of experimental duration. Bars are mean values (+ SE).

Table 3: Three mo old communities: the red alga *C. strictum* decreased in cover while two green algae were monotonuosly increasing across the UV exposure gradient after 7 wk.

	lrR^2	p
C. strictum	0.43	< 0.001
Enteromorpha sp.	0.11	< 0.050
C. tortuosa	0.20	< 0.010

This was also true for the barnacle *B. improvisus*: proportions of the barnacle were significantly smaller on the panels of the severest UVBR treatment than on those of the 0.5 h level (Kruskal-Wallis ANOVA multiple comparisons: $U_{observed} = 36$, $U_{critical} = 35.79$, $p = 0.05$, all are corrected for ties; Fig. 31).

After 7 mo of continuous enhanced UVBR treatment diversity-disturbance relationships were non-significant. All communities were dominated by benthic diatoms. No dissimilarities in community composition emerged between controls and treated assemblages. Communities of the severest UVBR treatment were dissimilar to those of the 2 h level (Appendix Table 14), and assemblages of the 1 and 4 h level were dissimilar to each other. (Appendix Table 14, Fig. 32). In the first case, dissimilarities were due to diverging proportions of diatoms (32 *), blue mussels (32 *), which were nearly absent from the 8 h panels, and *Enteromorpha sp.* (16 *), which was more abundant under conditions of the longest UVBR exposure. Dissimilarities between assemblages of the 1 and 4 h level were due to different proportions of diatoms (38 *), blue mussels (17 *), and *Laminaria sp.* (14 *).

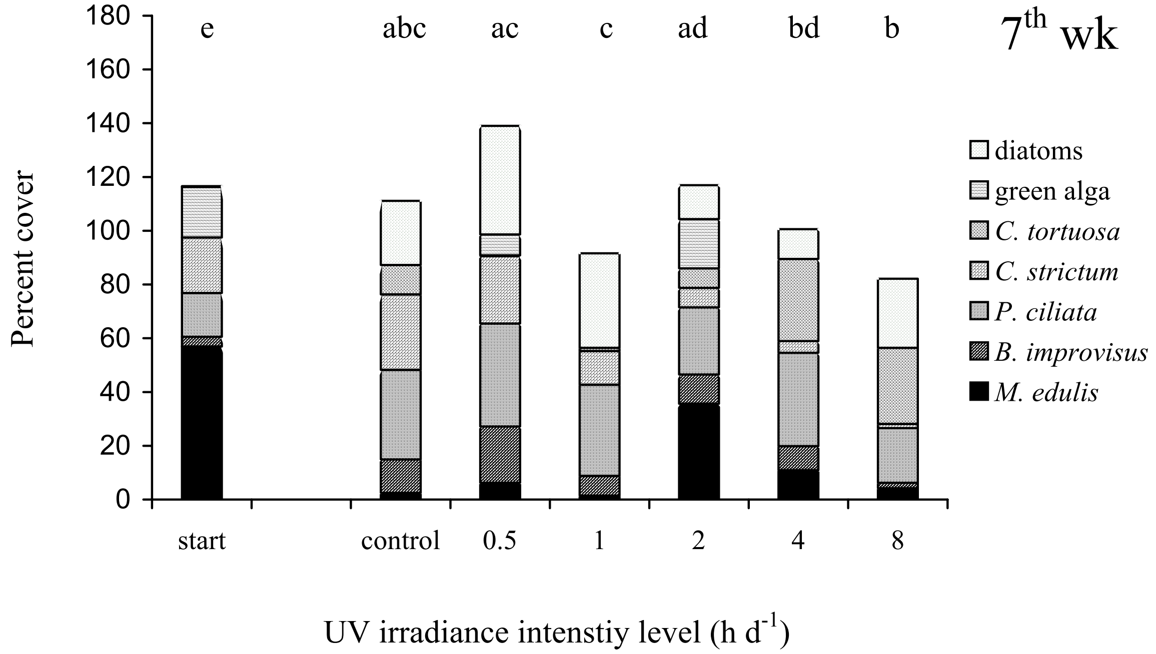


Fig. 31. Mean percent cover of the predominant settlers (presented species accounted for 86 % of total cover on average) in the 3 mo old communities after 7 wk of experimental duration across the UV exposure gradient. Their proportions in the 3 mo old start communities are shown in the very left column. Different letters indicate significant differences in community composition (ANOSIM: $p < 0.05$).

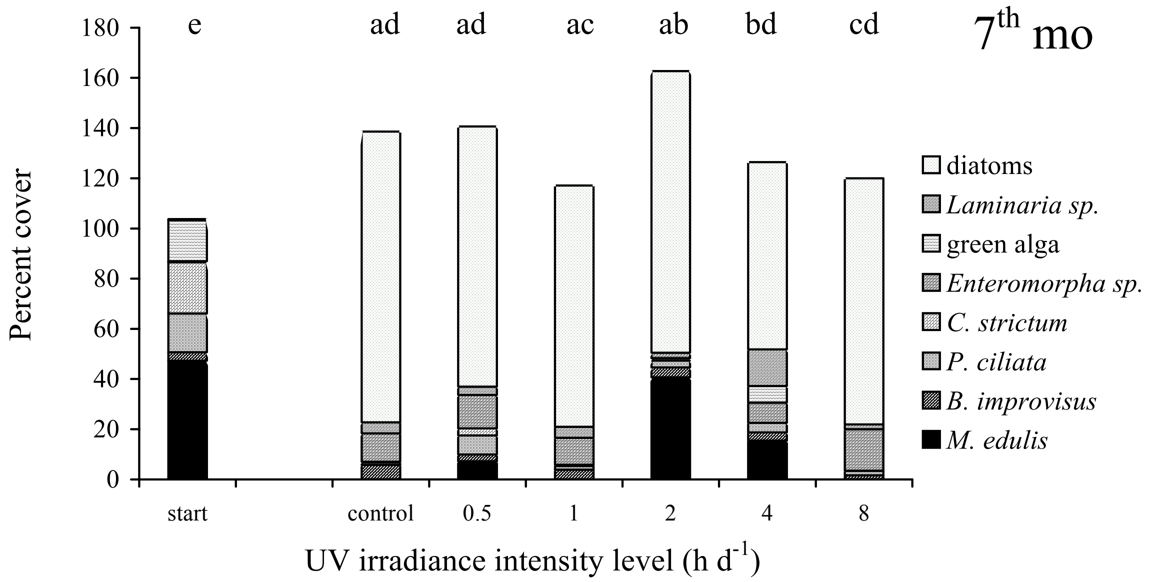


Fig. 32. Mean percent cover of the predominant settlers (presented species accounted for 96 % of total cover on average) in the 3 mo old communities after 7 mo of experimental duration across the UV exposure gradient. Their proportions in the 3 mo old start communities are shown in the very left column. Different letters indicate significant differences in community composition (ANOSIM: $p < 0.05$).

8.4 Twelve month old communities

At the beginning of the experiment, all communities were dominated by the red alga *C. strictum*, covering 47.5 % of the panel surfaces on average. The polychaete *P. ciliata* contributed 21 % to total surface cover while *B. improvisus* (7.5 %) and *L. flexuosa* (5 %) were of minor importance. The blue mussel *M. edulis*, which is the dominant space competitor in this hardbottom ecosystem (Dürr & Wahl in review, see chapter 4.1), was nearly absent (4 %).

After 4 wk of exposure to enhanced UVBR, all three diversity parameters declined monotonously across the disturbance gradient (species richness: $lrR^2 = 0.11$, $p < 0.05$; Shannon index: $lrR^2 = 0.18$, $p < 0.01$; evenness: $lrR^2 = 0.12$, $p < 0.05$; Fig. 33).

All communities changed incisively in their composition during the first month (Appendix Table 15, Fig 34). This was due to changes in the proportions of *C. strictum* (24 *) that decreased in cover proportions on all panels. The spionid *P. ciliata* (17 *) was nearly absent after one month while *Laomedea* (10 *) accrued in its abundance in all assemblages except in those of the severest treatment level. The latter fact indicates the sensitivity of the hydrozoan to conditions of prolonged exposure to enhanced UVBR.

Mytilus cover (8 *) increased during the experiment due to individual growth. The green alga *Enteromorpha sp.* (10 *) increased in abundance with increasing UVBR level ($lrR^2 = 0.25$, $p < 0.01$), and its proportions were inversely correlated with those of the red alga *C. strictum* (srcR = -0.5, $p < 0.01$). Diatom cover (10 *) showed no distinct response towards the various UVBR treatment levels (Fig. 35).

Control communities were dissimilar to the assemblages of the 0.5, 2 and 8 h treatment level (Appendix: Table 15, Fig. 35). This was due to higher proportions of *C. strictum* (33 *) in the treated communities, benthic diatoms (15 *) that were nearly absent on the panels of the 0.5 and 8 h levels, *L. flexuosa* (10 *) that were more abundant in the 0.5 and 2 h assemblages, but were scarce in the communities of the severest treatment level, and blue mussels (8 *) that were most abundant on the 0.5 and 8 h treatment panels.

Communities of the 0.5 and the 2 h level were distinct from those of the two severer treatment levels (Appendix: Table 15, Fig. 35). The former were clearly dominated by *C. strictum* (24 *) while this dominance was restricted by the green alga *Enteromorpha sp*. (26 *) on the latter. *Enteromorpha* cover increased significantly with increasing duration of exposure to enhanced UVBR ($lrR^2 = 0.25$, $p < 0.01$) and was inversely correlated with the abundance of *C. strictum* (srcR = -0.50, $p < 0.01$). No further significant effects of enhanced UVBR on the remaining colonizers were detected at this sampling date.

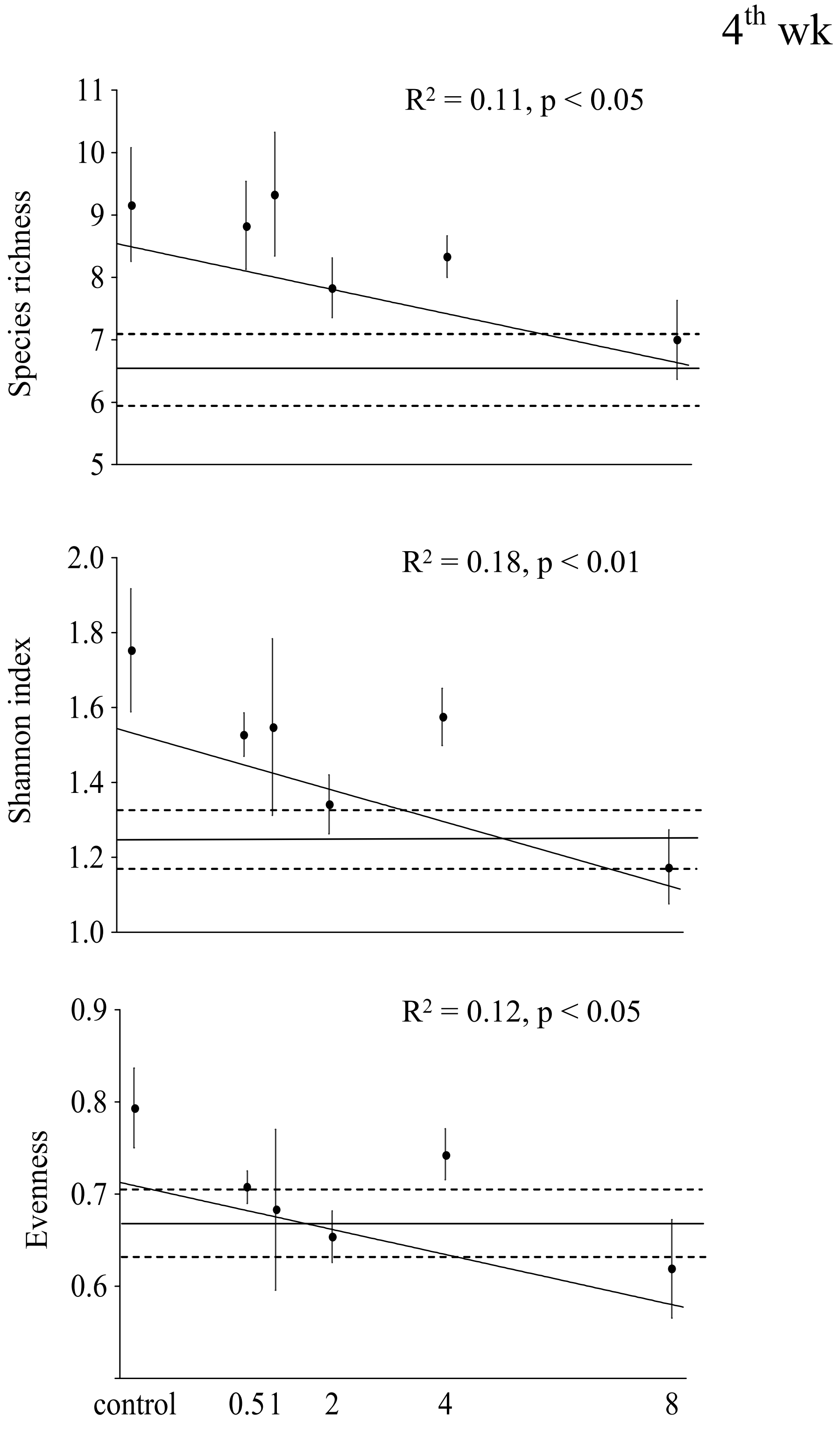


Fig. 33. Diversity parameters of 12 mo old communities after 4 wk of experimental duration. Dots are mean values (± SE) from replicate panels (n = 6). The solid horizontal line is the respective start parameter value and the dashed lines its SE. Regression lines are shown only for significant relationships ($p < 0.05$). Note ordinate scaling.

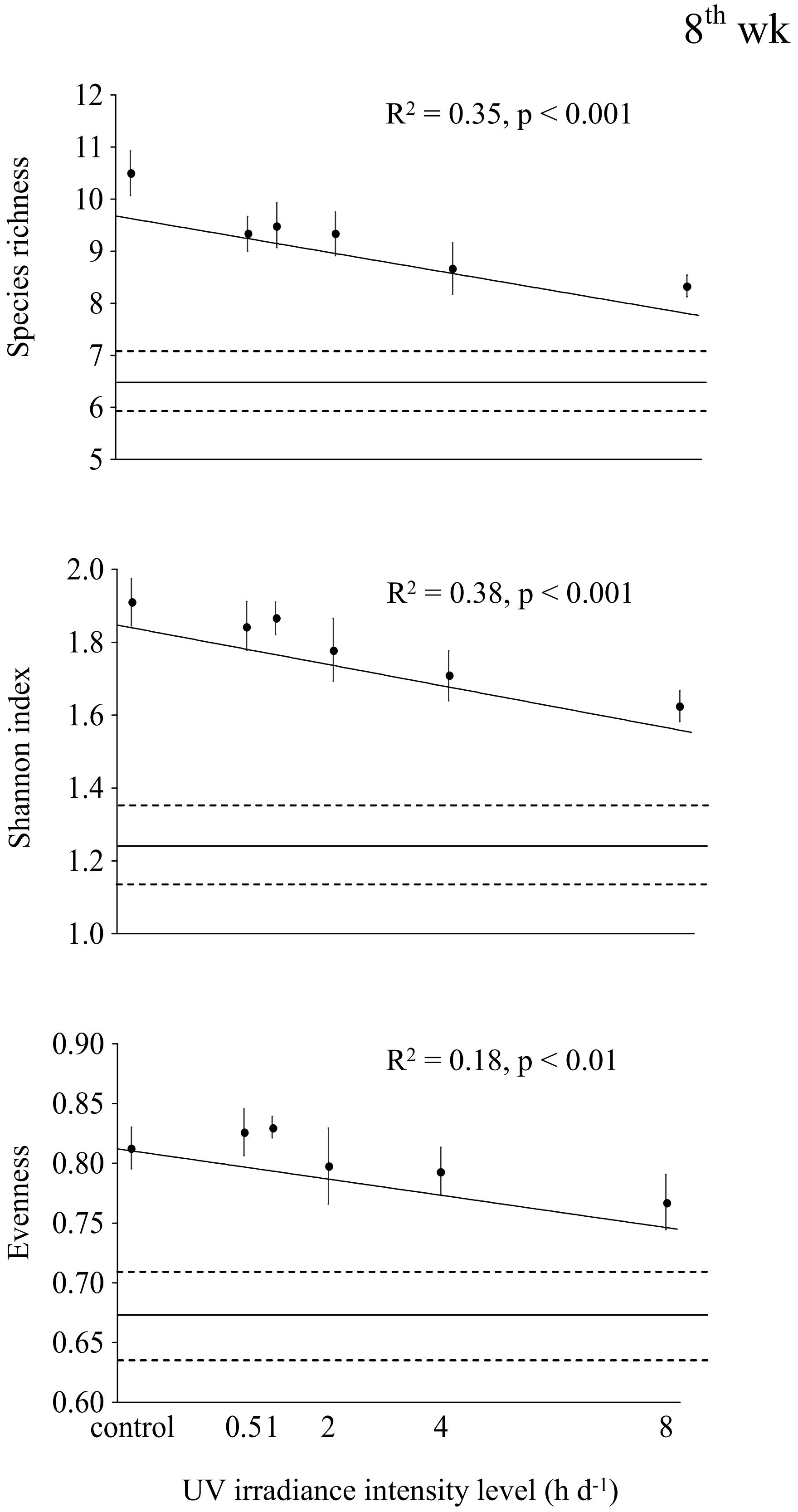


Fig. 34. Diversity parameters of 12 mo old communities after 8 wk of experimental duration. Dots are mean values (± SE) from replicate panels (n = 6). The solid horizontal line is the respective start parameter value and the dashed lines its SE. Regression lines are shown only for significant relationships ($p < 0.05$). Note ordinate scaling.

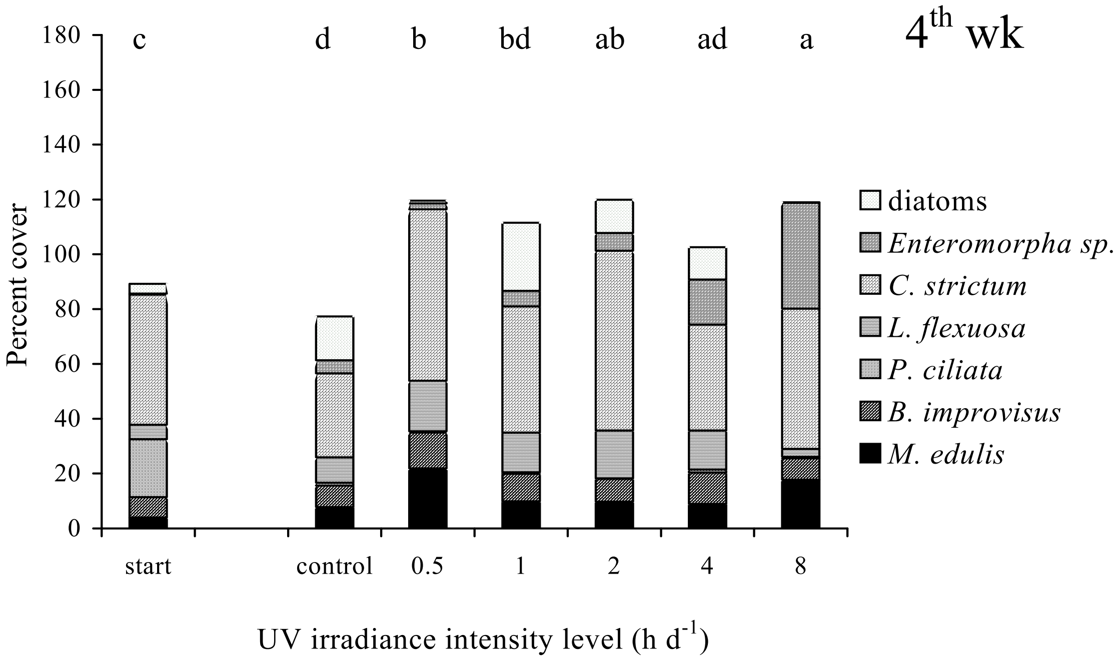


Fig. 35. Mean percent cover of the predominant settlers (presented species accounted for 85 % of total cover on average) in the 12 mo old communities after 4 wk of experimental duration across the UV exposure gradient. Their proportions in the 12 mo old start communities are shown in the very left column. Different letters indicate significant differences in community composition (ANOSIM: $p < 0.05$).

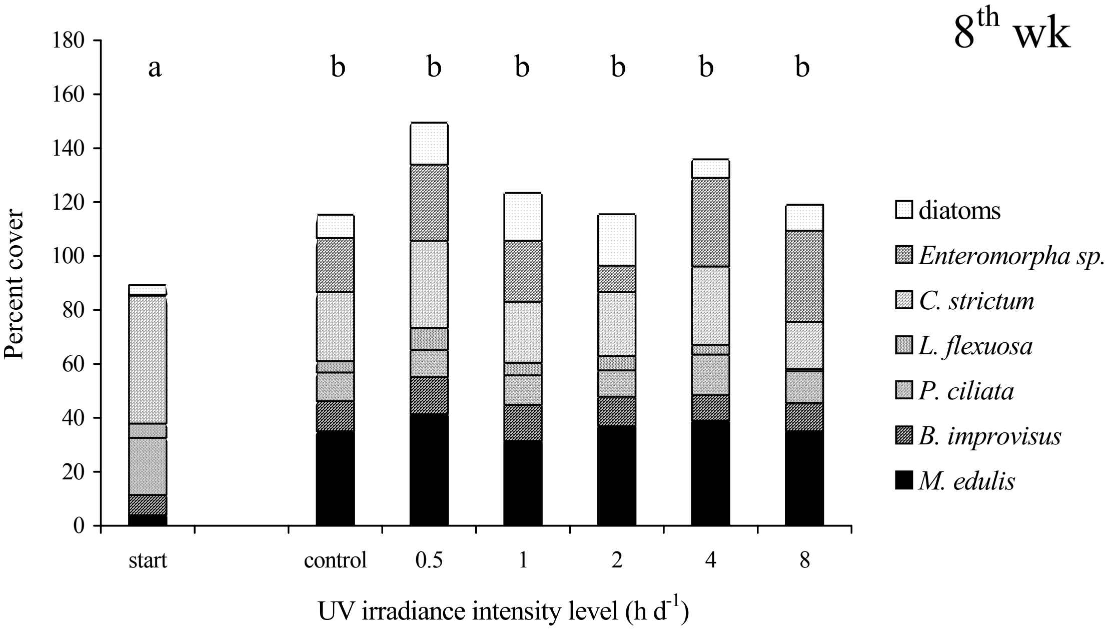


Fig. 36. Mean percent cover of the predominant settlers (presented species accounted for 72 % of total cover on average) in the 12 mo old communities after 8 wk of experimental duration across the UV exposure gradient. Their proportions in the 12 mo old start communities are shown in the very left column. Different letters indicate significant differences in community composition (ANOSIM: $p < 0.05$).

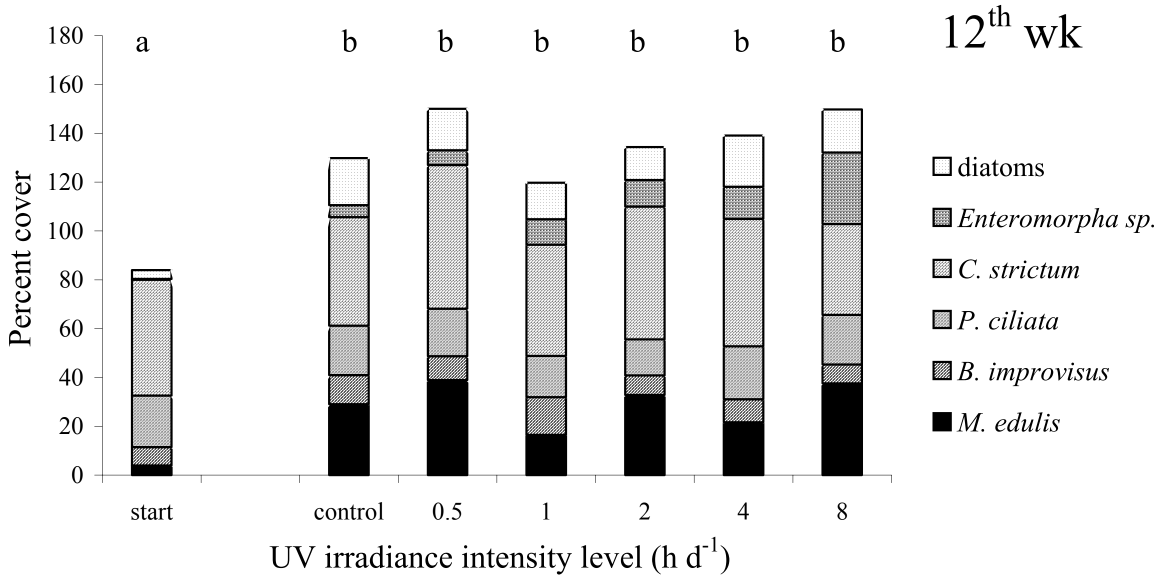


Fig. 37. Mean percent cover of the predominant settlers (presented species accounted for more than 80 % of total cover on average) in the 12 mo old communities after 12 wk of experimental duration across the UV exposure gradient. Their proportions in the 12 mo old start communities are shown in the very left column. Different letters indicate significant differences in community composition (ANOSIM: $p < 0.05$).

After 8 wk all diversity parameters still decreased monotonously across the disturbance gradient (species richness: $lrR^2 = 0.35$, $p < 0.001$; Shannon index: $lrR^2 = 0.38$, $p < 0.001$; evenness: $lrR^2 = 0.18$, $p < 0.01$; Fig. 34). All communities were similar in their compositions and remained similar until the end of the experiment (Appendix Table 16 + 17). Initial differences in the proportions of settlers among communities became indistinct during the second month of the study while *M. edulis*, *Enteromorpha sp.* and *C. strictum* were dominant on all panels. *Laomedea flexuosa* decreased towards the severe end of the UVBR exposure gradient ($lrR^2 = 0.21$, $p < 0.05$, controls excluded, Fig. 36). *Enteromorpha* was most abundant on panels of the severest treatment level while *C. strictum* cover decreased on all treatment panels when compared to the start assemblages. The spionid *P. ciliata* was generally scarce (Fig 36). No significant differences in the proportions of these species across the UVBR exposure gradient were detected.

After 12 wk no significant relationships between the UVBR exposure gradient and diversity parameters were present**.** C*eramium strictum* was still the dominant colonizer, and it was present on all panels in equal proportions. Under the conditions of the severest UVBR exposure level only, its percent cover was reduced while the green alga *Enteromorpha sp.* was more abundant on these than in the intermediate range. *Enteromorpha* abundances increased significantly with increasing duration of enhanced UVBR exposure ($lrR^2 = 0.22$, $p < 0.01$). Remaining settlers occurred in similar proportions on all panels as well, and they were obviously not impacted by the UVBR regimes (Fig. 37).

9. Discussion: UVBR exposure

In contrast to the majority of studies that approached the effects of enhanced UVR regimes on marine benthic communities, this study was conducted in the field under fully natural conditions. This approach was chosen to improve the relevance of the results with regard to interactions between UVBR and environmental factors such as nutrient conditions, shading, competition, and trophic interactions.

Since the late 1960s an average increase of UVBR (with a wavelength of 300 nm) of 13 % per decade was observed in Central Europe (Wallasch & Beilke 1999). Should these rate last more or less constant - a further increase could be compensated by first achievements in climate protection (e.g. Kerr 2002) - the enhanced UVBR level applied in this study matches the expected local, ambient UVBR level in the second half of this century.

The various UVBR intensity treatment levels affected the 1 yr old fouling communities with regard to their species composition. Here, the most conspicuous change in community composition across the radiation gradient concerned the proportions of red and green algae. At the beginning of the experimental phase, 1 yr old communities were dominated by the perennial red alga *Ceramium strictum* while green algae were scarce. During the experiment *Enteromorpha sp.* increased on all panels, and its abundances were positively correlated with the UVBR levels on two sampling dates (4th and 12th wk). The former observation presumably was a seasonal effect, since the annual green alga establishes in late spring and summer. The latter observation is consistent with the results of other experimental studies that worked either with optical filters, in order to modify UVR regimes, or with lamps that enhanced ambient UVR: Cabrera et al. (1997) reported highest densities of a unicellular green alga under highest UVR conditions during an experiment using UV-filters in a high-altitude Andean lake. Santas et al. (1998) found that *Enteromorpha prolifera* dominated young algal reef assemblages under artificially enhanced (20 % over ambient level) UVR regimes and was replaced by another green alga during the course of succession. After the high UVR treatment was ceased, a brown alga became the dominant form. Xiong (1996) applied enhanced UVR levels (2 W m^{-2} for 2 h) to 67 different species of unicellular freshwater algae (*Chlorophyta-Chromophyta*) and found *Chromophyta* species to be more UVR-sensitive than *Chlorophyta* species. Bischof et al. (1998) found photosynthesis rates in Antarctic *Chlorophytae* marginally inhibited while *Rhodophytae* showed more pronounced inhibition effects due to UVR. Figueroa & Gomez (2001) revealed by a transplantation experiment that intertidal macroalgae are better adapted to conditions of high UVBR than subtidal forms. These observations coincide with the results of the study at hand: *Enteromorpha sp.* is a typical inhabitant of intertidal areas while *C. strictum* normally occurs in the lower intertidal and subtidal (Kornmann & Sahling 1983). Both forms invaded the Baltic Sea from the North Sea and presumably reflect the adaptations of their progenitors with regard to conditions of prolonged emersion (see chapter 2 + 5).

Furthermore, a number of studies indicated that UVR tolerance in algae is a function of their vertical distribution: Arctic shallow water macroalgae are better adapted to UVR than deep water species (Hanelt et al. 1997, Aguilera et al. 1999, Karsten et al. 2001). Hoyer et al. (2001) demonstrated that the content of UVR screening MAAs is inversely correlated with depth distribution in Antarctic macroalgae. Generally, red algae are adapted to low light regimes and occur in greater depths than green algae. Corresponding to this, *C. strictum* was able to dominate the 1 yr old communities under ambient irradiance and short-term UVBR enhancement during the entire study while it was reduced under conditions of long-term UVBR exposure. However, this could have been due to two effects or a combination of both: (1) direct impairment through UVBR restricted biomass and photosynthesis rates in *C. strictum*, (2) *Enteromorpha sp.* benefited directly from the enhanced UVBR regimes and outcompeted *C. strictum*.

A further influencing factor could have been the presence or absence of swimming grazers like *Idotea sp*. Bothwell et al. (1994) reported increased primary productivity under conditions of enhanced UVRB because grazer population growth was suppressed by the treatment. It is also possible that swimming grazers were deterred by the artificial UVR source and avoided feeding on illuminated panels. Aarseth & Schram (1999) reported active avoidance of UVR by copepodids of the salmon louse *Lepeophtheirus salmonis* and by adults of *Calanus finmarchius*. Zagarese et al. (1997) showed that the freshwater copepod *Boeckella gracilipes* depends exclusively on avoidance in protecting its vital structures from UVR. No similar behaviour has been reported from isopods. In any case a reduction in grazer density should have favoured the more vulnerable but, in shallow water, competitively superior green alga. This general picture concerning the response of green and red algae towards exposure to enhanced levels of UVBR, obtained from the study on 12 mo old communities, was also confirmed by the results of the second study on younger assemblages. After 7 wk of enhanced UVR treatment, green alga abundances increased while *C. strictum* cover decreased significantly across the gradient.

Significant UVBR effects on the diversity of fouling communities were transient in the study on one 1 yr old communities while they were permanently absent in the study on the younger communities. During the first experiment, all three diversity parameters declined monotonously across the UVBR gradient at the first and second sampling date. This was mainly due to the dominance of *Enteromorpha sp.* and *C. strictum* on panels that experienced 8 h of enhanced UV radiation d^{-1}. Simultaneously, species like *Laomedea flexuosa* and *Membranipora membranacea* decreased in their abundances or vanished towards the extreme end of the gradient. These two species are presumably sensitive to UV radiation because of their transparent cuticles. Benthic diatoms were not significantly impacted in their total cover proportions. However, adverse effects of UVR on marine and freshwater diatoms have been reported in a number of very recent studies (Hernando & San Roman 1999, Danilov & Ekelund 2000, van Donk et al. 2001, Watkins et al. 2001). The absence of effects on diatoms could have been due to shading by macroalgae that protected diatom mats from the incident radiation. Since diatom communities were not analysized with regard to their species composition, it is not known whether a change in community composition, due to the favouring of more UVR-resistant species, took place.

Effects of UVBR exposure on blue mussels differed in the two studies. In the 12 mo old start communities, blue mussels were scarce. Nevertheless, they increased in abundance during the course of the experiment due to spat recruitment. No differential response of mussels towards the various levels of UVBR exposure was detected in this study. This was presumably due to the presence of a high standing stock of *C. strictum* that shaded the young recruits from the enhanced UVB radiation. Supposably, effects of UVBR on the small and almost transparent post-veliger larvae should have appeared in the absence of shading. Chalker-Scott et al. (1994) demonstrated the vulnerability of veliger and post-veliger larvae of *Dreissena polymorpha* towards UV irradiance. In contrast to this, blue mussels were abundant in the 3 mo old start communities but decreased heavily in all but one treatment within the first 7 wk of the experiment. No conclusive explanation has been found for this observation. It was certainly not a treatment effect, since mussels disappeared from the untreated controls as well. Due to the season, almost no subsequent recruitment took place that could have led to a recovery of mussel populations.

Balanus improvisus was not impacted by enhanced UVBR in the study on 1 yr old communities. Adult barnacles are very likely insensitive towards UVR because of their opaque exoskeleton. At the same time, cypris larvae and young adults were presumably protected by the algal canopy. During the second study on 3 mo old assemblages, barnacles increased in cover during the first 7 wk on all but the most severely treated panels. This indicates a sensibility of younger barnacles to prolonged exposure to enhanced UVBR. Algal cover was not as extensive as on the panels of the older communities and was therefore presumably an insufficient protection against UVBR. No records were found in the literature concerning the sensitivity of cypris larvae or adult barnacles towards UVR.

Polydora ciliata (present at the 8th and 12th wk sampling of the older communities), which can retreat itself in its nontransparent tube, showed no response to the UVBR treatment.

UVBR effects on diversity parameters were transient and vanished between the 8th and 12th week of the experiment. Santas et al. (1997, 1998) reported transient UVR effects from two different systems: Mediterranean benthic diatom assemblages experienced community change through different irradiance regimes (PAR, PAR + UVAR, PAR + UVAR + UVBR) during the first 3 wk of the study but effects diminished thereafter (Santas et al. 1997). The author suggested the existence of adjustment mechanisms to UVR stress within the communities under investigation. A similar observation is reported by the same author (Santas et al. 1998) from a tropical reef algal community. Ambient and artificially enhanced UVRB levels resulted in a reduction in biomass productivity and a change in species composition. However, these effects diminished while succession proceeded. Further effects of UVR on community composition have also been reported from assemblages of unicellular algae: Worrest et al. (1981) conducted one of the earliest laboratory studies on the influence of enhanced UVR on the structure of phytoplankton communities, and they found community compositions altered with increased UVBR exposure.

Generally, species composition change can result from a reduction in primary productivity and changes in carbon allocation (Odmark et al. 1998, Wulff et al. 1999). However, McNamara & Hill (2000) found no change in community composition in freshwater periphyton even under high levels (400 % of ambient irradiance) of UVBR.

Unexpected effects were observed in this study with regard to communities' sensitivity towards UVBR exposure as a function of community age. Lüning (1980) and Santas et al. (1998) underlined the sensitivity of early successional algal communities, due to the high sensitivity of spores and germlings, while adult individuals are better protected against UV radiation. It is therefore remarkable that communities of both successional stages were significantly influenced in their composition by long-term exposure to enhanced UVBR.

Santas et al. (1998) reported that experimentally enhanced UVBR reduced the biomass of filamentous algal assemblages significantly when compared to treatments that experienced PAR or PAR + UVA irradiance (Santas et al. 1998). This observation was not confirmed. Conclusions: Exposure to enhanced UVBR favoured the green algae *Enteromorpha sp*. and *Chaetomorpha tortuosa* and restricted the dominance of *C. strictum*. However, significant effects on community composition and diversity were transient.

The results of this study suggest that an ozone-related increase in ambient UVBR presumably will change the algal composition of benthic communities in the upper subtidal of the Western Baltic - at least during the summer months. Conditions of enhanced UVBR should favour green algae and will lead to a retreat of the perennial red algae into deeper water. This will result in an alteration of the vertical zonation of shallow water habitats, associated with a reduction of red algae communities in areas that do not provide sufficient water depths or suitable settlement substratum for macroalgae in deeper waters. The fact that UVBR effects on community diversity were transient in this study shows that buffering mechanisms within benthic assemblages (see chapter 10.2) are able to compensate for radiation-induced perturbations on the community level. Nevertheless, ecosystem functioning is very likely to be altered due to a change from red to green algae dominance in shallow water algal communities. As long as no information is available whether Western Baltic green algae communities provide ecosystem services similar to those of red algae assemblages, large scale ecological consequences of a UVBR-induced community change remain unpredictable. They could include the reduction of important nursery areas for macroinvertebrates and fish species or, in very shallow areas, even their total loss. Such a development will adversely effect the whole Baltic ecosystem and, last but not least, the fishing industry.

One should also keep in mind that UVBR penetration depths depend on the transparency of the sea water, i.e. content of dissolved and particular organic matter, and are therefore correlated with the degree of eutrophication. An decrease in organic matter, as a consequence of a reduced eutrophication, will result in a more profound impact of enhanced UVBR on the vertical distribution of macroalgae, restricting red algae to deeper waters were suitable substratum is scarce due to high sedimentation rates. Interactions of this kind should be considered when UVBR scenarios of the next decades are discussed for the Western Baltic.

10. General discussion

10.1 Spatial orientation of fouling communities

Twelve mo old fouling communities of the emersion and the UVBR exposure experiments differed markedly in their composition. The former were dominated by the blue mussel *Mytilus edulis,* whereas mussels were scarce on the latter and the red alga *Ceramium strictum* was the dominant competitor for space. Assemblages used in the emersion experiments matured, corresponding to their spatial orientation during the experimental phase, in a vertical position while those that were used for the UVBR exposure experiment were horizontally orientated. Though no conclusive explanation can be provided for the diverging community structures, it seems obvious that spatial orientation of the settlement panels was crucial for the determination of the respective fouling communities. This was confirmed by different compositions of the 3 mo old starting communities of the second study series of 2000. Once again, blue mussels were more abundant on vertically orientated panels. Though blue mussels were also present on the horizontally orientated ones, the latter orientation again favoured the red alga *C. strictum*. Furthermore, the barnacle *Balanus improvisus* was scarcer on the horizontal panels while the contrary was the case for the spionid polychaete *Polydora ciliata.*

A number of factors could have been responsible for the emergence of the observed differences in community character (plant vs animal dominance). (1) With regard to their settlement, algal sporelings presumably depend more on passive sedimentation processes than on active attachment. Fucoid sporelings in an in vitro experiment showed higher settlement rates on horizontally than on vertically surfaces (Karez, personal communication). No further reports concerning this topic were found in the literature. Nevertheless, passive settlement behaviour would explain the small amount of algae on vertically orientated surfaces. (2) Higher sedimentation rates choked the majority of animal colonizers on the horizontal panels while algae were able to escape this danger due to their fast and upright growth. (3) Generally, algae should benefit from a horizontally orientated position, since shading by neighbour individuals is reduced when compared to a vertical orientated substrate. The latter reason could also have led to higher growth rates in horizontally positioned algae. This resulted in the suppression of animal colonizers due to a restricted food supply through the dense algal canopy. This effect did not occur on the vertically positioned panels.

(4) Spatial orientation of the substrata could be an important cue for the settlement behaviour of larvae or sporelings, and preferences presumably differ between phylas or at least between kingdoms. Lauer et al. (2001) reported an increase in the density of freshwater

sponges when the orientation of an attachment substrate changed from horizontal to vertical. Glasby (2000) compared the influence of substrate spatial orientation (vertical vs horizontal undersides) with the influence of other substrate properties on the development of fouling communities. The author reported that assemblages were greatly influenced by spatial orientation. Vandermeulen & DeWreede (1982) found larvae of *Obelia sp*. and green algae germlings (*Ulva sp*. and *Enteromorpha sp*.) influenced by the spatial orientation of the settlement substratum. They observed more *Obelia* larvae on the vertical surfaces and higher densities of green algae germlings on horizontal surfaces. In contrast, Baker (1992) found the spatial orientation (facing up, down, and sideways) of the substratum to be of minor importance for the settlement behaviour of oyster larvae.

10.2 Testing the IDH: emersion vs UVBR

Emersion treatments proved to be suitable for an experimental test of the IDH in the focal system. The blue mussel *M. edulis*, which was the dominant space competitor on the vertically orientated settlement panels, was effectively harmed, at least in one study year, by this disturbance type. In contrast, various periods of exposure to enhanced UVBR did not generate the predicted unimodal disturbance-diversity relationship. One possible reason for the contrasting effects of the two disturbance types were the differing characters of the concerned communities. This fact hampers the direct comparison of effects. Diversity in the controls of the horizontally orientated communities (UVBR treatments) was not reduced during the course of the study. Neither *C. strictum*, that was initially dominant, nor blue mussels, which increased in cover proportions on the controls during the study, were able to exclude the majority of other colonizers. As discussed in chapter 5, the presence of competitive exclusion is a premise for the emergence of the unimodal pattern. The initially dominant red algae *C. strictum* experienced a decline in cover proportions along the UVBR exposure gradient. It remained unclear whether this was through direct impairment by the treatment or through overgrow by *Enteromorpha sp*., which possibly benefited from enhanced radiation regimes (see chapter 9). Thus, the green alga compensated for the retreat of *C. strictum* and no space was opened for further colonizers. No range of maximum diversity could emerge along the disturbance gradient, since one of the dominant species was not impaired by the UVBR treatments. The transient character of a monotonous decrease in diversity along the gradient was due to the suppression of benthic diatoms and the hydrozoan *Laomedea flexuosa* during the first 8 wk of the study on 1 yr old communities under the harshest UVBR exposure level. Diversity was not enduringly suppressed under these most extreme conditions, since diatoms recovered between the 8th and 12th wk. Simultaneously, the hydrozoan became scarce on all panels.

A temporal extension of daily exposure to enhanced UVBR would have led to more unbalanced irradiance regimes due to a superproportional increase of UVBR enhancement in the morning and evening hours. In this study UVBR exposure lengths (8 h at maximum) were adjusted to local day length, i.e. the zenith angle of the sun. Possibly, an enhancement of ambient UVBR by more than 100 % would have generated more pronounced effects. However, with regard to this question no references have been found in the literature on IDH-related experiments using UVR as a disturbance agent.

Effects of both disturbance types were generally mitigated by the complex structures of the fouling communities. This can be referred to as an associational protection. In the case of emersion treatments, the retention of water by the blue mussel matrix was beneficial for smaller colonizers, which inhabited interstices between mussel individuals, as well as for the blue mussels themselves (e.g. cooling through evaporation). The same applies, to a presumably even greater extent, to algal dominated communities that experience doses of enhanced UVBR. Shading should favour all organisms that live beneath the shelter of an algal canopy. No measurements of UVBR have been conducted within the algal canopy, but radiation doses should have been significantly reduced. Because of this, detrimental effects were presumably absent. Future studies on the effects of UVR on macrobenthos communities should consider mutual shading and should address the role of canopy-engineering species for the maintenance of communities under conditions of harsh UVR regimes.

11. References

Aarseth KA, Schram TA (1999) Wavelength-specific behaviour in *Lepeophtheirus salmonis* and *Calanus finmarchius* to ultraviolet and visible light in laboratory experiments (Crustacea: Copepoda). Mar Ecol Prog Ser 186:211-217

Abensperg-Traun M, Smith GT, Arnold GW, Steven DE (1996) The effect of habitat fragmentation and livestock grazing on animal communities in remnants of gimlet *Eucalyptus salubris* woodland in the Western Australia wheatbelt. I. Arthropods. J Appl Ecol 33:1281-1301

Adams JB, Bate GC (1994) The tolerance to desiccation of two submerged macrophytes *Ruppia cirrhosa* (Petagna) Grande and *Zostera capensis* Setchell. J Exp Mar Biol Ecol 183:53-62

Adams NL, Shick JM (1996) Mycosporine-like amino acids provide protection against ultraviolet radiation in eggs of the green sea urchin *Strongylocentrotus droebachiensis*. Photochem Photobiol 64:149-158

Adams NL, Shick JM (2001) Mycosporine-like amino acids prevent UVB-induced abnormalities during early development of the green sea urchin *Strongylocentrotus droebachiensis*. Mar Biol 138:267-280

Aguilera J, Karsten U, Lippert H, Vögele B, Philipp E, Hanelt D, Wiencke C (1999) Effects of solar radiation on growth, photosynthesis and respiration of marine macroalgae from the Artic. Mar Ecol Prog Ser 191:109-119

Allen TFH, Starr TB (1982) Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago

Ambrose WGJ (1993) Effects of predation and disturbance by ophiuroids on soft-bottom community structure in Oslofjord: results of a mesocosm study. Mar Ecol Prog Ser 97:225-236

Anderson NH (1992) Influence of disturbance on insect communities in Pacific Northwest streams. Hydrobiologia 248:79-92

Arasaki S (1981) A comparison of the phenology of intertidal *Porphyra* on the coasts of Japan and western North America. Proc Int Seaweed Symp 8:273-277

Armesto JJ, Pickett STA (1985) Experiments on disturbance in old-field plant communities: impact on species richness and abundance. Ecology 66:230-240

Aronson RB, Precht WF (1995) Landscape patterns of reef coral diversity: a test of the intermediate disturbance hypothesis. J Exp Mar Biol Ecol 192:1-14

Arts MT, Rai H (1997) Effects of enhanced ultraviolet-B radiation on the production of lipid, polysaccharide and protein in three freshwater algal species. Freshwat Biol 38:597-610

Aubréville A (1938) La forêt coloniale: les forêts de l'Afrique occidentale francaise. Ann Acad Sci Colon Paris 9

Austen MC, Widdicombe S, Villano-Pitacco N (1998) Effects of biological disturbance on diversity and structure of meiobenthic nematode communities. Mar Ecol Prog Ser 174:233-246

Ayling AM (1981) The role of biological disturbance in temperate subtidal encrusting communities. Ecology 62:830-847

Baker P (1992) Roles of physical cues in oyster larval settlement site choice. J Shellfish Res 11:189

Barbiero RP, James WF, Bako J W (1999) The effects of disturbance events on phytoplankton community structure in a small temperate reservoir. Freshwat Biol 42:503-512

Barnes H, Barnes M (1958) Note on the opening response of *Balanus balanoides* (L.) in relation to salinity and certain inorganic ions. Veröff Inst f Meeresforsch Bremerhaven 5:160-164

Bayne BL, Hawkins AJS, Navarro E (1988) Feeding and digestion in suspension-feeding bivalve molluscs: the relevance of physiological compensations. Am Zool 28:147-159

Beach KS, Smith CM (1997) Ecophysiology of a tropical rhodophyte III: recovery from emersion stress in *Ahnfeltiopsis concinna* (J. Ag.) Silva et DeCew. J Exp Mar Biol Ecol 211:151-167

Begon M, Harper JL, Townsend CR (1996) Ecology, 3rd edn, Blackwell Science, Oxford

Bell EC (1995) Environmental and morphological influences on thallus temperature and desiccation of the intertidal alga *Mastocarpus papillatus* Krützing. J Exp Mar Biol Ecol 191:29-55

Bischof K, Hanelt D, Wiencke C (1998) UV radiation can affect depth-zonation of Antarctic macroalgae. Mar Biol 131:597-605

Booth CR, Madronich S (1994) Radiation amplification factors: improved formulation accounts for large increases in ultraviolet radiation associated with Antarctic ozone depletion. In: Weiler CS, Penhale PA (eds) Ultraviolet radiation in Antarctica: measurements and biological effects. American Geophysical Union, Washington, DC, p 39-42

Bothwell ML, Sherbot D, Pollock CM (1994) Ecosystem response to solar ultraviolet-B radiation: influence of trophic-level interactions. Science 265:97-100

Bothwell ML, Sherbot D, Roberge AC, Daley RJ (1993) Influence of natural ultraviolet radiation on lotic periphytic diatom community growth, biomass accrual, and species composition: short-term versus long-term effects. J Phycol 29:24-35

Bradley BP, Olsson P, Brown DC, Tedengren M (1998) HSP70 levels in physiologically stressed Baltic Sea mussels. Mar Environ Res 46:1-5

Brawley SH, Johnson LE, Pearson GA, Speransky V, Li R, Serrao E (1999) Gamete release at low tide in fucoid algae: maladaptive or advantageous? Am Zool 39:218-229

Brewer R (1994) The science of ecology. Saunders, Ft. Worth, Texas

Brinkhuis BH, Tempel NR, Jones RF (1976) Photosynthesis and respiration of exposed salt marsh fucois. Mar Biol 34:349-359

Britton JC (1993) The effects of experimental protocol and behaviour on evaporative water loss during emersion in three species of rocky shore gastropods. In: The marine flora and fauna of Rottnest Island, Western Australia. Western Australian Museum, Perth, WA, p 539-563

Burnett LE, Jorgensen DD, Carrol AK, Scholnick D (1991) Physiological responses of the barnacle *Balanus nubilis* to air exposure. Am Zool 31:68A

Cabrera S, López M, Tartarotti B (1997) Phytoplankton and zooplankton response to ultraviolet radiation in a high-altitude Andean lake: short versus long-term effects. J Plankton Res 19:1565-1582

Calkins J, Thordardottir T (1980) The ecological significance of solar UV radiation on aquatic organisms. Nature 283:563-566

Carpenter RC (1981) Grazing by *Diadema antillarum* (Phillipi) and its effects on the benthic algal community. J Mar Res 39:749-765

Chalker-Scott L, Scott J, Titus J (1994) Brief exposure to ultraviolet radiation inhibits locomotion of veligers and juvenile *D. polymorpha*. In: International association for Great Lakes research B. 37. Conference of the international association of Great Lakes research and estuarine research federation. Iaglr, Buffalo, NY (USA), Windsor, ON (Canada)

Chapple JP, Smerdon GR, Berry RJ, Hawkins AJS (1998) Seasonal changes in stress-70 protein levels reflect thermal tolerance in the marine bivalve *Mytilus edulis* L. J Exp Mar Biol Ecol 229:53-68

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117-143

Clements FE (1916) Plant succession: an analysis of the development of vegetation. Carnegie Inst Washington Publ 242

Cohen AL, Singhakimara BMP, Aston PMS (1995) Releasing rain forest succession: a case study in the *Dicranopteris linearis* fernlands of Sri Lanka. Restor Ecol 3:261-270

Cohen AS, Bills R, Cocquyt CZ, Caljon AG (1993) The impact of sediment pollution on biodiversity in Lake Tanganyika. Conserv Biol 7:667-677

Coleman N (1973) Water loss from aerially exposed mussels. J Exp Mar Biol Ecol 12:145-155

Colinvaux P (1993) Ecology 2. Wiley, New York

Collen J, Davison IR (1997) In vivo measurement of active oxygen production in the brown alga *Fucus evanescens* using 2',7'-dichlorohydrofluorescein diacetate. J Phycol 33:643-648

Collins SL (1992) Fire frequency and community heterogeneity in tallgrass prairie vegetation. Ecology 73:2001-2006

Collins SL, Glenn SM, Gibson DJ (1995) Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology 76:486-492

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302-1309

Connell JH, Keough MJ (1985) Disturbance and patch dynamics of subtidal marine animals on hardsubstrata. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Fl, p 125-151

Cooper WS (1913) The climax forest of Isle Royale, Lake Superior and its development. Bot Gaz 15: p 1-44, p 115-140, p 189-235

Danilov RA, Ekelund NGA (2000) Effects of different levels of UV-B radiation on marine epilithic communities: a short-term microcosm study. Sci Mar 64:363-368

Davidson AT, Bramich D, Marchant HJ, McMinn A (1994) Effects of UV-B irradiation on growth and survival of Antarctic marine diatoms. Mar Biol 119:507-515

Davidson AT, Marchant HJ, de la Mare WK (1996) Natural UVB exposure changes the species composition of Antarctic phytoplankton in mixed culture. Aquat Microb Ecol 10:299-305

Davison IR, Dudgeon SR, Ruan H-M (1989) The effect of freezing on seaweed photosynthesis. Mar Ecol Prog Ser 58:123-131

Davison IR, Pearson GA (1996) Stress tolerance in intertidal seaweeds. J Phycol 32:197-211

Dayton PK (1971) Competition, predation, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol Monogr 41:351-389

Death RG, Winterbourn MJ (1995) Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. Ecology 76:1446-1460

de Zwaan A (1977) Anaerobic energy metabolism in bivalve molluscs. Oceanogr Mar Biol Annu Rev 15:103-187

Doeg TJ, Lake PS, Marchant R (1989) Colonization of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. Aust J Ecol 14:207-220

Döhler G (1997) Effect of UVB radiation on utilization of inorganic nitrogen by Antarctic microalgae. Photochem Photobiol 66:831-836

Döhler G, Biermann I (1987) Effect of UV-B irradiance on the response of 15N-ammonia and 15N-nitrate by phytoplankton of the Wadden Sea. J Plankton Res 9:881-890

Döhler G, Hagmeier GE, Krause K-D (1991) Impact of solar UV radiation on uptake of 15N-ammonia and 15N-nitrate by marine diatoms and natural phytoplankton. Biochem Physiol Pflanzen 181:533-539

Dromgoole FI (1980) Desiccation resistance of intertidal and subtidal algae. Bot Mar 23:143-159

Dudgeon SR, Davison IR, Vadas RL (1989) Effect of freezing on photosynthesis of intertidal algae: relative tolerance of *Chondrus crispus* and *Mastocarpus stellatus*. Mar Biol 101:107-114

Dürr S, Wahl M Species exclusion, simulated specific predation and diversity in a fouling community. In review.

Eggeling WJ (1947) Observations on the ecology of the Budongo rain forest, Uganda. J Ecol 34:20-87

Einav R, Beer S (1993) Photosynthesis in air and water of *Acanthophora najadiformis* growing within a narrow zone in the intertidal. Mar Biol 117:133-138

Ekelund NGA (1990) Effects of UV-B radiation on growth and motility of four phytoplankton species. Physiol Plant 78:590-594

Elliott KJ, Schwank WT (1994) Changes in tree species diversity after successive clearcuts in the Southern Appalachians. Vegetatio 115:11-18

Elvin DW, Gonor JJ (1979) The thermal regime of an intertidal *Mytilus californianus* Conrad population on the central oregon coast. J Exp Mar Biol Ecol 39:265-279

Feder JH, Rossi JM, Solomon J, Solomon N, Lindquist S (1992) The consequences of expressing hsp70 in *Drosophila* cells at normal temperatures. Genes Dev 6:1402-1413

Figueroa FL, Gomez I (2001) Photosynthetic acclimation to solar UV radiation of marine red algae from the warm-temperate coast of southern Spain: a review. J Appl Phycol 13:233-245

Flöder S, Sommer U (1999) Diversity in planktonic communities: an experimental test of the intermediate disturbance hypothesis. Limnol Oceanogr 44:1114-1119

Fork DC, Oequist G (1981) The effects of desiccation on excitation energy transfer at physiological temperatures between the photosystems of the red alga *Porphyra perforata*. Z Pflanzenphysiol 104:385-393

Foster BA (1971) Desiccation as a factor in the intertidal zonation of barnacles. Mar Biol 8:12-29

Fox JF (1985) Plant diversity in relation to plant production and disturbance by voles in Alaskan tundra communities. Arct Alp Res 17:199-204

Frederick JE, Snell HE, Haywood EK (1989) Solar ultraviolet radiation at the Earth's surface. Photochem Photobiol 50:443-450

Gaedeke A, Sommer U (1986) The influence of the frequency of periodic disturbances on the maintenance of phytoplankton diversity. Oecologia 71:25-28

Gause GF (1937) Experimental populations of microscopic organisms. Ecology 18:173-179

Glasby TM (2000) Surface composition and orientation interact to affect subtidal epibiota. J Exp Mar Biol Ecol 248:177-190

Grainger F, Newell GE (1965) Aerial respiration in *Balanus balanoides*. J Mar Biol Ass UK 45:469-479

Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nature 242:344-347

Grime JP (1979) Plant strategies and vegetation processes. Wiley, Chichester

Gutterman Y, Golan T, Garsani M (1990) Porcupine diggings as a unique ecological system in a desert environment. Oecologia 85:122-127

Häder D-P, Worrest RC (1991) Effects of enhanced solar ultraviolet radiation on aquatic ecosystems. Photochem Photobiol 53:717-725

Häder D-P, Worrest RC, Kumar HD, Smith RC (1995) Effects of increased solar ultraviolet radiation on aquatic ecosystems. Ambio 24:174-180

Hanelt D, Wiencke C, Nultsch W (1997) Influence of UV radiation on the photosynthesis of Arctic macroalgae in the field. J Photochem Photobiol B: Biol 38:40-47

Havaux M (1992) Stress tolerance of photosystem II in vivo. Plant Physiol 100:424-432

Hayward PJ, Ryland JS (1995) Handbook of the marine fauna of North-West Europe. Oxford University Press, Oxford, GB

Helbling EW, Villafane V, Ferrario M, Holm-Hansen O (1992) Impact of natural ultraviolet radiation on rates of photosynthesis and on specific marine phytoplankton species. Mar Ecol Prog Ser 80:89-100

Helbling EW, Villafane V, Holm-Hansen O (1994) Effects of ultraviolet radiation on Antarctic marine phytoplankton photosynthesis with particular attention to the influence of mixing. In: Weiler CS, Penhale PA (eds) Ultraviolet radiation in Antarctica: measurements and biological effects. Antarctic Research Series. American Geophysical Union, Washington, DC, p 207-228

Helmuth B (1998) Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. Ecol Monogr 68:51-74

Helmuth B (1999) Thermal biology of rocky intertidal mussels: quantifying body temperatures using climatological data. Ecology 80:15-34

Hernando MP, San Roman NA (1999) Preliminary data on chronic effects of ultraviolet radiation on the growth of some phytoplankton species of the Beagle Channel, Argentina. Sci Mar 63:81-88

Hessen DO (1996) Competitive trade-off strategies in Arctic *Daphnia* linked to melanism and UV-B stress. Polar Biol 16:573-579

Hessen DO, de Lange HJ, van Donk E (1997) UV-induced changes in phytoplankton cells and its effects on grazers. Freshwat Biol 38:513-524

Hessen DO, van Donk E, Andersen T (1995) Growth response, P-uptake and loss of flagellain *Clamydomonas reinhardtii* exposed to UV-B. J Plankton Res 17:17-27

Hiura T (1995) Gap formation and species diversity in Japanese beech forests: a test of the intermediate disturbance hypothesis on a geographic scale. Oecologia 104:265-271

Hixon MA, Brostoff WN (1983) Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. Science 220:511-513

Hofmann GE (1999) Ecologically relevant variation in induction and function of heat shock proteins in marine organisms. Am Zool 39:889-900

Hoopes MF, Harrison S (1998) Metapopulation, source-sink and disturbance dynamics. In: Sutherland WJ (ed) Conversation science and action. Blackwell, Oxford, p 135-151

Horn HS (1975) Markovian properties of forest succession. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Belknap Press, Cambridge, MA, p 196-211

Hoyer K, Karsten U, Sawall T, Wiencke C (2001) Photoprotective substances in Antarctic macroalgae and their variation with respect to depth distribution, different tissues and developmental stages. Mar Ecol Prog Ser 211:117-129

Huntly N, Inouye RS (1987) Small mammal populations of an old-field chronosequence: successional patterns and associations with vegetation. J Mammalogy 68:739-745

Huston MA (1979) A general hypothesis of species diversity. Am Nat 113:81-101

Hutchinson GE (1959) Homage to Santa Rosalia, or, why are there so many kinds of animals? Am Nat 93:145-159

Hutchinson GE (1961) The paradox of the plankton. Am Nat 95:137-145

Incze LA, Lutz RA, Watling L (1980) Relationships between effects of environmental temperature and seston on growth and mortality of *Mytilus edulis* in a temperate northern estuary. Mar Biol 57:147-156

Inouye RS, Huntly NJ, Tilman D, Tester JR, Stillwell M, Zinnel KC (1987) Old-field succession on a Minnesota sand plain. Ecology 68:12-26

Jackson GP, Fox BJ (1996) Comparison of regeneration following burning, clearing or mineral sand mining at Tomago, NSW: II. Succession of ant assemblages in a coastal forest. Aust J Ecol 21:200-216

Jacob A, Kirst GO, Wiencke C, Lehmann H (1991) Physiological responses of the Antarctic green alga *Prasiola crispa ssp. antarctica* to salinity stress. J Plant Physiol 139:57-62

Johnston AM, Raven JA (1986) The analysis of photosynthesis in air and water of *Ascophyllum nodosum* (L.) Le Jol. Oecologia 69:288-295

Jokiel PL, York Jr RH (1984) Importance of ultraviolet radiation in photoinhibition of microalgal growth. Limnol Oceanogr 29:192-199

Jones EW (1945) The structure and reproduction of the virgin forest of the north temperate zone. New Phytol 44:130-148

Jones MB, Greenwood JG (1982) Water loss of a porcelain crab, *Petrolisthes elongatus* (Milne Edwards, 1837) (Decapoda, Anomura), during atmospheric exposure. Comp Biochem Physiol A 72:631-636

Karentz D (1994) Considerations for evaluating ultraviolet radiation-induced genetic damage relative to Antarctic ozone depletion. Environ Health Perspectives 102:61-64

Karentz D (2001) Chemical defense of marine organisms against solar radiation exposure: UV-absorbing mycosporine-like amino acids and scytonemin. In: McClintock JB, Baker BJ (eds) Marine chemical ecology. CRC Marine Science Series, Boca Raton, p 481-521

Karentz D, Bosch J (2001) Influence of ozone-related increases in ultraviolet radiation on Antarctic marine organisms. Am Zool 41:3-16

Karentz D, Spero HJ (1995) Response of a natural *Phaeocystis* population to ambient fluctuations of UVB radiation caused by Antarctic ozone depletion. J Plankton Res 17:1771-1789

Karsten U, Barrow KD, West JA, King RJ (1997) Mannitol metabolism in the intertidal mangrove red alga *Caloglossa leprieurii:* salinity effects on enzymatic activity. Phycologia 36:150-156

Karsten U, Bischof K, Wiencke C (2001) Photosynthetic performance of Arctic macroalgae after transplantation from deep to shallow waters. Oecologia 127:11-20

Karsten U, Sawall T, Hanelt D, Bischof K, Figueroa F, Flores-Moya A, Wiencke C (1998) An inventory of UV-absorbing mycosporine-like amino acids in macroalgae from polar to warm-temperate regions. Bot Mar 41:443-453

Keddy PA (1983) Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. Ecology 64:331-344

Keddy PA (1985) Wave disturbance on lakeshores and the within-lake distribution of Ontario's Atlantic coastal plain flora. Can J Bot 63:656-660

Keeley SC, Keeley JE, Hutchinson SM, Johnson AW (1981) Postfire succession of the herbaceous flora in Southern California chaparral. Ecology 62:1608-1621

Kennedy VS (1976) Desiccation, higher temperatures and upper intertidal limits of three species of sea mussels (Mollusca: Bivalvia) in New Zealand. Mar Biol 35:127-137

Kerr RA (2002) Ozone depletion: a brighter outlook for good ozone. Science 297:1623-1625

Kerr RA, McElroy CT (1993) Evidence for a large upward trends of ultraviolet-B radiation linked to ozone depletion. Science 262:1032-1034

Kirk JTO (1994) Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge

Kornmann P, Sahling P-H (1983) Meeresalgen von Helgoland. Biologische Anstalt Helgoland, Hamburg

Krebs CJ (2001) Ecology: the experimental analysis of distribution and abundance. Benjamin Cummings, an imprint of Addison Wesley Longman, Inc.

Krebs RA, Loeschke V (1994) Costs and benefits of activation of the heat-shock response in *Drosophila melanogaster.* Funct Ecol 8:730-737

Kukert H, Smith CR (1992) Disturbance, colonization and succession in a deep-sea sediment community: artificial-mound experiments. Deep-Sea Res 39:1349-1371

Kumar HD, Häder D-P (1999) Global aquatic and atmospheric environment. Springer-Verlag

Lake PS, Doeg TJ (1995) Macroinvertebrate colonization of stones in two upland southern Australian streams. Hydrobiologia 126:199-211

Lake PS, Doeg TJ, Marchant R (1989) Effects of multiple disturbance on macroinvertebrate communities in the Acheron River, Victoria. Aust J Ecol 14:507-514

Lass HU, Magaard L (1995) Wasserstandsschwankungen und Seegang. In: Rheinheimer G (ed) Meereskunde der Ostsee, Springer Verlag, p 68-74

Lauer TE, Spacies A, Barnes DK (2001) The distribution and habitat preferences of freshwater sponges (Porifera) in four southern Lake Michigan harbors. Am Midl Nat 146:243-253

Li R, Brawley SH, Close TJ (1998) Proteins immunologically related to dehydrins in fucoid algae. J Phycol 34:642-650

Liu C-H, Shih M-C, Lee T-M (2000) Free proline levels in *Ulva* (Chlorophyta) in response to hypersalinity: elevated NaCl in seawater versus concentrated seawater. J Phycol 36:118-119

Loomis SH (1995) Freezing tolerance of marine invertebrates. Oceanogr Mar Biol Annu Rev 33:337-350

Lubchenco J, Menge BA (1978) Community development and persistence in a low rocky intertidal zone. Ecol Monogr 59:67-94

Lubin D, Jensen EH (1995) Effects of clouds and stratospheric ozone depletion on ultraviolet radiation trends. Nature 377:710-713

Lüning K (1980) Critical levels of light and temperature regulating the gametogenesis of three *Laminaria* species (Phaeophyceae). J Phycol 16:1-15

MacArthur RH (1965) Patterns of species diversity. Biol Rev 40:510-533

Mackey RL, Currie DJ (2001) The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82:3479-3492

Madronich S, McKenzie RL, Caldwell MM, Björn LO (1995) Changes in ultraviolet radiation reaching the Earth's surface. Ambio 24:143-152

Madsen TV, Maberly SC (1990) A comparison of air and water as environments for photosynthesis by the intertidal alga *Fucus spiralis* (Phaeophyta). J Phycol 26:24-30

Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton, NJ

Margalef R (1972) Homage to Evelyn Hutchinson, or why is there an upper limit to diversity. Trans Connect Acad Arts Sci 44:211-235

Marsden ID (1991) A comparison of water loss and gill areas in two supralittoral amphipods from New Zealand. Hydrobiologia 223:149-158

Martinsen GD, Cushman JH, Whitham TG (1990) Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community. Oecologia 83:132-138

McCabe DJ, Gotelli NJ (2000) Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. Oecologia 124:270-279

McIntyre S, Lavorel S, Tremont RM (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. J Ecol 83:31-44

McMahon RF (1990) Thermal tolerance, evaporative water loss, air-water oxygen consumption and zonation of intertidal prosobranchs: a new synthesis. Hydrobiologia 193:241-260

McNamara AE, Hill WR (2000) UV-B irradiance gradient affects photosynthesis and pigments but not food quality of periphyton. Freshwat Biol 43:649-662

Mehlman DW (1992) Effects of fire on plant community composition of North Florida second growth pineland. Bull Torrey Bot Club 119:376-383

Meier AJ, Bratton SP, Duffy DC (1995) Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecol Appl 5:935-946

Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. Am Nat 130:730-757

Mingoa-Licuanan S (1993) Oxygen consumption and ammonia excretion in juvenile *Tridacna gigas* (Linne, 1758): effects of emersion. J Exp Mar Biol Ecol 171:119-137

Mitchell DL, Karentz D (1993) The induction and repair of DNA photodamage in the environment. In: Young AR, Björn LO, Moan J, Nultsch W (eds) Environmental UV photobiology. Plenum Press, New York, p 345-377

Mook DH (1981) Effects of disturbance and initial settlement on fouling community structure. Ecology 62:522-526

Morgan K, Freedman B (1986) Breeding bird communities in a hardwood forest succession in Nova Scotia. Can Field-Nat 100:506-519

Mostaert AS, Karsten U, King RJ (1995) Inorganic ions and mannitol in the red alga *Caloglossa leprieurii* (Ceramiales, Rhodophyta): response to salinity change. Phycologia 34:501-507

Moulton JM (1962) Intertidal clustering of an Australian gastropod. Biol Bull Wood's Hole 123:170-178

Muslin EH, Homann PH (1992) Light as a hazard for the desiccation-resistant “resurrection” fern *Polypodium polypodioides* L. Plant Cell Environm 15:81-89

Nery LEM, Santos EA (1993) Carbohydrate metabolism during osmoregulation in *Chasmagnathus granulata* (Dana, 1851) (Crustacea, Decapoda). Comp Biochem Physiol B 106:747-753

Nilsson C (1987) Distribution of stream-edge vegetation along a gradient of current velocity. J Ecol 75:513 – 522

Nordic Council of Ministers (1996) UV-B effects on nordic marine ecosystems. Nordic Council of Ministers, Copenhagen.

Norton TA (1986) The zonation of seaweeds on rocky shores. In: Moore PG, Seed R (eds) The ecology of rocky coasts. Columbia University Press, New York, p 7-21

Odmark S, Wulff A, Wänberg S-A, Nilsson C, Sundbäck K (1998) Effects of UVB radiation in a microbenthic community of a marine shallow-water sandy sediment. Mar Biol 132:335-345

Odum EP (1963) Ecology. Holt, Rinehart and Winston, New York

Ohno M, Miyanoue K (1980) The ecology of the food alga *Enteromorpha prolifera*. Rep Usa Mar Biol Inst Kochi Univ 2:11-17

O’Neill RV, DeAngelis DL, Waide JB, Allen TFH (1986) A hierarchical concept of ecosystems. Princeton University Press, Princeton, NJ

Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and the dynamics of pattern. Ecol Monogr 51:145-178

Palmer MW (1994) Variation in species richness: towards a unification of hypothesis. Folia Geobot Phytotaxon 29:511-530

Parker GR (1989) Effects of reforestation upon small mammal communities in New Brunswick. Can Field-Nat 103:509-519

Pearson G, Krautsky L, Serrao E (2000) Recent evolution in Baltic *Fucus vesiculosus*: reduced tolerance to emersion stress compared to intertidal (North Sea) populations. Mar Ecol Prog Ser 202:67-79

Pearson GA, Davison IR (1993) Freezing rate and duration determine the physiological response of intertidal fucoids to freezing. Mar Biol 115:353-362

Pequeux A (1995) Osmotic regulation in crustaceans. J Crust Biol 15:1-60

Petraitis PS, Latham RE, Niesenbaum RA (1989) The maintenance of species diversity by disturbance. Q Rev Biol 64:393-418

Phillips OL, Hall P, Gentry AH, Sawyer SA, Vasquez R (1994) Dynamics and species richness of tropical rain forests. Proc Natl Acad Sci USA 91:2805-2809

Pickett STA, Kolasa J, Armesto JJ, Collins SL (1989) The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129-136

Pickett STA, White PS (1985) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Fl.

Pielou EC (1969) An introduction to mathematical ecology. Wiley, New York

Qiu J-W, Qian P-Y (1997) Effects of food availability, larval source and culture method on larval development of *Balanus amphitrite amphitrite* Darwin: implications for experimental design. J Exp Mar Biol Ecol 217:47-61

Quadir A, Harrison PJ, De Wreede RE (1979) The effects of emergence and submergence on the photosynthesis and respiration of marine macrophytes. Phycologia 18:83-88

Raphael MG, Morrison ML, Yoder-Williams MP (1987) Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. The Condor 89:614-626

Rawlings TA (1996) Shields against ultraviolet radiation: an additional protective role for the egg capsules of benthic marine gastropods. Mar Ecol Prog Ser 136:81-95

Reice SR (1985) Experimental disturbance and the maintenance of species diversity in stream community. Oecologia 67:90-97

Ricklefs RE (1990) Ecology, 3 edn. Freeman, New York

Ritz DA, Crisp DJ (1970) Seasonal changes in feeding rate in *Balanus balanoides*. J Mar Biol Ass UK 50:223-240

Rosser ZC, Pearson RG (1995) Responses of rock fauna to physical disturbance in two Australian tropical rainforest streams. J N Am Benthol Soc 14:183-196

Roxburgh SH, Wilson JB, Mark AF (1988) Succession after disturbance of a New Zealand high-alpine cushionfield. Arct Alp Res 20:230-236

Russel G (1988) The seaweed flora of a young semi-enclosed sea: the Baltic. Salinity as a possible agent of flora divergence. Helgol Meeresunters 42:243-250

Rykiel EJJ (1985) Towards a definition of ecological disturbance. Aust J Ecol 10:361-365

Sadok S, Uglow RF, Haswell SJ (1997) Haemolymph and mantle fluid ammonia and ninhydrin positive substances variations in salinity-challenged mussels (*Mytilus edulis* L.). J Exp Mar Biol Ecol 211:195-212

Sadok S, Uglow RF, Haswell SJ (1999) Some aspects of nitrogen metabolism in *Mytilus edulis:* effects of aerial exposure. Mar Biol 135:297-305

Sammarco PW (1982) Effects of grazing by *Diadema antillarum* Phillipi (Echinodermata: Echinoidea) on algal diversity and community structure. J Exp Mar Biol Ecol 65:83-105

Sanchez Y, Taulien J, Borkovich KA, Lindquist S (1992) HSP104 is required for tolerance to many forms of stress. EMBO J 11:2357-2364

Sandmann H (2001) Über die ultraviolette Sonnenstrahlung. Aus Bildung und Wissenschaft 54:260-265

Santas R, Korda A, Lianou C, Santas P (1998) Community responses to UV radiation. I. Enhanced UVB effects on biomass and community structure of filamentous algal assemblages growing in a coral reef mesocosm. Mar Biol 131:153-162

Santas R, Lianou C, Danielidis D (1997) UVB radiation and depth interaction during primary succession of marine diatom assemblages of Greece. Limnol Oceanogr 42:986-991

Schmidt-Nielsen K (1997) Animal physiology: adaptation and environment. Cambridge University Press, Cambridge

Schnitzer SA, Carson WP (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82:913-919

Schonbeck M, Norton TA (1979) The effects of brief periodic submergence on intertidal fucoid algae. Estuar Coast Mar Sci 8:205-211

Schonbeck MW, Norton TA (1980) Effects on intertidal fucoid algae of exposure to air under various conditions. Bot Mar 23:141-147

Setlow RB (1974) The wavelengths in sunlight effective in producing skin cancer: a theoretical analysis. Proc Natl Acad Sci USA 71:3363-3366

Sheath RG, Vis ML, Hambrooke JA, Cole KM (1996) Tundra stream macroalgae of North America: composition, distribution and physiological adaptations. Hydrobiologia 336:67-82

Shick JM, Widdows J, Gnaiger E (1988) Calorimetric studies of behavior, metabolism and energetics of sessile intertidal animals. Am Zool 28:161-181

Smith CM (1984) Drying enhances tolerance to high temperature stress for an intertidal alga, *Porphyra perforata* J Ag. Am Zool 24:29A

Smith RC, Prézelin BB, Baker KS, Bidegare RR, Boucher NP, Colery T, Karentz D MacIntyre S, Matlick HA, Menzies D, Ondrusek M, Wan Z, Waters KJ (1992) Ultraviolet radiation and phytoplankton biology in Antarctic waters. Science 255:952-959

Sommer U (1995) An experimental test of the intermediate disturbance hypothesis using cultures of marine phytoplankton. Limnol Oceanogr 40:1271-1277

Sousa WP (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225-1239

Steinman AD, Lamberti GA (1988) Lotic algal communities in the Mt. St. Helens region six years following the eruption. J Phycol 24:482-489

Stienen CH (1986) Die Phytoplanktonentwicklung in Abhängigkeit von der Nährsalzkonzentration. Ein Vergleich zwischen Kieler Förde und Kieler Bucht. PhD thesis, Mathematisch-Naturwissenschaftliche Fakultät, Christian-Albrechts-Universität, Kiel

Strid AC, Chow WS, Anderson JM (1994) UV-B damage and protection at the molecular level in plants. Photosynthesis Res 39:475-489

Swamikannu X, Hoagland KD (1989) Effects of snail grazing on the diversity and structure of a periphyton community in a eutrophic pond. Can J Fish Aquat Sci 46:1698-1704

Tansley AG (1949) Britain's green mantle. George Allen and Unwin, London

Tester JR (1989) Effects of fire frequency on oak savanna in east-central Minnesota. Bull Torrey Bot Club 116:134-144

Tevini M, Häder D-P (1985) Allgemeine Photobiologie. Thieme-Verlag, Stuttgart

Thomas TE, Turpin DH, Harrison PJ (1987) Adaptation of *Gracilaria pacifica* (Rhodophyta) to nitrogen procurement at different intertidal locations. Mar Biol 93:569-580

Thurman CL (1998) Evaporative water loss, corporal temperature and the distribution of sympatric fiddler crabs (*Uca*) from south Texas. Comp Biochem Physiol 119A:279-286

Tilmann D (1982) Resource competition and community structure. Princeton University Press, Princeton, NJ

Townsend CR, Scarsbrook MR, Doledec S (1997) The intermediate disturbance hypothesis, refugia, and biodiversity in streams. Limnol Oceanogr 42:938-949

Uhl C (1987) Factors controlling succession following slash-and-burn agriculture in Amazonia. J Ecol 75:377-407

Valiela I, Rietsma CS (1995) Disturbance of salt marsh vegetation by wrack mats in Great Sippewissett Marsh. Oecologia 102:106-112

van Donk E, Faafeng BA, de Lange HJ, Hessen DO (2001) Differential sensitivity to natural ultraviolet radiation among phytoplankton species in Arctic lakes (Spitsbergen, Norway). Plant Ecol 154:247

Vandermeulen H, DeWreede RE (1982) The influence of orientation of an artificial substrate (Transite) on settlement of marine organisms. Ophelia 21:41-48

Vayda ME, Yuan M-L (1994) The heat shock response of an Antarctic alga is evident at 5° C. Plant Mol Biol 24:229-233

Vincent WF, Neale PJ (2000) Mechanisms of UV damage to aquatic organisms. In: de Mora S, Demers S, Vernet M (eds) The effects of UV radiation in the marine environment. Cambridge University Press, Cambridge

Vincent WF, Roy S (1993) Solar ultraviolet-B radiation and aquatic primary production: damage, protection and recovery. Env Rev 1:1-12

Wallasch M, Beilke S (1999) Spezielle Umweltprobleme: Die UV-B Strahlung in Deutschland. In: Jahresbericht 1999 aus dem Messnetz des Umweltbundesamtes. Umweltbundesamt, Berlin

Watkins EM, Schindler DW, Turner MA, Findlay D (2001) Effects of solar ultraviolet radiation on epilithic metabolism, and nutrient and community composition in a clear-water boreal lake. Can J Fish Aquat Sci 58:2059-2070

Watt AS (1947) Pattern and process in the plant community. J Ecol 35:1-22

Weiler SA, Penhale PA (1994) Ultraviolet radiation in Antarctica: measurements and biological effects. Antarctic Research Series. American Geophysical Union, Washington, DC

Whitehead RF, de Mora SJ, Demers S (2000) Enhanced UV radiation – a new problem for the marine environment. In: de Mora SJ, Demers S, Vernet M (eds) The effects of UV radiation in the marine environment. Cambridge University Press, Cambridge

Widdicombe S, Austen MC (1998) Experimental evidence for the role of *Brissopsis lyrifera* (Forbes, 1841) as a critical species in the maintenance of benthic diversity and the modification of sediment chemistry. J Exp Mar Biol Ecol 228:214-255

Widdicombe S, Austen MC (1999) Mesocosm investigation into the effects of bioturbation on the diversity and structure of a subtidal macrobenthic community. Mar Ecol Prog Ser 189:181-193

Widdows J, Bayne BL, Livingstone DR, Newell RIE, Donkin P (1979) Physiological and biochemical responses of bivalve molluscs to exposure to air. Comp Biochem Physiol A 62:301-308

Widdows J, Shick JM (1985) Physiological responses of *Mytilus edulis* and *Cardium edule* to aerial exposure. Mar Biol 85:217-232

Wiencke C, Davenport J (1987) Respiration and photosynthesis in the intertidal alga *Cladophora rupestris* (L.) Kuetz. under fluctuating salinity regimes. J Exp Mar Biol Ecol 114:183-197

Wilkinson DM (1999) The disturbing history of intermediate disturbance. Oikos 84:145-147

Wilson SD, Keddy PA (1988) Species richness, survivorship, and biomass accumulation along an environmental gradient. Oikos 53:375-380

Wilson SD, Shay JM (1990) Competition, fire, and nutrients in a mixed-grass prairie. Ecology 71:1959-1967

Winston GW, Di Guilio RT (1991) Prooxidant and antioxidant mechanisms in aquatic organisms. Aquat Toxicol 19:137-161

Worrest RC, Thomson BE, Van Dyke H (1981) Impact of UVB upon estuarine microcosms. Photochem Photobiol 33:861-867

Wulff A, Nilsson C, Sundbäck K, Wängberg ST, Odmark S (1999) UV radiation effects on microbenthos - a four month field experiment. Aquat Microb Ecol 19:269-278

Xiong FS, Lederer F, Lukavsky J, Nedbal L (1996) Screening of fresh-water algae (Chlorophyta, Chromophyta) for ultraviolet-B sensitivity of the photosynthetic apparatus. J Plant Physiol 148:42-48

Zagarese HE, Feldman M, Williamson CE (1997) UV-B-induced damage and photoreactivation in three species of *Boeckella* (Copepoda, Calanoida). J Plankton Res 19:357-367

Zhao S, Dong S, Wu Y, Shan J (2000) Biochemical and physiological effects of salinity stress on *Ulva purtusa.* Mar Sci/Haiyang Kexue 24:52-55

Acknowledgements

First of all, I'm grateful to my supervisor Dr. Martin Wahl for guiding me into this fascinating field of science and for his advice and help concerning all scientific, technical or logistical problems.

Furthermore, I would like to thank:
my colleague Markus Molis and the members of the Marine Ecology working group that were helpful in various ways on various occasions: Simone Dürr, Peter Enderlein, and Sandra Gohse;
the staff of the Biozentrum's workshop for their indispensable help in designing, building, and maintaining the experimental set-up: Michael Bachmann, Hannes Freitag, Thomas Walter, Thomas Winter, and Jürgen Sachau for his technical and personal support concerning problems that were mostly not commonplace for a terrestrial electrician;
the Wasser- und Schifffahrtsamt Lübeck who kindly provided access to the study site and provided the rafts;
the staff of the locks of Kiel-Holtenau who were always generous with technical help;
the Pausch company for providing free UV tubes;
Dr. Anton-Erxleben and Dr. Künnemann from the Zoological Institute at the CAU Kiel for their technical support;
Rolf Karez, Helmut Hillebrandt, and Thorsten Reusch for their scientific advice.

I thank my parents for their overall support and their believe in my skills.

Critical reading of my manuscript was done by Jennifer Dannheim and Ute Kossak. Their efforts significantly improved the quality of this text. Maike Funk was helpful with the cover design.
The following friends contributed to the success of my study in very different and sometimes rather indirect ways: Ralf Huuck and Thorsten Lammers primarily by sharing similar problems but also by their occasional logistic support, Hartmut Riedel by maintaining my inner equilibrium, and Stefanie Moorthi and Valentin Mayr by diving with me in inappropriate seasons.

This study was funded by the Deutsche Forschungsgemeinschaft (WA 708/6-1 + 6-2).

Appendix I: ANOSIM analyses

Table 4: Emersion frequencies. ANOSIM: R-values and p-levels of the pairwise comparisons between start assemblages, controls, and all treatments of the 3 mo old communities after 6 wk.

	R	*P*
Start x Control	0.452	< 0.01
Start x 1 x 15	0.408	< 0.01
Start x 4 x 15	0.693	< 0.01
Start x 8 x 15	0.670	< 0.01
Start x 24 x15	0.604	< 0.01
Start x 48 x15	0.921	< 0.01
Control x 1 x 15	0.056	n.s.
Control x 4 x 15	0.176	n.s.
Control x 8 x 15	0.235	< 0.1
Control x 24 x 15	0.263	< 0.05
Control x 48 x 15	0.572	< 0.01
1 x 15 x 4 x 15	0.057	n.s.
1 x 15 x 8 x 15	0.100	n.s.
1 x 15 x 24 x15	0.143	< 0.1
1 x15 x 48 x 15	0.765	< 0.01
4 x 15 x 8 x 15	-0.131	n.s.
4 x 15 x 24 x 15	0.030	n.s.
4 x 15 x 48 x 15	0.609	< 0.01
8 x 15 x 24 x 15	0.076	n.s.
8 x 15 x 48 x 15	0.594	< 0.01
24 x 15 x 48 x15	0.289	< 0.05

Table 5: Emersion frequencies. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 3 mo old communities after 14 wk.

	R	*P*
Start x Control	0.328	< 0.01
Start x 1 x 15	0.675	< 0.01
Start x 4 x 15	0.749	< 0.01
Start x 8 x 15	0.603	< 0.01
Start x 24 x15	0.831	< 0.01
Start x 48 x15	0.926	< 0.01
Control x 1 x 15	0.013	n.s.
Control x 4 x 15	0.031	n.s.
Control x 8 x 15	0.015	n.s.
Control x 24 x 15	0.261	< 0.05
Control x 48 x 15	0.635	< 0.01
1 x 15 x 4 x 15	-0.056	n.s.
1 x 15 x 8 x 15	-0.069	n.s.
1 x 15 x 24 x15	0.261	< 0.05
1 x15 x 48 x 15	0.728	< 0.01
4 x 15 x 8 x 15	-0.057	n.s.
4 x 15 x 24 x 15	0.024	n.s.
4 x 15 x 48 x 15	0.578	< 0.01
8 x 15 x 24 x 15	0.154	< 0.1
8 x 15 x 48 x 15	0.630	< 0.01
24 x 15 x 48 x15	0.200	< 0.1

Table 6: Emersion frequencies. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 12 mo old communities after 8 wk.

	R	*P*
Start x Control	0.817	< 0.01
Start x 1 x 15	0.802	< 0.01
Start x 4 x 15	0.734	< 0.01
Start x 8 x 15	0.968	< 0.01
Start x 24 x15	0.762	< 0.01
Start x 48 x15	0.589	< 0.01
Control x 1 x 15	0.708	< 0.05
Control x 4 x 15	0.708	< 0.05
Control x 8 x 15	0.708	< 0.05
Control x 24 x 15	0.875	< 0.05
Control x 48 x 15	0.600	< 0.01
1 x 15 x 4 x 15	0.292	n.s.
1 x 15 x 8 x 15	0.188	n.s.
1 x 15 x 24 x15	0.292	n.s.
1 x15 x 48 x 15	0.569	< 0.01
4 x 15 x 8 x 15	0.115	n.s.
4 x 15 x 24 x 15	-0.021	n.s.
4 x 15 x 48 x 15	0.450	< 0.05
8 x 15 x 24 x 15	0.375	< 0.1
8 x 15 x 48 x 15	0.444	< 0.05
24 x 15 x 48 x15	0.213	< 0.1

Table 7: Emersion frequencies. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 12 mo old communities after 12 wk.

	R	*P*
Start x Control	0.679	< 0.01
Start x 1 x 15	0.861	< 0.01
Start x 4 x 15	0.762	< 0.05
Start x 8 x 15	0.873	< 0.01
Start x 24 x15	0.992	< 0.01
Start x 48 x15	0.811	< 0.01
Control x 1 x 15	0.323	< 0.1
Control x 4 x 15	0.260	n.s.
Control x 8 x 15	0.146	n.s.
Control x 24 x 15	0.531	< 0.05
Control x 48 x 15	0.663	< 0.01
1 x 15 x 4 x 15	0.208	n.s.
1 x 15 x 8 x 15	0.115	n.s.
1 x 15 x 24 x15	0.198	n.s.
1 x15 x 48 x 15	0.575	< 0.01
4 x 15 x 8 x 15	-0.156	n.s.
4 x 15 x 24 x 15	0.500	< 0.05
4 x 15 x 48 x 15	0.413	< 0.05
8 x 15 x 24 x 15	0.271	n.s.
8 x 15 x 48 x 15	0.294	< 0.05
24 x 15 x 48 x15	0.619	< 0.01

Table 8: Emersion intensities. ANOSIM: R-values and p-levels of the pairwise comparisons between start assemblages, controls, and all treatments of the 3 mo old communities after 6 wk.

	R	*p*
Start x Control	.452	< 0.01
Start x 0.25 h	.408	< 0.01
Start x 1 h	.463	< 0.01
Start x 2 h	.343	< 0.01
Start x 6 h	.342	< 0.01
Start x 12 h	.598	< 0.01
Control x 0.25 h	.056	n.s.
Control x 1 h	.128	n.s.
Control x 2 h	.083	n.s.
Control x 6 h	.163	< 0.1
Control x 12 h	.219	< 0.05
0.25 h x 1 h	.044	n.s.
0.25 h x 2 h	.009	n.s.
0.25 h x 6 h	.044	n.s.
0.25 h x 12 h	.500	< 0.01
1 h x 2 h	-.091	n.s.
1 h x 6 h	.109	n.s.
1 h x 12 h	.454	< 0.1
2 h x 6 h	.031	n.s.
2 h x 12 h	.263	< 0.05
6 h x 12 h	.135	n.s.

Table 9: Emersion intensities. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 3 mo old communities after 14 wk.

	R	*p*
Start x Control	.328	< 0.01
Start x 0.25 h	.675	< 0.01
Start x 1 h	.836	< 0.01
Start x 2 h	.640	< 0.01
Start x 6 h	.630	< 0.01
Start x 12 h	.625	< 0.01
Control x 0.25 h	.013	n.s.
Control x 1 h	.165	n.s.
Control x 2 h	.057	n.s.
Control x 6 h	.000	n.s.
Control x 12 h	.317	< 0.05
0.25 h x 1 h	-.078	n.s.
0.25 h x 2 h	-.015	n.s.
0.25 h x 6 h	-.054	n.s.
0.25 h x 12 h	.487	< 0.01
1 h x 2 h	-.078	n.s.
1 h x 6 h	- .004	n.s.
1 h x 12 h	.539	< 0.01
2 h x 6 h	- .006	n.s.
2 h x 12 h	.439	< 0.01
6 h x 12 h	.346	< 0.01

Table 10: Emersion intensities. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 12 mo old communities after 4 wk.

	R	*p*
Start x Control	.548	< 0.05
Start x 0.25 h	.429	< 0.05
Start x 1 h	.639	< 0.01
Start x 2 h	.488	< 0.05
Start x 6 h	.500	< 0.05
Start x 12 h	.667	< 0.01
Control x 0.25 h	.156	n.s.
Control x 1 h	.448	< 0.05
Control x 2 h	.823	< 0.05
Control x 6 h	.948	< 0.05
Control x 12 h	.625	< 0.05
0.25 h x 1 h	-.125	n.s.
0.25 h x 2 h	.240	n.s.
0.25 h x 6 h	.604	< 0.05
0.25 h x 12 h	.417	< 0.05
1 h x 2 h	.208	n.s.
1 h x 6 h	.677	< 0.05
1 h x 12 h	.521	< 0.05
2 h x 6 h	.229	n.s.
2 h x 12 h	.198	< 0.1
6 h x 12 h	.177	< 0.05

Table 11: Emersion intensities. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 12 mo old communities after 8 wk.

	R	*p*
Start x Control	.817	< 0.01
Start x 0.25 h	.802	< 0.01
Start x 1 h	.619	< 0.01
Start x 2 h	.802	< 0.01
Start x 6 h	.563	< 0.01
Start x 12 h	.710	< 0.01
Control x 0.25 h	.729	< 0.05
Control x 1 h	.506	< 0.05
Control x 2 h	.906	< 0.05
Control x 6 h	.958	< 0.05
Control x 12 h	.625	< 0.05
0.25 h x 1 h	.000	n.s.
0.25 h x 2 h	.271	< 0.1
0.25 h x 6 h	.479	< 0.05
0.25 h x 12 h	.625	< 0.05
1 h x 2 h	.106	n.s.
1 h x 6 h	.138	n.s.
1 h x 12 h	.456	< 0.05
2 h x 6 h	-.052	n.s.
2 h x 12 h	.167	n.s.
6 h x 12 h	.146	n.s.

Table 12: Emersion intensities. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 12 mo old communities after 12 wk.

	R	*p*
Start x Control	.659	< 0.01
Start x 0.25 h	.861	< 0.01
Start x 1 h	.995	< 0.01
Start x 2 h	.857	< 0.01
Start x 6 h	.782	< 0.01
Start x 12 h	.742	< 0.01
Control x 0.25 h	.323	< 0.1
Control x 1 h	.775	< 0.01
Control x 2 h	.438	< 0.05
Control x 6 h	.635	< 0.05
Control x 12 h	.583	< 0.05
0.25 h x 1 h	.069	n.s.
0.25 h x 2 h	.188	n.s.
0.25 h x 6 h	.313	n.s.
0.25 h x 12 h	.510	< 0.05
1 h x 2 h	.731	< 0.01
1 h x 6 h	.906	< 0.01
1 h x 12 h	.644	< 0.01
2 h x 6 h	-.052	n.s.
2 h x 12 h	.396	< 0.05
6 h x 12 h	.302	< 0.05

Table 13: UVBR exposure. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 3 mo old communities after 7 wk.

	R	*p*
Start x Control	0.764	< 0.01
Start x 0.5 h	0.863	< 0.01
Start x 1 h	0.943	< 0.01
Start x 2 h	0.344	< 0.05
Start x 4 h	0.762	< 0.01
Start x 8 h	0.932	< 0.01
Control x 0.5 h	-0.031	n.s.
Control x 1 h	0.043	n.s.
Control x 2 h	0.161	n.s.
Control x 4 h	0.081	n.s.
Control x 8 h	0.220	n.s.
0.5 h x 1 h	0.057	n.s.
0.5 h x 2 h	0.189	< 0.1
0.5 h x 4 h	0.415	< 0.01
0.5 h x 8 h	0.643	< 0.01
1 h x 2 h	0.244	< 0.05
1 h x 4 h	0.281	< 0.01
1 h x 8 h	0.454	< 0.05
2 h x 4 h	0.093	n.s.
2 h x 8 h	0.296	< 0.05
4 h x 8 h	0.050	n.s.

Table 14: UVBR exposure. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 3 mo old communities after 7 mo.

	R	*p*
Start x Control	0.725	< 0.01
Start x 0.5 h	0.693	< 0.01
Start x 1 h	0.708	< 0.01
Start x 2 h	0.647	< 0.01
Start x 4 h	0.569	< 0.01
Start x 8 h	0.719	< 0.01
Control x 0.5 h	- 0.085	n.s.
Control x 1 h	0.100	n.s.
Control x 2 h	0.032	n.s.
Control x 4 h	0.155	n.s.
Control x 8 h	-0.046	n.s.
0.5 h x 1 h	0.113	n.s.
0.5 h x 2 h	-0.053	n.s.
0.5 h x 4 h	0.052	n.s.
0.5 h x 8 h	-0.037	n.s.
1 h x 2 h	0.189	< 0.1
1 h x 4 h	0.349	< 0.05
1 h x 8 h	-0.007	n.s.
2 h x 4 h	0.025	n.s.
2 h x 8 h	0.240	< 0.05
4 h x 8 h	0.218	< 0.1

Table 15: UVBR exposure. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 12 mo old communities after 4 wk.

	R	*p*
Start x control	0. 649	< 0.01
Start x 0.5 h	0.598	< 0.01
Start x 1 h	0.543	< 0.01
Start x 2 h	0.576	< 0.01
Start x 4 h	0.509	< 0.01
Start x 8 h	0.528	< 0.01
Control x 0.5 h	0.402	< 0.05
Control x 1 h	- 0.022	n.s.
Control x 2 h	0.330	< 0.05
Control x 4 h	0.007	n.s.
Control x 8 h	0.394	< 0.05
0.5 h x 1 h	0.141	n.s.
0.5 h x 2 h	-0.052	n.s.
0.5 h x 4 h	0.198	< 0.05
0.5 h x 8 h	0.230	< 0.05
1 h x 2 h	-0.063	n.s.
1 h x 4 h	0.015	n.s.
1 h x 8 h	0.306	< 0.05
2 h x 4 h	0.100	n.s.
2 h x 8 h	0.187	< 0.1
4 h x 8 h	0.031	n.s.

Table 16: UVBR exposure. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 12 mo old communities after 8 wk.

	R	*p*
Start x Control	0.888	< 0.01
Start x 0.5 h	0.628	< 0.01
Start x 1 h	0.780	< 0.01
Start x 2 h	0.801	< 0.01
Start x 4 h	0.705	< 0.01
Start x 8 h	0.804	< 0.01
Control x 0.5 h	0.024	n.s.
Control x 1 h	-0.111	n.s.
Control x 2 h	-0.124	n.s.
Control x 4 h	-0.022	n.s.
Control x 8 h	-0.056	n.s.
0.5 h x 1 h	-0.102	n.s.
0.5 h x 2 h	-0.031	n.s.
0.5 h x 4 h	-0.006	n.s.
0.5 h x 8 h	0.007	n.s.
1 h x 2 h	-0.091	n.s.
1 h x 4 h	0.028	n.s.
1 h x 8 h	-0.048	n.s.
2 h x 4 h	0.063	n.s.
2 h x 8 h	0.043	n.s.
4 h x 8 h	-0.113	n.s.

Table 17: UVBR exposure. ANOSIM: Pairwise comparisons between start assemblages, controls, and all treatments of the 12 mo old communities after 12 wk.

	R	*P*
Start x control	0.452	< 0.01
Start x 0.5 h	0.584	< 0.01
Start x 1 h	0.323	< 0.01
Start x 2 h	0.397	< 0.01
Start x 4 h	0.423	< 0.01
Start x 8 h	0.615	< 0.01
Control x 0.5 h	-0.072	n.s.
Control x 1 h	-0.143	n.s.
Control x 2 h	-0.141	n.s.
Control x 4 h	-0.100	n.s.
Control x 8 h	0.007	n.s.
0.5 h x 1 h	-0.052	n.s.
0.5 h x 2 h	-0.093	n.s.
0.5 h x 4 h	-0.167	n.s.
0.5 h x 8 h	0.015	n.s.
1 h x 2 h	-0.144	n.s.
1 h x 4 h	-0.117	n.s.
1 h x 8 h	0.035	n.s.
2 h x 4 h	-0.091	n.s.
2 h x 8 h	-0.039	n.s.
4 h x 8 h	-0.050	n.s.

Curriculum vitae

Name	Mark Lenz		
Nationalität	Deutsch		
Anschrift	Medusastrasse 11 24143 Kiel		
Geboren	02.04.1971 in Kiel		
Ausbildung	1990	Abitur	Kiel
	1991	Grundstudium Biologie	CAU Kiel
	1993	Hauptstudium Biologie	CAU Kiel
	1996	Diplomhauptprüfung Hauptfach: Zoologie 1. Nebenfach: Biologische Meereskunde 2. Nebenfach: Biochemie	CAU Kiel
	1997	Diplomarbeit „Verteidungsmechanismen der Miesmuschel *Mytilus edulis* gegen Aufwuchs“	CAU Kiel
	1998 - 2003	Promotion: Ein experimenteller Test der Intermediate Disturbance Hypothesis (IDH)	CAU Kiel

Erklärung

Hiermit versichere ich, dass diese Abhandlung – abgesehen von der Beratung durch meinen akademischen Lehrer – nach Inhalt und Form meine eigene Arbeit ist und dass ich keine als die angegebenen Quellen und Hilfsmittel verwandt habe. Die Arbeit hat bisher weder ganz noch zum Teil an anderer Stelle im Rahmen eines Prüfungsverfahrens vorgelegen. Teile dieser Arbeit wurden, mit Markus Molis und Martin Wahl als Koautoren, als Manuskripte bei Zeitschriften eingereicht. Die Ergebnisse aus Kapitel 4.5, einschließlich zugehöriger Methodik und Diskussion, wurden beim Journal of Experimental Marine Biology and Ecology eingereicht, die in Kapitel 4.6 dargestellten Daten, mit Methodik und Diskussion, bei den Marine Ecological Progress Series.

Kiel, den 17.03.2003 Mark Lenz

Appendix II: raw data

Emersion 1999

3 mo old communities start values (data are percent cover values)

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6	replicate 7	replicate 8
Enteromorpha sp.	0,33	0,00	0,00	2,33	1,00	0,00	1,00	5,00
Melosira sp.	0,33	0,00	1,67	18,33	18,33	0,33	1,00	10,00
C. strictum	0,67	2,33	1,00	16,67	3,67	3,67	2,33	6,67
L. flexuosa	0,00	2,33	2,00	0,00	2,33	13,67	0,33	0,33
M. edulis	96,67	25,00	100,00	100,00	20,00	80,00	100,00	56,67
B. improvisus	26,67	11,67	20,00	36,67	7,00	13,33	53,33	11,67
P. ciliata	0,00	0,00	0,00	0,00	0,00	0,00	0,33	0,67
C. volutator	0,00	0,00	1,67	0,00	0,00	0,00	1,67	0,00
M. membranacea	3,33	0,00	0,00	0,00	0,00	0,00	0,00	6,67
diatoms	0,00	0,00	0,00	0,00	0,00	0,00	0,00	8,33
chironomids	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	0,00	0,67	0,33	0,67	0,00	0,00
	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
total cover	128,00	41,33	126,33	174,67	52,67	111,67	160,00	106,00
Shannon index	0,69	0,99	0,69	1,19	1,43	0,91	0,86	1,54
species number	5,00	4,00	6,00	5,00	7,00	6,00	8,00	9,00
evenness	0,43	0,71	0,39	0,74	0,74	0,51	0,41	0,70

Emersion 1999 **4th wk**

3 mo old communities in 1999 after 4 wk of experimental duration. 0.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	5,33	0,00	4,00	0,00
Melosira sp.	53,33	11,67	28,33	10,33
C. strictum	3,33	10,00	1,67	1,67
L. flexuosa	3,67	1,67	0,00	8,33
M. edulis	10,33	43,33	70,00	86,67
B. improvisus	10,00	43,33	6,67	10,00
P. ciliata	2,00	5,00	3,33	5,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	20,00	0,00	0,00	0,00
diatoms	23,33	33,33	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	131,33	148,33	114,00	122,00
Shannon index	1,74	1,60	1,09	1,03
species number	9,00	7,00	6,00	6,00
evenness	0,79	0,82	0,61	0,57

3 mo old communities in 1999 after 4 wk of experimental duration. 0.75 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	3,67	0,67	0,67	2,33
Melosira sp.	63,33	80,00	10,33	8,33
C. strictum	0,67	0,67	0,67	0,33
L. flexuosa	2,00	0,00	30,00	0,00
M. edulis	6,67	13,33	63,33	63,33
B. improvisus	3,33	2,33	20,00	26,67
P. ciliata	2,00	2,33	5,33	2,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	2,00	0,00
diatoms other than *Melosira* sp.	0,00	0,00	3,67	2,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	81,67	99,33	136,00	105,33
Shannon index	0,89	0,69	1,51	1,12
species number	7,00	6,00	9,00	7,00
evenness	0,46	0,38	0,69	0,57

3 mo old communities in 1999 after 4 wk of experimental duration. 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	3,67	1,00	1,00	15,00
Melosira sp.	11,67	26,67	70,00	30,00
C. strictum	2,00	0,67	18,33	2,00
L. flexuosa	1,00	13,33	1,00	0,33
M. edulis	90,00	17,00	58,33	86,67
B. improvisus	40,00	20,00	26,67	23,33
P. ciliata	1,00	0,67	3,67	5,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	26,67	0,00	0,00
diatoms	7,33	0,00	0,00	0,33
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	3,33	0,00
total cover	156,67	106,00	182,33	162,67
Sahnnon index	1,21	1,67	1,45	1,33
species number	8,00	8,00	8,00	8,00
evenness	0,58	0,80	0,70	0,64

3 mo old communities in 1999 after 4 wk of experimental duration. 1.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	1,00	1,00	3,67	missing
Melosira sp.	40,00	40,00	26,67	missing
C. strictum	0,67	0,33	0,00	missing
L. flexuosa	13,67	5,33	3,33	missing
M. edulis	61,67	60,00	100,00	missing
B. improvisus	46,67	56,67	30,00	missing
P. ciliata	0,67	2,00	1,00	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	2,00	13,67	0,00	missing
diatoms other than Melosira sp.	6,67	0,00	0,00	missing
chironomids	0,00	0,67	0,00	missing
Nereis sp.	0,00	0,00	0,00	missing
total cover	173,00	179,67	164,67	missing
Shannon index	1,51	1,48	1,10	missing
species number	9,00	9,00	6,00	missing
evenness	0,69	0,67	0,62	missing

3 mo old communities in 1999 after 4 wk of experimental duration. 2 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	1,00	2,33	0,67	0,67
Melosira sp.	11,67	5,33	40,00	60,00
C. strictum	0,00	0,67	1,00	0,33
L. flexuosa	80,00	0,00	8,33	2,00
M. edulis	23,33	13,33	50,00	26,67
B. improvisus	30,00	40,00	30,00	50,00
P. ciliata	0,00	0,00	0,00	5,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	66,67	0,00	46,67	0,00
diatoms other than Melosira sp.	0,00	1,67	1,67	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	212,67	63,33	178,33	144,67
Shannon index	1,43	1,09	1,58	1,26
species number	6,00	6,00	8,00	7,00
evennes	0,80	0,61	0,76	0,65

3 mo old communities in 1999 after 4 wk of experimental duration. 4 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,33	3,33	3,33	0,00
Melosira sp.	0,33	23,33	2,33	0,00
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	20,00	33,33	50,00	80,00
B. improvisus	30,00	33,33	36,67	23,33
P. ciliata	0,00	0,00	0,00	1,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	40,00	0,00	10,00	3,33
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	90,67	93,33	102,33	108,33
Shannon index	1,10	1,20	1,14	0,73
species number	5,00	4,00	5,00	4,00
evenness	0,68	0,87	0,71	0,52

3 mo old communities in 1999 after 4 wk of experimental duration. 6 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	2,33	0,00	0,33	0,00
Melosira sp.	0,33	1,67	3,33	0,00
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	18,33	6,67	20,00	0,00
B. improvisus	56,67	28,00	53,33	6,67
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	77,67	36,33	77,00	6,67
Shannon index	0,70	0,65	0,76	0,00
species number	4,00	3,00	4,00	1,00
evenness	0,50	0,59	0,55	error

3 mo old communities in 1999 after 4 wk of experimental duration. 8 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	1,00	3,33	0,00	0,67
Melosira sp.	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	26,67	1,00	0,00	1,67
B. improvisus	33,33	5,33	20,00	33,33
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	36,67	10,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	97,67	19,67	20,00	35,67
Shannon index	1,14	1,15	0,00	0,28
species number	4,00	4,00	1,00	3,00
evenness	0,82	0,83	error	0,26

3 mo old communities in 1999 after 4 wk of experimental duration. 1 x 15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	8,33	5,33	0,33	23,67
Melosira sp.	28,33	5,33	30,00	20,33
C. strictum	36,67	7,00	5,00	6,67
L. flexuosa	3,33	0,33	0,00	0,33
M. edulis	60,00	93,33	100,00	86,67
B. improvisus	5,00	5,00	5,00	33,33
P. ciliata	11,67	7,00	3,33	3,67
C. volutator	1,67	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,33
diatoms other than Melosira sp.	1,67	3,33	0,00	6,67
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	156,67	126,67	143,67	181,67
Shannon index	1,65	1,05	0,91	1,52
species number	9,00	8,00	6,00	9,00
evenness	0,75	0,51	0,51	0,69

3 mo old communities in 1999 after 4 wk of experimental duration. 2x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	2,33	0,00	7,00	3,67
Melosira sp.	53,33	8,33	1,00	11,67
C. strictum	11,67	0,67	17,00	0,33
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	70,00	90,00	100,00	100,00
B. improvisus	20,00	8,33	30,00	10,00
P. ciliata	10,00	5,00	7,00	6,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	13,33	0,00	0,00	0,00
diatoms other than Melosira sp.	6,67	0,00	3,33	1,67
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	187,33	112,33	165,33	134,00
Shannon index	1,66	0,73	1,23	0,94
species number	8,00	5,00	7,00	7,00
evenness	0,80	0,46	0,63	0,48

3 mo old communities in 1999 after 4 wk of experimental duration. 3x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	6,67	11,67	2,33	3,67
Melosira sp.	15,00	8,33	2,00	13,33
C. strictum	1,67	13,67	0,00	15,00
L. flexuosa	1,67	3,67	1,67	1,67
M. edulis	96,67	83,33	96,67	23,33
B. improvisus	3,33	16,67	3,33	16,67
P. ciliata	10,00	5,33	6,67	8,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	31,67
diatoms other than Melosira sp.	30,00	20,00	16,67	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Vorticella sp.	0,00	3,33	0,00	0,00
total cover	165,00	166,00	129,33	113,67
Shannon index	1,31	1,65	0,92	1,85
species number	8,00	9,00	7,00	8,00
evenness	0,63	0,75	0,47	0,89

3 mo old communities in 1999 after 4 wk of experimental duration. 4x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	3,33	3,33
Melosira sp.	18,33	16,67	30,00	26,67
C. strictum	10,00	0,00	0,00	26,67
L. flexuosa	0,33	0,00	0,00	0,33
M. edulis	96,67	100,00	69,67	76,67
B. improvisus	3,33	0,00	0,00	10,00
P. ciliata	10,00	0,00	3,67	8,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	6,67
diatoms other than Melosira sp.	3,33	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	142,00	116,67	106,67	158,67
Shannon index	1,09	0,41	0,86	1,51
species number	7,00	2,00	4,00	8,00
evenness	0,56	0,59	0,62	0,72

3 mo old communities in 1999 after 4 wk of experimental duration. 6x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	18,33	2,33	13,33	1,00
Melosira sp.	16,67	40,00	10,33	33,33
C. strictum	50,00	2,00	11,67	0,33
L. flexuosa	30,00	13,33	2,00	5,00
M. edulis	76,67	26,67	50,00	43,33
B. improvisus	63,33	11,67	56,67	23,33
P. ciliata	2,33	5,33	5,33	2,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	5,00	1,67	0,00	0,00
chironomids	0,00	0,00	0,00	0,33
Nereis sp.	0,00	0,00	0,00	0,00
total cover	262,33	103,00	149,33	109,00
Shannon index	1,75	1,61	1,51	1,36
species number	8,00	8,00	7,00	8,00
evenness	0,84	0,77	0,78	0,65

3 mo old communities in 1999 after 4 wk of experimental duration. 8x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	10,00	0,33	3,67	13,33
Melosira sp.	6,67	10,00	50,00	0,00
C. strictum	5,00	0,00	3,33	1,67
L. flexuosa	18,33	11,67	1,67	0,00
M. edulis	33,33	96,67	60,00	43,33
B. improvisus	25,00	3,33	26,67	50,00
P. ciliata	10,00	0,00	8,33	8,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	3,33	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	108,33	122,00	157,00	116,67
Shannon index	1,76	0,73	1,49	1,23
species number	7,00	5,00	8,00	5,00
evenness	0,90	0,45	0,72	0,76

3 mo old communities in 1999 after 4 wk of experimental duration. 16x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	13,33	33,33	1,67	6,67
Melosira sp.	16,67	10,00	18,33	2,00
C. strictum	1,00	3,33	5,00	1,67
L. flexuosa	3,33	1,67	17,00	3,33
M. edulis	83,33	73,33	60,00	86,67
B. improvisus	16,67	16,67	23,33	6,67
P. ciliata	0,00	0,33	1,67	5,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	1,67	0,00	3,33	0,00
diatoms other than Melosira sp.	0,00	10,00	20,00	0,00
chironomids	0,00	0,00	0,00	0,33
Nereis sp.	0,00	0,00	0,00	0,00
total cover	136,00	148,67	150,33	112,33
Shannon index	1,22	1,44	1,72	0,93
species number	7,00	8,00	9,00	8,00
evenness	0,63	0,69	0,78	0,45

3 mo old communities in 1999 after 4 wk of experimental duration. 32x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	10,00	40,00	20,00	23,33
Melosira sp.	13,33	5,33	10,00	6,67
C. strictum	6,67	11,67	6,67	8,33
L. flexuosa	1,67	0,33	8,33	0,00
M. edulis	50,00	46,67	40,00	76,67
B. improvisus	36,67	10,00	30,00	18,33
P. ciliata	1,67	0,00	0,33	0,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	1,67	23,33	10,00	0,00
diatoms other than Melosira sp.	0,00	13,33	0,00	33,33
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	121,67	150,67	125,33	167,00
Shannon index	1,51	1,73	1,76	1,49
species number	8,00	8,00	8,00	7,00
evenness	0,73	0,83	0,84	0,76

3 mo old communities in 1999 after 4 wk of experimental duration. controls

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	missing
Melosira sp.	0,33	1,67	0,00	missing
C. strictum	6,67	5,00	3,67	missing
L. flexuosa	0,00	0,33	0,00	missing
M. edulis	100,00	90,00	100,00	missing
B. improvisus	0,00	10,00	0,00	missing
P. ciliata	0,00	0,33	0,00	missing
C. volutator	0,00	0,00	0,00	missing
M membranacea	0,00	0,00	0,00	missing
diatoms	0,00	0,00	0,00	missing
chironomids	0,00	0,00	0,00	missing
Nereis sp.	0,00	0,00	0,00	missing
total cover	107,00	107,33	103,67	missing
Shannon index	0,25	0,61	0,15	missing
species number	3,00	6,00	2,00	missing
evenness	0,23	0,34	0,22	missing

Emersion 1999 **8th wk**

3 mo old communities in 1999 after 8 wk of experimental duration. 1x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	1,00	0,67	0,67	5,00
Melosira sp.	33,33	21,67	23,33	38,33
C. strictum	8,33	2,00	2,33	10,00
L. flexuosa	0,00	0,00	1,67	5,00
M. edulis	93,33	100,00	86,67	63,33
B. improvisus	11,67	0,00	18,33	26,67
P. ciliata	5,33	0,67	2,33	15,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	11,67	13,67
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	153,00	125,00	147,33	177,33
Shannon index	1,14	0,60	1,28	1,76
species number	6,00	5,00	9,00	8,00
evenness	0,64	0,38	0,58	0,84

3 mo old communities in 1999 after 8 wk of experimental duration. 2x15 min

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	2,33	8,33	8,33
Melosira sp.	23,33	11,67	66,67	15,00
C. strictum	6,67	8,33	3,67	4,00
L. flexuosa	0,00	0,00	16,67	1,67
M. edulis	96,67	43,33	73,33	96,67
B. improvisus	3,33	73,33	10,00	10,00
P. ciliata	8,33	2,33	6,67	2,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,33	0,00	0,00
diatoms other than Melosira sp.	23,33	0,00	0,00	2,33
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	0,00	0,00
total cover	161,67	141,67	185,33	140,33
Shannon index	1,23	1,22	1,45	1,14
species number	6,00	7,00	7,00	8,00
evenness	0,69	0,63	0,74	0,55

3 mo old communities in 1999 after 8 wk of experimental duration. 3x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	5,00	2,33	16,67	3,67
Melosira sp.	35,00	21,67	10,00	11,67
C. strictum	3,67	2,33	1,00	0,33
L. flexuosa	0,00	10,00	1,00	3,67
M. edulis	80,00	56,67	60,00	10,00
B. improvisus	26,67	60,00	70,00	56,67
P. ciliata	6,67	3,67	3,67	1,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	15,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	172,00	156,67	162,33	87,00
Shannon index	1,49	1,40	1,28	1,14
species number	7,00	7,00	7,00	7,00
evenness	0,77	0,72	0,66	0,58

3 mo old communities in 1999 after 8 wk of experimental duration. 4x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	3,67	missing
Melosira sp.	8,33	26,67	43,33	missing
C. strictum	0,00	0,00	3,33	missing
L. flexuosa	0,00	0,00	1,67	missing
M. edulis	96,67	100,00	76,67	missing
B. improvisus	0,00	0,00	20,00	missing
P. ciliata	8,33	10,00	10,00	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	missing
diatoms other than Melosira sp.	3,33	0,00	0,00	missing
chironomids	0,00	0,00	0,00	missing
Nereis sp.	0,00	0,00	0,00	missing
total cover	116,67	136,67	158,67	missing
Shannon index	0,63	0,74	1,36	missing
species number	4,00	3,00	7,00	missing
evenness	0,46	0,67	0,70	missing

3 mo old communities in 1999 after 8 wk of experimental duration. 6x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	8,33	2,33	2,33	10,00
Melosira sp.	18,67	10,00	35,00	16,67
C. strictum	8,33	4,00	4,00	5,00
L. flexuosa	16,67	13,33	15,00	23,33
M. edulis	60,00	93,33	96,67	86,67
B. improvisus	36,67	40,00	16,67	40,00
P. ciliata	3,67	3,67	2,33	5,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	13,33	0,00	3,33	5,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	165,67	166,67	175,33	192,00
Shannon index	1,77	1,27	1,36	1,60
species number	8,00	7,00	8,00	8,00
evenness	0,85	0,65	0,65	0,77

3 mo old communities in 1999 after 8 wk of experimental duration. 8x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,33	2,00	0,00	0,00
Melosira sp.	40,00	50,00	3,67	36,67
C. strictum	0,33	0,00	0,00	0,00
L. flexuosa	3,33	1,67	0,00	0,00
M. edulis	83,33	83,33	90,00	100,00
B. improvisus	10,00	20,00	3,33	0,00
P. ciliata	3,67	6,67	5,00	2,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	141,00	163,67	102,00	139,00
Shannon index	1,07	1,19	0,49	0,66
species number	7,00	6,00	4,00	3,00
evenness	0,55	0,67	0,35	0,60

3 mo old communities in 1999 after 8 wk of experimental duration. 16x15 min

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,33	3,33	0,33
Melosira sp.	20,00	11,67	10,00	11,67
C. strictum	1,67	0,00	0,00	3,33
L. flexuosa	0,33	10,33	0,00	6,67
M. edulis	100,00	73,33	90,00	76,67
B. improvisus	0,00	20,00	13,33	13,33
P. ciliata	13,33	1,67	5,00	11,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	6,67	0,00	0,00
diatoms other than Melosira sp.	6,67	0,00	3,33	36,67
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
green algae	10,00	0,00	0,00	20,00
C. multicornis	0,00	5,00	0,00	0,00
total cover	152,00	129,00	125,00	180,33
Shannon index	1,13	1,38	1,00	1,69
species number	7,00	8,00	6,00	9,00
evenness	0,58	0,66	0,56	0,77

3 mo old communities in 1999 after 8 wk of experimental duration. 32x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	13,33	20,00	8,33	11,67
Melosira sp.	2,33	13,33	2,33	11,67
C. strictum	10,33	0,67	0,33	13,33
L. flexuosa	0,00	4,00	0,00	0,33
M. edulis	100,00	70,00	83,33	70,00
B. improvisus	23,33	53,33	43,33	26,67
P. ciliata	1,00	1,00	2,33	2,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	5,00	1,67	21,67
diatoms other than Melosira sp.	3,33	0,00	0,00	10,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	0,00	2,00
total cover	153,67	167,33	141,67	169,67
Shannon index	1,14	1,43	1,04	1,78
species number	7,00	8,00	7,00	10,00
evenness	0,59	0,69	0,54	0,77

3 mo old communities in 1999 after 8 wk of experimental duration. 0.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	3,67	6,67	0,00	0,00
Melosira sp.	26,67	63,33	36,67	10,67
C. strictum	0,00	8,33	0,00	0,00
L. flexuosa	13,33	1,67	0,00	2,00
M. edulis	83,33	50,00	100,00	86,67
B. improvisus	16,67	0,00	0,00	15,00
P. ciliata	6,67	6,67	5,33	10,00
C. volutator	0,00	0,00	1,67	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	11,67	0,00	1,67	6,67
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	162,00	136,67	145,33	131,00
Shannon index	1,48	1,24	0,83	1,14
species number	7,00	6,00	5,00	6,00
evenness	0,76	0,69	0,51	0,63

3 mo old communities in 1999 after 8 wk of experimental duration. 0.75 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Melosira sp.	20,00	40,00	96,67	43,33
C. strictum	0,00	0,00	0,33	0,33
L. flexuosa	0,33	0,00	0,00	5,00
M. edulis	86,67	100,00	35,00	63,33
B. improvisus	16,67	0,00	0,33	16,67
P. ciliata	7,00	0,33	3,33	10,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	13,33
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	130,67	140,33	135,67	152,00
Shannon index	0,99	0,61	0,71	1,48
species number	5,00	3,00	5,00	7,00
evenness	0,62	0,56	0,44	0,76

3 mo old communities in 1999 after 8 wk of experimental duration. 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Melosira sp.	26,67	56,67	43,33	24,00
C. strictum	0,00	3,33	0,33	0,00
L. flexuosa	0,33	0,00	0,00	0,00
M. edulis	80,00	96,67	53,33	96,67
B. improvisus	0,00	0,00	13,33	0,00
P. ciliata	8,33	7,00	10,00	11,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	6,67	0,00	15,00	0,00
diatoms other than Melosira sp.	3,33	6,67	0,33	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	6,67	0,00	0,00
total cover	125,33	177,00	135,67	132,33
Shannon index	1,06	1,14	1,42	0,75
species number	6,00	6,00	7,00	3,00
evenness	0,59	0,64	0,73	0,69

3 mo old communities in 1999 after 8 wk of experimental duration. 1.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	2,00	0,33	0,67	missing
Melosira sp.	86,67	30,00	18,67	missing
C. strictum	0,00	0,00	0,00	missing
L. flexuosa	3,67	1,67	0,00	missing
M. edulis	96,67	100,00	93,33	missing
B. improvisus	13,33	21,67	23,67	missing
P. ciliata	10,00	3,67	5,00	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	missing
diatoms other than Melosira sp.	0,00	0,00	0,00	missing
chironomids	0,00	0,00	0,00	missing
Nereis sp.	0,00	0,00	0,00	missing
total cover	212,33	157,33	141,33	missing
Shannon index	1,16	1,03	0,98	missing
species number	6,00	6,00	5,00	missing
evenness	0,65	0,57	0,61	missing

3 mo old communities in 1999 after 8 wk of experimental duration. 2 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	1,67	3,33	13,33	3,67
Melosira sp.	13,33	46,67	36,67	20,33
C. strictum	0,00	0,00	0,00	0,67
L. flexuosa	21,67	0,33	0,00	0,00
M. edulis	50,00	60,00	63,33	30,00
B. improvisus	30,00	13,33	30,00	43,33
P. ciliata	3,33	8,33	8,33	2,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	13,33	13,33	0,00	0,00
diatoms other than Melosira sp.	0,00	1,67	0,00	23,33
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,33	0,00	0,00
total cover	133,33	147,33	151,67	123,33
Shannon index	1,61	1,49	1,40	1,52
species number	7,00	9,00	5,00	7,00
evenness	0,83	0,68	0,87	0,78

3 mo old communities in 1999 after 8 wk of experimental duration. 4 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,33	1,00	6,67	3,67
Melosira sp.	13,67	20,00	40,00	6,67
C. strictum	0,67	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	30,00	90,00	66,67	100,00
B. improvisus	56,67	31,67	46,67	8,33
P. ciliata	2,00	0,00	0,67	0,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	6,67	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
U. grevillei	0,67	0,00	7,00	0,00
Porphyra sp.	1,00	2,00	13,33	0,00
total cover	111,67	144,67	181,00	119,33
Shannon index	1,32	0,99	1,51	0,63
species number	9,00	5,00	7,00	5,00
evenness	0,60	0,62	0,78	0,39

3 mo old communities in 1999 after 8 wk of experimental duration. 6 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	3,33	2,33	0,00	1,00
Melosira sp.	15,00	3,67	2,00	0,33
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	13,33	6,67	0,33	0,33
B. improvisus	63,33	60,00	21,67	63,33
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	15,00	20,00	80,00	23,33
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
U. grevillei	0,67	0,67	10,00	6,67
Porphyra sp.	5,00	6,67	26,67	8,33
total cover	115,67	100,00	140,67	103,33
Shannon index	1,38	1,23	1,19	1,10
species number	7,00	7,00	6,00	7,00
evenness	0,71	0,63	0,66	0,56

3 mo old communities in 1999 after 8 wk of experimental duration. 8 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,33	0,33	0,33
Melosira sp.	17,33	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	23,33	5,00	0,33	0,00
B. improvisus	66,67	56,67	30,00	10,00
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	1,67	0,00	0,00
diatoms other than Melosira sp.	0,00	43,33	70,00	90,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
U. grevillei	7,00	0,67	0,67	0,00
Porphyra sp.	0,67	5,00	0,67	0,00
total cover	115,00	112,67	102,00	100,33
Shannon index	1,13	1,10	0,72	0,35
species number	5,00	7,00	6,00	3,00
evenness	0,70	0,57	0,40	0,32

3 mo old communities in 1999 after 8 wk of experimental duration. controls

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	missing
Melosira sp.	0,00	0,00	0,00	missing
C. strictum	0,67	0,33	6,67	missing
L. flexuosa	0,00	0,00	0,00	missing
M. edulis	100,00	100,00	100,00	missing
B. improvisus	0,00	0,00	0,00	missing
P. ciliata	3,33	3,33	1,67	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	missing
diatoms other than Melosira sp.	0,00	0,00	0,00	missing
chironomids	0,00	0,00	0,00	missing
Nereis sp.	0,00	0,00	0,00	missing
total cover	104,00	103,67	108,33	missing
Shannon index	0,18	0,16	0,31	missing
species number	3,00	3,00	3,00	missing
evenness	0,16	0,15	0,28	missing

3 mo old communities in 1999 after 8 wk of experimental duration. recruitment panels

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,33	0,33
Melosira sp.	60,00	53,33	36,67	53,33
C. strictum	0,33	10,00	3,67	13,33
L. flexuosa	0,00	0,00	0,00	0,33
M. edulis	0,33	0,00	1,67	0,00
B. improvisus	0,00	8,67	0,00	0,00
P. ciliata	0,00	0,00	0,00	0,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	100,00	73,33	96,67	100,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
A. aurita	0,00	10,00	0,33	0,00
total cover	160,67	155,33	139,33	167,67
Shannon index	0,69	1,24	0,78	0,91
species number	4,00	5,00	5,00	6,00
evenness	0,50	0,77	0,49	0,51

Emersion 1999 **12th wk**

3 mo old communities in 1999 after 12 wk of experimental duration. 1x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,33	0,67	0,67	0,00
Melosira sp.	53,33	7,33	30,00	63,33
C. strictum	0,00	3,33	10,00	0,67
L. flexuosa	20,00	8,33	10,33	10,00
M. edulis	1,00	53,33	70,00	31,67
B. improvisus	40,00	40,00	46,67	43,33
P. ciliata	1,00	20,00	18,33	15,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	1,67	0,00
total cover	115,67	133,00	187,67	164,00
Shannon index	1,13	1,46	1,61	1,45
species number	6,00	7,00	8,00	6,00
evenness	0,63	0,75	0,78	0,81

3 mo old communities in 1999 after 12 wk of experimental duration. 2x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	8,67	0,00	0,00	0,33
Melosira sp.	21,67	18,33	33,33	73,33
C. strictum	0	0	0	1,666667
L. flexuosa	1,67	15,00	30,00	10,00
M. edulis	33,33	6,67	13,33	13,33
B. improvisus	43,33	56,67	26,67	26,67
P. ciliata	36,67	16,67	11,67	13,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	3,33	0,00
diatoms other than Melosira sp.	0,00	46,67	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,33	1,67	0,00
Callithamnion sp.	0,00	0,00	0,00	0,00
green algae	0,00	0,33	0,00	0,00
total cover	145,33	160,67	120,00	138,67
Shannon index	**1,55**	**1,59**	**1,67**	**1,36**
species number	6,00	8,00	7,00	7,00
evenness	**0,86**	**0,76**	**0,86**	**0,70**

3 mo old communities in 1999 after 12 wk of experimental duration. 3x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,33	0,00	0,00	7,00
Melosira sp.	73,33	23,33	40,00	26,67
C. strictum	0,33	6,67	1,00	1,00
L. flexuosa	16,67	8,67	3,33	0,67
M. edulis	16,67	63,33	70,00	26,67
B. improvisus	46,67	46,67	46,67	63,33
P. ciliata	13,33	20,00	30,00	16,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	167,33	168,67	191,00	142,00
Shannon index	1,40	1,53	1,43	1,45
species number	7,00	6,00	6,00	7,00
evenness	0,72	0,85	0,80	0,74

3 mo old communities in 1999 after 12 wk of experimental duration. 4x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	missing
Melosira sp.	33,33	11,67	8,67	missing
C. strictum	0,00	0,00	0,00	missing
L. flexuosa	1,67	80,00	6,67	missing
M. edulis	8,33	1,67	11,67	missing
B. improvisus	43,33	15,00	33,33	missing
P. ciliata	8,33	0,00	8,33	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	missing
diatoms other than Melosira sp.	0,00	0,00	0,00	missing
chironomids	0,00	0,00	0,00	missing
Nereis sp.	0,00	0,00	0,00	missing
total cover	95,00	108,33	68,67	missing
Shannon index	1,22	0,80	1,40	missing
species number	5,00	4,00	5,00	missing
evenness	0,76	0,58	0,87	missing

3 mo old communities in 1999 after 12 wk of experimental duration. 6x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	2,00	1,00	0,33
Melosira sp.	3,67	10,00	8,67	8,67
C. strictum	0,67	0,67	1,00	1,00
L. flexuosa	53,33	15,00	38,33	38,33
M. edulis	33,33	36,67	6,67	6,67
B. improvisus	86,67	50,00	43,33	43,33
P. ciliata	6,67	36,67	11,67	11,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,00	2,33	0,33
total cover	184,33	151,00	113,00	110,33
Shannon index	1,24	1,54	1,50	1,42
species number	6,00	7,00	8,00	8,00
evenness	0,69	0,79	0,72	0,68

3 mo old communities in 1999 after 12 wk of experimental duration. 8x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Melosira sp.	16,67	23,33	26,67	11,67
C. strictum	0,00	0,00	0,33	0,00
L. flexuosa	11,67	10,33	12,00	6,67
M. edulis	8,33	3,33	23,33	53,33
B. improvisus	53,33	40,00	50,00	43,33
P. ciliata	10,00	5,00	11,67	23,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	3,33
total cover	100,00	82,00	124,00	141,67
Shannon index	1,32	1,27	1,48	1,46
species number	5,00	5,00	6,00	6,00
evenness	0,82	0,79	0,82	0,82

3 mo old communities in 1999 after 12 wk of experimental duration. 16x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	2,33
Melosira sp.	20,33	16,67	2,33	1,00
C. strictum	0,00	0,00	0,33	2,00
L. flexuosa	7,00	33,33	3,67	1,67
M. edulis	13,33	10,00	51,67	40,00
B. improvisus	43,33	26,67	26,67	43,33
P. ciliata	6,67	20,00	16,67	30,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	1,67	0,00	0,00	0,00
diatoms other than Melosira sp.	3,33	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	95,67	106,67	101,33	120,33
Shannon index	1,53	1,54	1,22	1,32
species number	7,00	5,00	6,00	7,00
evenness	0,78	0,95	0,68	0,68

3 mo old communities in 1999 after 12 wk of experimental duration. 32x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	1,00	2,33	3,67	missing
Melosira sp.	11,67	13,33	8,33	missing
C. strictum	0,67	5,33	10,00	missing
L. flexuosa	0,00	0,00	0,00	missing
M. edulis	70,00	50,00	83,33	missing
B. improvisus	73,33	30,00	30,00	missing
P. ciliata	11,67	8,33	5,33	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	5,00	0,00	missing
diatoms other than Melosira sp.	0,00	16,67	0,00	missing
chironomids	0,00	0,00	0,00	missing
Nereis sp.	1,67	0,00	0,00	missing
Callithamnion sp.	0,00	0,33	0,00	missing
Porphyra sp.	1,00	0,00	1,00	missing
total cover	171,00	131,33	141,67	missing
Shannon index	1,22	1,72	1,25	missing
species number	8,00	9,00	7,00	missing
evenness	0,59	0,78	0,64	missing

3 mo old communities in 1999 after 12 wk of experimental duration. 0.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,33	1,67
Melosira sp.	5,00	15,00	28,33	10,00
C. strictum	2,00	0,67	0,00	0,33
L. flexuosa	20,00	6,67	10,00	11,67
M. edulis	10,67	23,33	0,00	26,67
B. improvisus	38,33	30,00	10,00	53,33
P. ciliata	15,00	10,00	8,33	10,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	3,33	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	36,67	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
total cover	91,00	89,00	93,67	113,67
Shannon index	1,49	1,62	1,44	1,44
species number	6,00	7,00	6,00	7,00
evenness	0,83	0,83	0,80	0,74

3 mo old communities in 1999 after 12 wk of experimental duration. 0.75 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Melosira sp.	13,33	63,33	73,33	40,00
C. strictum	0,00	0,00	0,33	0,00
L. flexuosa	33,33	0,00	5,00	53,33
M. edulis	2,33	40,67	6,67	8,33
B. improvisus	56,67	0,00	2,00	10,67
P. ciliata	13,33	16,67	8,33	3,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,67	0,00	0,00
Fucus sp.	0,00	0,00	0,33	0,00
total cover	119,00	121,33	96,00	116,00
Shannon index	1,28	1,01	0,88	1,24
species number	5,00	4,00	7,00	5,00
evenness	0,79	0,73	0,45	0,77

3 mo old communities in 1999 after 12 wk of experimental duration. 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,33
Melosira sp.	33,33	30,00	26,67	56,67
C. strictum	0,00	0,00	0,33	0,00
L. flexuosa	53,33	10,00	46,67	0,00
M. edulis	7,00	33,33	13,33	30,00
B. improvisus	40,00	23,33	20,00	30,00
P. ciliata	2,33	40,00	26,67	13,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	10,00	0,00	3,33
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	0,00	0,00
total cover	136,00	146,67	133,67	133,67
Shannon index	1,29	1,67	1,54	1,37
species number	5,00	6,00	6,00	6,00
evenness	0,80	0,93	0,86	0,77

3 mo old communities in 1999 after 12 wk of experimental duration. 1.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,33	0,33	1,00	missing
Melosira sp.	30,00	13,33	40,00	missing
C. strictum	0,00	0,33	0,00	missing
L. flexuosa	10,00	33,33	26,67	missing
M. edulis	33,33	26,67	23,33	missing
B. improvisus	56,67	66,67	60,00	missing
P. ciliata	13,33	10,00	16,67	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	missing
diatoms other than Melosira sp.	0,00	0,00	0,00	missing
chironomids	0,00	0,00	0,00	missing
Nereis sp.	0,00	0,00	0,00	missing
Porphyra sp.	0,00	0,00	0,33	missing
C. multicornis	0,00	0,00	0,33	missing
total cover	143,67	150,67	168,33	missing
Shannon index	1,45	1,42	1,56	missing
species number	6,00	7,00	8,00	missing
evenness	0,81	0,73	0,75	missing

3 mo old communities in 1999 after 12 wk of experimental duration. 2 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	8,67	0,00	0,00	0,33
Melosira sp.	21,67	18,33	33,33	73,33
C. strictum	0,00	0,00	0,00	1,67
L. flexuosa	1,67	15,00	30,00	10,00
M. edulis	33,33	6,67	13,33	13,33
B. improvisus	43,33	56,67	26,67	26,67
P. ciliata	36,67	16,67	11,67	13,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	3,33	0,00
diatoms other than Melosira sp.	0,00	46,67	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,33	1,67	0,00
Callithamnion sp.	0,00	0,00	0,00	0,00
green algae	0,00	0,33	0,00	0,00
total cover	145,33	160,67	120,00	138,67
Shannon index	1,55	1,59	1,67	1,36
species number	6,00	8,00	7,00	7,00
evenness	0,86	0,76	0,86	0,70

3 mo old communities in 1999 after 12 wk of experimental duration. 4 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,67
Melosira sp.	6,67	0,00	46,67	8,33
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,33	0,00	0,00
M. edulis	13,33	0,67	3,67	10,33
B. improvisus	90,00	73,33	83,33	100,00
P. ciliata	0,00	2,33	2,33	1,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,67
Ulva sp.	0,00	0,00	0,00	0,00
Porphyra sp.	0,67	10,33	2,00	0,00
total cover	110,67	87,00	138,00	121,00
Shannon index	0,62	0,55	0,90	0,65
species number	4,00	5,00	5,00	6,00
evenness	0,45	0,34	0,56	0,36

3 mo old communities in 1999 after 12 wk of experimental duration. 6 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Melosira sp.	1,67	5,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	0,00	0,00	0,00	0,00
B. improvisus	63,33	63,33	40,00	50,00
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	16,67	23,33	60,00	16,67
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	5,00	0,00	0,00
Ulva sp.	3,67	2,50	30,00	0,00
Porphyra sp.	8,33	0,33	0,67	0,00
total cover	93,67	99,50	130,67	66,67
Shannon index	0,99	1,04	1,08	0,56
species number	5,00	6,00	4,00	2,00
evenness	0,61	0,58	0,78	0,81

3 mo old communities in 1999 after 12 wk of experimental duration. 8 h

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,33	0,33
Melosira sp.	0,33	0,00	43,33	0,67
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	0,00	0,33	20,00	0,00
B. improvisus	10,00	60,00	83,33	33,33
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	80,00	21,67	16,67	66,67
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Ulva sp.	2,33	8,33	6,67	13,33
Porphyra sp.	23,33	18,33	1,00	8,33
total cover	116,00	108,67	171,33	122,67
Shannon index	0,89	1,16	1,34	1,15
species number	5,00	5,00	7,00	6,00
evenness	0,55	0,72	0,69	0,64

3 mo old communities in 1999 after 12 wk of experimental duration. controls

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	missing
Melosira sp.	0,00	0,00	0,00	missing
C. strictum	1,67	0,00	3,33	missing
L. flexuosa	0,00	0,00	0,00	missing
M. edulis	100,00	100,00	100,00	missing
B. improvisus	0,00	0,00	0,00	missing
P. ciliata	1,67	3,33	3,33	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	missing
diatoms other than Melosira sp.	0,00	0,00	0,00	missing
chironomids	0,00	0,00	0,00	missing
Nereis sp.	0,00	0,00	0,00	missing
total cover	103,33	103,33	106,67	missing
Shannon index	0,16	0,14	0,28	missing
species number	3,00	2,00	3,00	missing
evenness	0,15	0,21	0,25	missing

3 mo old communities in 1999 after 12 wk of experimental duration. recruitment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,67	3,67	1,00	0,67
Melosira sp.	26,67	5,33	27,00	40,00
C. strictum	0,00	0,33	0,33	0,33
L. flexuosa	0,00	0,00	0,00	1,67
M. edulis	1,00	1,00	0,33	1,00
B. improvisus	6,67	0,33	0,67	1,67
P. ciliata	0,00	0,33	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	100,00	86,67	100,00	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
A. aurita	0,00	0,00	0,00	0,33
	5,00	0,00	5,00	13,33
total cover	140,00	97,67	134,33	59,00
Shannon index	0,88	0,49	0,76	0,98
species number	6,00	7,00	7,00	8,00
evenness	0,49	0,25	0,39	0,47

Emersion **28th wk**

3 mo old communities in 1999 after 7 mo of experimental duration. 1x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,33	0,00	0,00
Melosira sp.	36,67	0,00	6,67	10,00
C. strictum	0,00	2,00	0,00	0,00
L. flexuosa	5,00	10,00	3,33	20,00
M. edulis	0,33	60,00	1,67	16,67
B. improvisus	1,67	30,00	18,33	30,00
P. ciliata	3,67	40,00	2,00	17,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	60,00	15,00	76,67	30,00
Ectocarpus sp.	0,00	0,00	16,67	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Fucus sp.	1,67	0,00	0,00	0,00
C. multicornis	0,33	0,00	0,00	6,67
total cover	109,33	157,33	125,33	130,33
Shannon index	1,11	1,50	1,23	1,84
species number	7,00	6,00	6,00	6,00
evenness	0,57	0,84	0,68	1,03

3 mo old communities in 1999 after 7 mo of experimental duration. 2x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,67	0,00	0,00
Melosira sp.	10,00	10,00	43,33	53,33
C. strictum	2,00	0,00	0,00	0,00
L. flexuosa	53,33	10,00	18,67	36,67
M. edulis	1,67	16,67	6,67	13,33
B. improvisus	30,00	43,33	5,00	1,33
P. ciliata	28,33	21,67	2,33	6,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	41,67	60,00	86,67	50,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	7,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
total cover	167,00	162,33	169,67	161,33
Shannon index	1,59	1,59	1,36	1,44
species number	6,00	6,00	6,00	5,00
evenness	0,89	0,89	0,76	0,90

3 mo old communities in 1999 after 7 mo of experimental duration. 3x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,33	1,67	0,00
Melosira sp.	15,00	50,33	60,00	76,67
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	36,67	13,67	5,00	30,00
M. edulis	36,67	13,33	11,67	6,67
B. improvisus	13,33	16,67	13,33	10,00
P. ciliata	18,33	10,00	10,33	11,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	50,00	40,00	20,00	30,00
chironomids	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,33	0,00	0,00
C. multicornis	0,00	3,33	0,00	0,33
Ectocarpus sp.	1,67	0,33	0,00	1,67
total cover	171,67	148,33	122,00	167,00
Shannon index	1,71	1,71	1,51	1,52
species number	6,00	9,00	6,00	7,00
evenness	0,96	0,78	0,84	0,78

3 mo old communities in 1999 after 7 mo of experimental duration. 4x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	1,67	0,00	missing
Melosira sp.	40,00	5,33	3,33	missing
C. strictum	0,00	0,00	1,67	missing
L. flexuosa	53,33	13,33	10,00	missing
M. edulis	0,00	0,00	16,67	missing
B. improvisus	6,67	0,00	6,67	missing
P. ciliata	5,00	5,33	16,67	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	missing
diatoms other than Melosira sp.	40,00	76,67	76,67	missing
chironomids	0,00	0,00	0,00	missing
Nereis sp.	0,00	0,00	0,00	missing
Ectocarpus sp.	0,00	1,67	3,33	missing
Ulva sp.	0,00	0,00	1,67	missing
total cover	145,00	104,00	136,67	missing
Shannon index	1,34	0,93	1,46	missing
species number	4,00	5,00	8,00	missing
evenness	0,96	0,57	0,70	missing

3 mo old communities in 1999 after 7 mo of experimental duration. 6x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,33	0,00	0,00	0,00
Melosira sp.	10,00	10,00	33,33	10,00
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	10,33	20,00	26,67	20,00
M. edulis	6,67	1,67	13,33	18,33
B. improvisus	23,67	23,33	60,00	40,00
P. ciliata	6,67	3,67	6,67	6,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	80,00	96,67	66,67	60,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Ectocarpus sp.	3,33	0,00	0,00	20,00
C. multicornis	0,00	3,33	0,00	0,00
total cover	141,00	158,67	206,67	175,00
Shannon index	1,39	1,24	1,57	1,72
species number	7,00	6,00	5,00	6,00
evenness	0,72	0,69	0,98	0,96

3 mo old communities in 1999 after 7 mo of experimental duration. 8x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Melosira sp.	17,00	23,33	46,67	10,33
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	13,33	20,00	11,67	26,67
M. edulis	3,33	53,33	46,67	1,67
B. improvisus	0,00	10,00	0,00	23,67
P. ciliata	2,00	30,00	6,67	13,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	86,67	46,67	23,33	73,33
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Ectocarpus sp.	1,67	0,00	0,00	0,00
Fucus sp.	0,00	6,67	0,00	0,00
total cover	124,00	190,00	135,00	149,00
Shannon index	0,98	1,76	1,40	1,40
species number	5,00	6,00	4,00	5,00
evenness	0,61	0,98	1,01	0,87

3 mo old communities in 1999 after 7 mo of experimental duration. 16x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	1,67	0,00	3,33
Melosira sp.	20,00	5,33	16,67	6,67
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	2,00	5,00	6,67	1,67
M. edulis	1,67	3,33	0,00	0,00
B. improvisus	0,00	23,33	1,67	15,00
P. ciliata	10,00	11,67	10,00	8,33
C. volutator	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	1,67
diatoms other than Melosira sp.	90,00	90,00	100,00	100,00
Ulva sp.	3,33	0,00	0,00	3,33
Porphyra sp.	1,67	0,00	0,00	0,33
Ectocarpus sp.	10,00	0,00	7,00	3,33
C. multicornis	0,00	11,67	0,00	0,00
total cover	138,67	152,00	142,00	143,67
Shannon index	1,20	1,36	1,03	1,18
species number	7,00	7,00	5,00	9,00
evenness	0,61	0,70	0,64	0,53

3 mo old communities in 1999 after 7 mo of experimental duration. 32x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	1,67	0,33	3,67	1,67
Melosira sp.	66,67	20,00	70,00	43,33
C. strictum	0,00	0,33	1,67	1,67
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	10,33	51,67	11,67	26,67
B. improvisus	76,67	40,00	27,00	56,67
P. ciliata	3,67	13,33	4,00	3,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	40,00	53,33	33,33	25,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	0,00	0,00
Ectocarpus sp.	0,00	3,33	0,00	0,00
total cover	199,00	182,33	151,33	158,67
Shannon index	1,32	1,58	1,43	1,50
species number	5,00	7,00	6,00	6,00
evenness	0,82	0,81	0,80	0,83

3 mo old communities in 1999 after 7 mo of experimental duration. 0.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,33	0,00	0,00	0,00
Melosira sp.	8,33	56,67	10,33	16,67
C. strictum	2,00	3,67	0,00	0,00
L. flexuosa	1,67	8,33	6,67	6,67
M. edulis	23,33	8,33	23,33	10,00
B. improvisus	10,00	5,00	10,00	6,67
P. ciliata	6,67	7,00	13,33	8,33
C. volutator	0,00	0,33	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	86,67	36,67	90,00	86,67
chironomids	0,00	0,00	0,00	0,00
Ectocarpus sp.	23,33	6,67	6,67	10,00
Gammarus sp.	0,33	0,00	0,00	0,00
P. litoralis	0,00	1,67	0,00	0,00
total cover	162,67	134,33	160,33	145,00
Shannon index	1,47	1,66	1,43	1,37
species number	9,00	9,00	6,00	6,00
evenness	0,67	0,75	0,80	0,77

3 mo old communities in 1999 after 7 mo of experimental duration. 0.75 h treatment

Arten	Replikat 1	Replikat 2	Replikat 3	Replikat 4
Enteromorpha sp.	0,00	0,00	0,33	0,00
Melosira sp.	56,67	13,33	0,00	80,00
C. strictum	0,00	1,67	1,67	0,00
L. flexuosa	16,67	41,67	10,33	20,00
M. edulis	10,00	0,00	0,00	0,00
B. improvisus	36,67	26,67	3,33	66,67
P. ciliata	3,33	0,00	0,33	6,67
C. volutator	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,33	0,00
diatoms other than Melosira sp.	63,33	56,67	83,33	76,67
P. litoralis	0,00	0,00	20,00	0,00
Fucus sp.	0,00	0,00	0,33	0,00
Ectocarpus sp.	1,67	6,67	16,67	8,33
C. multicornis	0,00	30,00	0,00	1,67
total cover	188,33	176,67	136,67	260,00
Shannon index	1,53	1,65	1,24	1,51
species number	6,00	6,00	9,00	6,00
evenness	0,85	0,92	0,56	0,84

3 mo old communities in 1999 after 7 mo of experimental duration. 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,33
Melosira sp.	43,33	13,33	53,33	50,00
C. strictum	1,67	0,00	0,00	0,00
L. flexuosa	20,00	61,67	10,00	1,67
M. edulis	1,67	8,33	1,67	20,00
B. improvisus	33,33	23,33	56,67	36,67
P. ciliata	10,00	16,67	5,00	8,33
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	5,00	0,00	1,67
diatoms other than Melosira sp.	26,67	26,67	50,00	50,00
chironomids	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,33	6,67
Ectocarpus sp.	2,00	5,00	7,00	1,67
Ulva sp.	0,33	0,00	0,00	0,33
total cover	139,00	160,00	184,00	177,33
Shannon index	1,67	1,76	1,51	1,71
species number	8,00	7,00	7,00	10,00
evenness	0,80	0,90	0,78	0,74

3 mo old communities in 1999 after 7 mo of experimental duration. 1.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	1,67	0,00	missing
Melosira sp.	53,33	43,33	46,67	missing
C. strictum	0,00	0,00	0,00	missing
L. flexuosa	27,00	6,67	33,33	missing
M. edulis	16,67	0,00	1,67	missing
B. improvisus	60,00	16,67	43,33	missing
P. ciliata	5,33	7,00	4,00	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	missing
diatoms other than Melosira sp.	30,00	53,33	33,33	missing
chironomids	0,00	0,00	0,00	missing
Ulva sp.	0,00	0,00	0,33	missing
Ectocarpus sp.	0,00	3,33	20,00	missing
C. multicornis	0,00	0,00	6,67	missing
total cover	192,33	132,00	189,33	missing
Shannon index	1,60	1,45	1,78	missing
species number	5,00	6,00	8,00	missing
evenness	0,99	0,81	0,86	missing

3 mo old communities in 1999 after 7 mo of experimental duration. 2 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,33	0,67	0,00	0,00
Melosira sp.	73,33	16,67	36,67	6,67
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	30,00	0,00	1,67	23,33
M. edulis	0,00	16,67	0,00	0,00
B. improvisus	50,00	36,67	80,00	53,33
P. ciliata	2,00	3,67	3,33	0,67
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	3,33	0,00	0,00	5,00
diatoms other than Melosira sp.	26,67	83,33	73,33	56,67
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	0,00	0,00
Ulva sp.	1,67	0,00	2,33	0,50
total cover	187,33	157,67	197,33	146,17
Shannon index	1,46	1,26	1,21	1,33
species number	7,00	5,00	5,00	5,00
evenness	0,75	0,78	0,75	0,83

3 mo old communities in 1999 after 7 mo of experimental duration. 4 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,33
Melosira sp.	46,67	50,00	3,67	10,33
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	3,33	0,33	1,67	0,00
M. edulis	0,00	6,67	10,00	1,67
B. improvisus	3,33	3,33	0,00	0,00
P. ciliata	7,00	5,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	66,67	46,67	96,67	93,33
chironomids	0,00	0,00	0,00	0,00
Ectocarpus sp.	0,00	3,33	6,67	3,33
Ulva sp.	0,00	3,33	0,00	1,67
Porphyra sp.	0,00	0,00	0,00	0,00
total cover	127,00	118,67	118,67	110,67
Shannon index	1,06	1,34	0,70	0,61
species number	4,00	7,00	4,00	5,00
evenness	0,76	0,69	0,51	0,38

3 mo old communities in 1999 after 7 mo of experimental duration. 6 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Melosira sp.	70,00	66,67	53,33	90,00
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	0,00	0,00	0,00	0,00
B. improvisus	6,67	0,00	0,00	0,00
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	18,33	40,00	70,00	23,33
chironomids	0,00	0,00	0,00	0,00
Fucus sp.	0,67	0,00	0,00	0,00
Ulva sp.	0,00	7,00	2,33	0,00
Porphyra sp.	0,00	0,00	0,00	0,00
total cover	95,67	113,67	125,67	113,33
Shannon index	0,77	0,85	0,76	0,51
species number	3,00	2,00	2,00	1,00
evenness	0,70	1,23	1,10	error

3 mo old communities in 1999 after 7 mo of experimental duration. 8 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Melosira sp.	93,33	46,67	56,67	70,00
C. strictum	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
M. edulis	0,00	18,33	0,00	0,00
B. improvisus	10,00	70,00	21,67	60,00
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	6,67	100,00	36,67	0,00
chironomids	0,00	0,00	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00
Ulva sp.	4,00	6,67	0,00	1,67
Porphyra sp.	0,00	0,00	0,00	0,00
total cover	114,00	241,67	115,00	131,67
Shannon index	0,66	1,34	1,03	0,75
species number	3,00	4,00	2,00	3,00
evenness	0,60	0,96	1,48	0,68

3 mo old communities in 1999 after 7 mo of experimental duration. controls

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	missing
Melosira sp.	6,67	0,00	0,00	missing
C. strictum	5,00	0,00	0,00	missing
L. flexuosa	0,00	0,00	0,00	missing
M. edulis	100,00	100,00	100,00	missing
B. improvisus	1,67	0,00	0,00	missing
P. ciliata	0,00	0,00	0,00	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	missing
diatoms other than Melosira sp.	0,00	0,00	0,00	missing
chironomids	0,00	0,00	0,00	missing
Nereis sp.	0,00	0,00	0,00	missing
total cover	113,33	100,00	100,00	missing
Shannon index	0,48	0,00	0,00	missing
species number	4,00	1,00	1,00	missing
evenness	0,34	error	error	missing

3 mo old communities in 1999 after 7 mo of experimental duration. recruitment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	missing
Melosira sp.	1,67	36,67	10,00	missing
C. strictum	0,33	0,00	0,00	missing
L. flexuosa	11,67	6,67	0,00	missing
M. edulis	0,00	0,00	0,00	missing
B. improvisus	0,00	0,00	0,00	missing
P. ciliata	0,00	0,00	0,00	missing
C. volutator	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	missing
diatoms other than Melosira sp.	0,00	0,00	0,00	missing
chironomids	0,00	0,00	0,00	missing
Ectocarpus sp.	13,33	3,33	20,00	missing
P. litoralis	13,33	30,00	16,67	missing
Fucus sp.	0,00	0,33	0,00	missing
total cover	40,33	77,00	46,67	missing
Shannon index	1,26	1,09	1,06	missing
species number	5,00	5,00	3,00	missing
evenness	0,78	0,68	0,97	missing

Emersion 2000 **3 mo old communities**

start communities (unlabelled data are percent cover values)

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6	replicate 7	replicate 8
Enteromorpha sp.	0,00	0,00	0,33	0,00	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	0,00	0,33	0,33	0,00	0,00	0,00	0,33
P. elongata	10,00	0,00	0,00	0,00	20,00	0,00	0,00	0,33
C. strictum	10,00	20,00	0,00	3,33	0,00	3,33	1,67	3,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	86,67	93,33	60,00	80,00	96,67	86,67	93,33	90,00
B. improvisus	23,33	10,00	10,00	22,00	20,00	33,33	3,33	6,67
P. ciliata	5,00	3,33	6,67	1,67	3,67	2,00	0,33	6,67
C. volutator	0,00	0,00	1,67	0,00	1,67	0,00	0,00	0,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	3,33	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	36,67	3,33	1,67	0,00	5,00	15,00
total cover	135,00	126,67	115,67	110,67	147,00	125,33	103,67	122,67
Shannon index	0,90	0,81	0,79	0,72	0,78	0,77	0,29	0,66
species number	5,00	4,00	7,00	6,00	7,00	4,00	5,00	8,00
evenness	0,56	0,59	0,41	0,40	0,40	0,56	0,18	0,32

Emersion 2000 **6th wk**

3 mo old communities in 2000 after 6 wk of experimental duration. 1x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	13,33	0,00	0,00	0,33	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	6,67	6,67	3,67	0,67	11,67	15,00
P. elongata	0,33	3,33	0,00	0,00	20,00	10,00
C. strictum	5,00	0,00	0,00	2,00	5,00	3,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	80,00	100,00	100,00	90,00	63,33	83,33
B. improvisus	16,67	0,00	1,67	10,00	46,67	10,33
P. ciliata	16,67	23,33	27,00	18,67	30,00	46,67
C. volutator	0,00	0,00	0,00	0,33	0,33	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	20,00	0,00	3,33	10,00	3,33	0,00
Achnanthes sp.	0,00	0,00	3,33	0,00	3,33	8,33
A. aurita	0,00	0,00	0,00	3,33	0,00	0,00
total cover	158,67	133,33	139,00	135,33	183,67	177,33
Shannon index	1,14	0,52	0,61	0,83	1,12	0,95
species number	8,00	4,00	6,00	9,00	9,00	7,00
evenness	0,55	0,38	0,34	0,38	0,51	0,49

3 mo old communities in 2000 after 6 wk of experimental duration. 4x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	3,33	1,67	0,00	0,00	0,00	1,67
Ulva sp.	0,00	0,00	0,00	0,00	3,33	0,00
Melosira sp.	8,33	36,67	11,67	8,33	26,67	36,67
P. elongata	0,00	0,00	0,00	10,00	0,00	0,00
C. strictum	2,00	5,00	0,00	0,33	16,67	0,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	3,33	1,67	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	1,67
M. edulis	80,00	56,67	100,00	93,33	100,00	33,33
B. improvisus	23,33	36,67	0,00	16,67	1,67	46,67
P. ciliata	30,00	43,33	33,33	56,67	56,67	33,33
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	23,33	3,33	1,67	23,33	13,33	13,33
Achnanthes sp.	3,33	1,67	0,00	6,67	0,00	0,00
total cover	173,67	188,33	148,33	215,33	218,33	167,00
Shannon index	1,06	1,23	0,65	0,92	1,01	1,10
species number	8,00	9,00	5,00	8,00	7,00	8,00
evenness	0,51	0,56	0,40	0,44	0,52	0,53

3 mo old communities in 2000 after 6 wk of experimental duration. 8x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	1,67	0,33	0,33	1,67	8,33	3,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	8,33	3,33	11,67	13,33	30,00	33,33
P. elongata	0,00	0,00	0,00	0,00	13,33	1,67
C. strictum	6,67	10,00	3,33	5,00	23,33	2,33
Porphyra sp.	0,00	1,67	0,00	0,00	0,00	0,33
P. litoralis	0,00	0,00	0,00	0,00	1,67	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,33	0,00	0,00	0,00
M. edulis	100,00	90,00	86,67	100,00	18,33	66,67
B. improvisus	5,00	10,00	36,67	6,67	46,67	20,00
P. ciliata	56,67	60,00	43,33	66,67	30,00	53,33
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,33
diatoms other than Melosira sp. or A	10,00	0,00	6,67	0,00	0,00	0,00
unidentified green alga	0,00	0,00	30,00	0,00	0,00	20,00
Achnanthes sp.	5,00	1,67	0,00	0,00	6,67	16,67
total cover	193,33	177,00	219,00	193,33	178,33	218,33
Shannon index	0,95	1,09	1,07	0,96	1,34	1,05
species number	8,00	8,00	8,00	6,00	9,00	11,00
evenness	0,46	0,52	0,51	0,54	0,61	0,44

3 mo old communities in 2000 after 6 wk of experimental duration. 24x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha	0,00	6,67	0,00	13,33	1,67	0,00
Ulvopsis	0,00	0,00	0,00	0,00	0,00	0,00
Melosira	5,33	8,33	0,33	5,00	20,00	26,67
Polysiphonia	0,00	0,00	6,67	2,00	0,00	0,00
Ceramium	0,33	1,67	0,00	3,33	0,00	0,33
Porphyra	0,00	1,67	0,33	0,00	3,33	0,00
Pilayella	3,33	0,00	0,00	3,33	0,00	1,67
Laomedea	0,00	0,00	0,00	0,00	0,00	0,00
Clava	0,00	0,00	0,00	0,00	0,00	0,00
Mytilus	100,00	76,67	100,00	76,67	23,33	0,33
Balanus	8,33	30,00	3,67	10,00	46,67	15,00
Polydora	30,00	40,00	10,00	43,33	33,33	5,00
Corophium	0,00	0,00	0,00	0,00	0,00	0,00
Chaetomorpha	0,00	0,00	0,00	0,00	6,67	0,00
Bryozoa	0,00	0,00	0,00	0,00	0,00	0,00
Fucus	0,00	0,00	0,00	0,00	0,00	0,00
Diaotmeenrasen	6,67	26,67	26,67	73,33	73,33	93,33
GA-Rasen	0,00	6,67	6,67	3,33	0,00	0,00
Achnanthes	0,00	3,33	0,00	3,33	0,00	0,00
total cover	154,00	201,67	154,33	237,00	208,33	142,33
Shannon index	0,85	1,16	0,56	1,09	1,09	0,44
species number	6,00	9,00	7,00	10,00	7,00	6,00
evenness	0,48	0,53	0,29	0,47	0,56	0,24

3 mo old communities in 2000 after 6 wk of experimental duration. 48x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	2,00	5,00	73,33	16,67	10,00	11,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	10,00	4,00	3,33	7,33	20,00	3,33
P. elongata	7,00	5,33	0,00	0,00	6,67	3,33
C. strictum	1,67	1,67	0,33	2,33	5,00	0,33
Porphyra sp.	0,33	0,00	0,00	1,67	0,00	1,67
P. litoralis	0,00	0,00	0,00	0,00	3,33	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	21,67	40,00	13,67	10,33	25,00	20,00
B. improvisus	66,67	53,33	40,00	43,33	8,33	3,33
P. ciliata	16,67	8,33	10,00	10,00	16,67	10,00
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	13,33	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	3,33	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	30,00	53,33	90,00	33,33
unidentified green alga	26,67	13,33	10,00	0,00	0,00	0,00
total cover	166,00	131,00	180,67	148,33	185,00	87,00
Shannon index	1,18	1,08	1,07	1,09	0,95	1,08
species number	10,00	8,00	7,00	8,00	8,00	8,00
evenness	0,51	0,52	0,55	0,52	0,46	0,52

3 mo old communities in 2000 after 6 wk of experimental duration. 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	0,00	0,00	0,00	10,00	3,33
Ulva sp.	0,00	0,00	0,00	0,00	26,67	0,00
Melosira sp.	8,33	8,33	3,67	10,00	33,33	20,00
P. elongata	0,33	0,00	0,00	0,00	15,00	0,00
C. strictum	0,00	0,00	0,00	1,67	1,67	3,33
Porphyra sp.	0,00	0,00	0,00	0,00	1,67	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	7,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	100,00	30,00	36,67
B. improvisus	0,33	0,33	0,00	3,33	11,67	36,67
P. ciliata	18,33	33,33	26,67	50,00	43,33	76,67
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	1,67
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	3,33	0,00	0,00	33,33
total cover	127,33	142,00	133,67	165,00	173,33	218,67
Shannon index	0,48	0,60	0,54	0,79	1,37	1,24
species number	5,00	4,00	4,00	5,00	9,00	9,00
evenness	0,30	0,43	0,39	0,49	0,63	0,56

3 mo old communities in 2000 after 6 wk of experimental duration. 2 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,33	0,00	0,33	1,67	6,67	1,67
Ulva sp.	0,33	0,00	0,00	0,00	0,00	0,00
Melosira sp.	1,67	13,67	10,33	6,67	16,67	36,67
P. elongata	0,00	0,00	0,00	0,00	1,67	0,00
C. strictum	0,00	0,00	0,00	0,00	3,67	0,00
Porphyra sp.	0,00	0,00	0,00	0,00	8,33	0,00
P. litoralis	0,00	0,00	1,67	10,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	30,00	1,67
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	86,67	100,00	100,00	100,00	26,67	26,67
B. improvisus	10,00	0,00	1,67	0,00	46,67	63,33
P. ciliata	13,33	16,67	26,67	36,67	26,67	63,33
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,33	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	1,67	0,00	0,00	13,33	0,00
Achnanthes sp.	3,33	0,00	0,00	0,00	0,00	0,00
total cover	116,00	132,00	140,67	155,00	180,33	193,33
Shannon index	0,71	0,47	0,68	0,85	1,56	1,09
species number	8,00	4,00	6,00	5,00	10,00	6,00
evenness	0,34	0,34	0,38	0,53	0,68	0,61

3 mo old communities in 2000 after 6 wk of experimental duration. 6 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	1,67	0,00	3,67	1,67	0,00
Ulva sp.	0,00	5,00	0,00	0,00	2,00	0,00
Melosira sp.	1,67	100,00	7,00	0,00	2,00	0,33
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	3,33	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,00	0,00	0,00	3,33	1,67
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	0,00	100,00	80,00	31,67	100,00
B. improvisus	0,67	12,00	0,33	20,00	40,00	0,00
P. ciliata	23,33	0,33	13,33	11,67	4,00	10,33
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	1,67	16,67
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	0,00	100,00	0,00	10,00	83,33	13,33
unidentified green alga	0,00	0,00	0,00	0,00	1,67	0,00
Achnanthes sp.	0,00	0,00	0,00	0,00	0,00	3,33
total cover	125,67	222,33	120,67	125,33	171,33	145,67
Shannon index	0,52	0,35	0,42	0,90	0,96	0,75
species number	4,00	6,00	4,00	4,00	9,00	6,00
evenness	0,38	0,20	0,30	0,65	0,44	0,42

3 mo old communities in 2000 after 6 wk of experimental duration. 12 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	10,00	26,67	6,67	12,00	3,33	0,00
Ulva sp.	0,67	0,00	1,67	0,00	0,00	5,00
Melosira sp.	2,33	8,33	0,67	0,00	0,67	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,67	0,00	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	8,33	0,00	0,00	1,67	3,33
P. litoralis	0,00	6,67	0,00	1,67	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	46,67	53,33	40,00	56,67	76,67	0,00
B. improvisus	43,33	40,00	16,67	36,67	13,33	0,00
P. ciliata	0,67	0,00	0,00	8,67	3,33	0,00
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	33,33	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	3,33	0,00	56,67	46,67	0,00	0,00
unidentified green alga	3,33	0,00	3,33	6,67	0,00	100,00
total cover	111,00	143,33	125,67	169,00	132,33	108,33
Shannon index	1,04	1,35	0,85	1,08	1,14	0,25
species number	8,00	6,00	6,00	6,00	7,00	3,00
evenness	0,50	0,75	0,47	0,60	0,58	0,23

3 mo old communities in 2000 after 6 wk of experimental duration. controls

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	0,00	3,67	3,67	0,67	0,33
Ulva sp.	0,00	0,00	0,00	1,67	0,00	0,00
Melosira sp.	5,00	3,33	3,33	0,33	3,67	6,67
P. elongata	23,33	0,00	1,67	0,00	10,00	6,67
C. strictum	3,67	3,33	5,00	2,00	11,67	6,67
Porphyra sp.	0,00	0,00	0,00	0,00	1,67	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,33	0,00	16,67	6,67
C. multicornis	0,00	0,00	0,00	0,00	3,33	0,00
M. edulis	46,67	100,00	73,33	80,00	50,00	50,00
B. improvisus	38,33	0,00	17,00	16,67	30,00	36,67
P. ciliata	10,00	20,00	13,33	26,67	40,00	20,00
C. volutator	0,00	0,00	0,00	0,00	0,33	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	0,00	0,00	1,67	0,00	0,00	0,00
unidentified green alga	0,00	30,00	0,00	30,00	3,33	6,67
Vorticella sp.	0,00	1,67	0,00	0,00	0,00	0,00
Achnanthes sp.	0,00	0,00	13,33	0,00	0,00	0,00
total cover	127,00	158,33	132,67	161,00	171,33	140,33
Shannon index	1,03	0,63	1,06	1,07	1,57	1,30
species number	6,00	6,00	9,00	8,00	12,00	9,00
evenness	0,58	0,35	0,48	0,51	0,63	0,59

3 mo old communities in 2000 after 6 wk of experimental duration. procedural controls

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	1,67	0,00	0,33	5,00	0,00	0,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,33	6,67	13,67	3,67	1,67	10,33
P. elongata	3,33	1,67	6,67	0,00	0,00	0,00
C. strictum	11,67	8,33	5,00	6,67	20,00	5,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	1,67	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,33	11,67	0,00	3,33
C. multicornis	0,00	0,00	0,00	0,00	0,00	5,00
M. edulis	96,67	60,00	90,00	26,67	86,67	63,33
B. improvisus	13,33	36,67	26,67	33,33	23,33	33,33
P. ciliata	10,00	26,67	23,33	13,33	23,33	43,33
C. volutator	0,00	0,00	0,00	0,67	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	10,00	0,00	18,33	0,00	0,00	3,33
unidentified green alga	0,00	0,00	0,00	43,33	0,00	0,00
Achnanthes sp.	10,00	16,67	10,00	0,00	3,33	0,00
Zoothamnion sp.	0,00	0,00	0,00	0,00	0,00	8,33
Total	157,00	156,67	196,00	144,33	158,33	175,67
H'	0,92	1,16	1,04	1,36	1,16	1,32
Artenzahl	8,00	7,00	10,00	9,00	6,00	9,00
Evenness	0,44	0,60	0,45	0,62	0,64	0,60

Emersion 2000 **14 th wk**

3 mo old communities in 2000 after 14 wk of experimental duration. 1x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	0,00	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	10,00	3,33	3,33	18,33	26,67	6,67
P. elongata	1,67	0,00	3,33	0,00	16,67	6,67
C. strictum	3,67	0,00	0,00	0,00	1,67	2,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	1,67	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,33	3,33	3,33	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	80,00	100,00	100,00	100,00	53,33	100,00
B. improvisus	13,33	0,00	3,33	6,67	23,33	3,33
P. ciliata	46,67	40,00	53,33	60,00	26,67	36,67
C. volutator	0,00	0,00	0,00	0,00	0,67	0,67
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	5,00	0,00	10,00
unidentified green alga	16,67	0,00	0,00	0,00	0,00	3,33
total cover	172,00	145,00	163,67	193,33	152,33	169,33
Shannon index	0,99	0,66	0,76	0,89	1,12	0,79
species number	7,00	4,00	6,00	5,00	8,00	8,00
evenness	0,51	0,48	0,42	0,55	0,54	0,38

3 mo old communities in 2000 after 14 wk of experimental duration. 4x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	2,00	0,00	0,00	0,00	1,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	16,67	30,00	0,00	11,67	23,33	30,00
P. elongata	3,33	0,00	0,00	0,00	0,00	0,00
C. strictum	1,67	5,33	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	3,33	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	1,67	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	5,00
M. edulis	56,67	66,67	100,00	100,00	100,00	33,33
B. improvisus	33,33	16,67	6,67	3,33	0,00	36,67
P. ciliata	76,67	73,33	40,00	43,33	43,33	36,67
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	20,00	0,00
unidentified green alga	0,00	0,00	0,00	6,67	0,00	5,00
total cover	188,33	197,33	146,67	165,00	188,33	148,33
Shannon index	1,08	1,16	0,76	0,73	0,72	1,19
species number	6,00	7,00	3,00	5,00	4,00	7,00
evenness	0,60	0,59	0,69	0,46	0,52	0,61

3 mo old communities in 2000 after 14 wk of experimental duration. 8x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,33	0,33	0,33	0,00	0,33	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	3,33	15,00	6,67	20,00	13,33
P. elongata	0,00	0,00	0,33	0,00	13,33	0,00
C. strictum	0,00	1,67	1,67	12,00	7,00	3,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	1,67
L. flexuosa	0,00	0,00	1,67	0,00	1,67	0,00
C. multicornis	0,00	0,00	0,00	0,00	3,33	0,00
M. edulis	100,00	86,67	96,67	100,00	16,67	100,00
B. improvisus	13,67	11,67	13,33	10,00	50,00	3,33
P. ciliata	26,67	60,00	60,00	43,33	70,00	53,33
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	1,67	0,00	0,00
diatoms other than Melosira sp. or A	0,00	0,00	16,67	0,00	1,67	26,67
unidentified green alga	0,00	0,00	3,33	0,00	3,33	0,00
Achnanthes sp.	0,00	1,67	0,00	0,00	0,00	0,00
total cover	140,67	165,33	209,00	173,67	187,33	201,67
Shannon index	0,80	0,95	0,98	1,01	1,18	0,87
species number	4,00	7,00	9,00	6,00	10,00	6,00
evenness	0,58	0,49	0,45	0,57	0,51	0,49

3 mo old communities in 2000 after 14 wk of experimental duration. 24x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	3,67	1,67	0,67	1,67	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	6,67	15,00	20,00	13,33	26,67	26,67
P. elongata	0,00	0,00	1,67	0,00	0,00	0,00
C. strictum	8,33	5,00	0,00	13,33	1,67	0,00
Porphyra sp.	1,67	16,67	23,67	0,00	1,67	0,33
P. litoralis	0,00	1,67	1,67	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	76,67	100,00	66,67	20,00	0,00
B. improvisus	13,33	40,00	0,00	10,00	40,00	26,67
P. ciliata	46,67	53,33	63,33	45,00	53,33	23,33
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	5,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	43,33	0,00	13,33	40,00	50,00	43,33
unidentified green alga	0,00	6,67	30,00	0,00	0,00	0,00
Achnanthes sp.	0,00	6,67	0,00	0,00	0,00	0,00
total cover	220,00	225,33	255,33	194,00	195,00	120,33
Shannon index	1,02	1,40	1,00	1,16	1,04	0,67
species number	6,00	10,00	8,00	7,00	7,00	4,00
evenness	0,57	0,61	0,48	0,59	0,53	0,48

3 mo old communities in 2000 after 14 wk of experimental duration. 48x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	5,00	2,33	13,33	23,33	3,33	13,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	23,33	7,00	23,33	23,33	46,67	40,00
P. elongata	5,33	0,00	0,00	3,33	15,00	1,67
C. strictum	3,67	0,33	6,67	5,00	3,67	0,67
Porphyra sp.	13,33	1,67	1,67	3,33	0,00	6,67
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,33
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,33
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	33,67	8,33	13,33	10,00	38,33	15,00
B. improvisus	10,00	40,00	33,33	50,00	20,00	1,67
P. ciliata	30,00	1,00	40,00	23,33	30,00	13,33
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	40,00	0,00	56,67	0,00	13,33	46,67
unidentified green alga	8,33	0,00	0,00	0,00	0,00	0,00
total cover	172,67	60,67	188,33	141,67	170,33	139,67
Shannon index	1,17	0,87	1,17	1,36	1,05	0,94
species number	9,00	7,00	7,00	8,00	7,00	10,00
evenness	0,53	0,45	0,60	0,65	0,54	0,41

3 mo old communities in 2000 after 14 wk of experimental duration. 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	0,33	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	6,67	0,00
Melosira sp.	10,00	20,00	18,33	6,67	5,00	13,33
P. elongata	0,00	0,00	0,00	0,00	0,00	3,67
C. strictum	0,00	0,00	0,00	0,00	0,00	1,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	10,00	0,00	0,33	0,00	0,00
C. multicornis	0,00	0,00	0,00	3,33	0,00	0,00
M. edulis	100,00	90,00	100,00	100,00	86,67	53,33
B. improvisus	3,33	3,33	0,00	6,67	13,33	16,67
P. ciliata	33,33	63,33	40,00	80,00	56,67	66,67
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	6,67	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	0,00	0,00	10,00	0,00	5,00	8,33
unidentified green alga	0,00	3,33	0,00	3,33	0,00	0,00
Achnanthes sp.	0,00	0,00	0,00	0,00	3,33	0,00
total cover	146,67	197,00	168,33	200,33	176,67	163,67
Shannon index	0,68	1,07	0,65	0,91	1,03	1,01
species number	4,00	8,00	3,00	7,00	6,00	6,00
evenness	0,49	0,51	0,59	0,47	0,58	0,56

3 mo old communities in 2000 after 14 wk of experimental duration. 2 h treatment

Arten	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	1,67	0,33	0,00	0,00	0,00	0,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	6,67	21,67	20,00	10,00	11,67	11,67
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00	0,00	2,00
Porphyra sp.	0,00	0,00	0,00	0,00	1,67	3,33
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	18,33	2,33
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	100,00	20,00	20,00
B. improvisus	3,33	6,67	5,00	6,67	53,33	50,00
P. ciliata	36,67	73,33	43,33	60,00	60,00	60,00
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	3,33	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	1,67	0,00	0,00	1,67	0,00	0,00
total cover	153,33	202,00	168,33	178,33	165,00	149,67
Shannon index	0,84	0,84	0,76	0,81	1,28	1,22
species number	7,00	5,00	4,00	5,00	6,00	8,00
evenness	0,43	0,52	0,55	0,51	0,71	0,59

3 mo old communities in 2000 after 14 wk of experimental duration. 6 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	1,67	0,00	2,00	0,00	1,67
Ulva sp.	0,00	11,67	0,00	0,00	0,00	0,00
Melosira sp.	1,67	6,67	10,00	2,00	15,00	16,67
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,33	0,00	3,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	3,33	0,00	0,00	0,00	1,67
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	0,33	100,00	80,00	70,00	70,00
B. improvisus	0,00	2,33	0,00	78,33	10,00	13,33
P. ciliata	43,33	40,00	46,67	53,33	50,00	33,33
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	10,00	0,00	3,33	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	36,67	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	3,33
total cover	145,00	112,67	156,67	219,33	145,00	143,33
Shannon index	0,62	1,08	0,65	1,20	0,90	1,10
species number	3,00	8,00	3,00	7,00	4,00	8,00
evenness	0,56	0,52	0,59	0,61	0,65	0,53

3 mo old communities in 2000 after 14 wk of experimental duration. 12 h treatment

Arten	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,67	6,67	16,67	0,67	5,00	0,00
Ulva sp.	0,33	6,67	0,00	3,33	0,00	26,67
Melosira sp.	0,67	1,67	0,00	0,00	1,67	0,33
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	66,67	50,00	43,33	28,33	90,00	0,00
B. improvisus	30,00	43,33	33,33	23,33	16,67	3,33
P. ciliata	5,33	26,67	1,67	2,00	13,33	0,00
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	23,33	0,00	26,67	16,67	6,67	20,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	13,33	43,33	63,33	86,67	23,33	0,00
unidentified green alga	0,00	0,00	6,67	0,00	0,00	23,33
total cover	140,33	178,33	191,67	161,00	156,67	73,67
Shannon index	1,15	1,23	1,17	0,98	1,01	0,86
species number	7,00	6,00	6,00	6,00	6,00	5,00
evenness	0,59	0,69	0,65	0,55	0,56	0,54

3 mo old communities in 2000 after 14 wk of experimental duration. controls

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	0,00	0,00	1,67	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	3,33	0,00	6,67	6,67	3,67	6,67
P. elongata	13,33	0,00	0,00	1,67	6,67	8,33
C. strictum	2,33	0,33	5,00	3,33	23,33	5,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	1,67	0,00	6,67	1,00	10,00
C. multicornis	0,00	0,00	0,00	0,00	10,00	3,33
M. edulis	70,00	100,00	100,00	86,67	30,00	78,33
B. improvisus	40,00	13,33	5,00	10,00	43,33	11,67
P. ciliata	23,33	3,33	60,00	36,67	36,67	20,00
C. volutator	0,00	0,00	0,00	0,00	0,33	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	10,00	0,00	20,00	0,00	0,00	0,00
unidentified green alga	3,33	0,00	0,00	16,67	3,33	6,67
Vorticella sp.	3,33	0,00	0,00	0,00	0,00	0,00
Achnanthes sp.	0,00	0,00	1,67	0,00	0,00	3,33
total cover	169,00	118,67	198,33	170,00	158,33	153,33
Shannon index	1,04	0,57	0,89	1,09	1,51	1,18
species number	8,00	5,00	6,00	9,00	10,00	10,00
evenness	0,50	0,35	0,50	0,50	0,66	0,51

3 mo old communities in 2000 after 14 wk of experimental duration. procedural controls

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	0,00	0,67	0,00	0,33	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	6,67	8,33	18,33	6,67	6,67	13,33
P. elongata	0,00	1,67	10,00	0,00	0,00	0,00
C. strictum	3,33	11,67	16,67	8,67	10,33	2,00
Porphyra sp.	0,00	0,00	1,67	0,00	0,00	0,00
P. litoralis	3,33	0,00	1,67	0,00	1,67	0,00
L. flexuosa	0,00	0,00	6,67	11,67	0,00	20,00
C. multicornis	0,00	0,00	0,00	0,00	0,33	13,33
M. edulis	86,67	56,67	83,33	33,33	100,00	36,67
B. improvisus	10,00	30,00	16,67	20,00	11,67	26,67
P. ciliata	43,33	50,00	46,67	26,67	33,33	21,67
C. volutator	0,00	0,00	0,00	0,67	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	1,67	0,33	0,00
diatoms other than Melosira sp. or A	13,33	0,00	0,00	0,00	0,00	6,67
unidentified green alga	0,00	0,00	0,00	30,00	1,67	0,00
Achnanthes sp.	0,00	0,00	1,67	10,00	6,67	0,00
Ectocarpus sp.	0,00	0,00	3,33	0,00	0,00	0,00
total cover	166,67	158,33	207,33	149,33	173,00	140,33
Shannon index	1,02	1,24	1,31	1,30	1,05	1,52
species number	6,00	6,00	12,00	10,00	11,00	7,00
evenness	0,57	0,69	0,53	0,56	0,44	0,78

3 mo old communities in 2000 after 14 wk of experimental duration. recruitment panels

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	1,00	1,00	11,67	5,00	1,00	5,00
Ulva sp.	0,00	0,33	0,67	0,00	0,00	0,00
Melosira sp.	1,00	3,67	1,00	1,00	1,00	43,33
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	1,00	0,33	1,00	0,67	1,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	17,00	23,33	30,00	26,67	36,67	33,33
L. flexuosa	0,00	0,33	0,00	0,00	7,33	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,33	0,00
M. edulis	0,00	0,33	0,00	0,00	0,00	0,00
B. improvisus	1,00	3,67	1,00	1,00	5,00	1,00
P. ciliata	0,67	2,33	1,00	1,00	1,00	0,67
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,33
diatoms other than Melosira sp.	100,00	100,00	100,00	100,00	100,00	100,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
chironomids	0,33	0,00	0,00	0,00	0,00	0,00
total cover	121,00	136,00	145,67	135,67	153,00	184,67
Shannon index	0,38	0,59	0,63	0,55	0,70	0,48
species number	7,00	10,00	8,00	7,00	9,00	8,00
evenness	0,20	0,25	0,31	0,28	0,32	0,23

Emersion 2000 **12 mo old communities**

start communities (unlabelled data are percent cover values)

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	0,00	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	0,00	0,00	2,00	1,67	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	21,67	6,67	23,33	40,00	0,00	46,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	3,33	0,00	7,00	0,00	0,00	0,33
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	100,00	100,00	100,00
B. improvisus	16,67	10,00	1,67	25,00	0,00	3,33
P. ciliata	6,67	0,00	0,00	0,00	0,33	0,33
C. volutator	0,00	0,00	0,00	0,00	0,00	0,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	10,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	40,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
Ectocarpus sp.	6,67	36,67	13,33	0,00	8,33	30,00
Zoothamnion sp.	2,00	0,00	8,33	0,33	8,00	0,33
Vorticella sp.	10,00	26,67	3,33	13,33	18,33	3,33
total cover	167,00	190,00	197,00	180,67	136,67	184,67
Shannon index	1,01	0,77	0,76	0,93	0,24	0,79
species number	8,00	6,00	8,00	6,00	6,00	9,00
evenness	0,49	0,43	0,36	0,52	0,14	0,36

Emersion 2000 **4th wk**

12 mo old communities in 2000 after 4 wk of experimental duration. 1x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	8,33	10,00	10,00	0,00
P. elongata	20,00	0,00	0,00	0,00
C. strictum	23,33	5,00	15,00	7,00
Porphyra sp.	0,00	0,00	0,00	1,67
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	8,33	15,00	26,67	10,00
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	83,33
B. improvisus	3,33	1,67	3,67	15,00
P. ciliata	3,67	2,00	0,33	7,00
C. volutator	0,00	0,00	0,00	1,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	6,67	0,00	63,33
unidentified green alga	0,00	0,00	0,00	0,00
Ectocarpus sp.	8,33	0,00	0,00	0,00
total cover	175,33	140,33	155,67	188,33
Shannon index	0,89	0,71	0,91	1,03
species number	8,00	6,00	6,00	7,00
evenness	0,43	0,40	0,51	0,53

12 mo old communities in 2000 after 4 wk of experimental duration. 4x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	0,00	0,00	3,33	6,67
P. elongata	0,00	0,00	0,00	0,00
C. strictum	8,33	13,33	0,00	0,67
Porphyra sp.	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	0,67	0,00	0,00	7,00
C. multicornis	1,67	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	100,00
B. improvisus	5,00	3,33	6,67	5,00
P. ciliata	5,00	2,00	0,00	0,00
C. volutator	0,33	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	20,00	18,33	16,67	21,67
unidentified green alga	0,00	0,00	0,00	0,00
Ectocarpus sp.	23,33	0,00	0,00	0,00
total cover	164,33	137,00	126,67	141,00
Shannon index	0,75	0,61	0,34	0,54
species number	8,00	4,00	3,00	5,00
evenness	0,36	0,44	0,31	0,33

12 mo old communities in 2000 after 4 wk of experimental duration. 8x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	5,33	5,00	10,33	0,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	0,00	0,00	3,33	1,67
P. elongata	0,00	0,00	0,00	0,00
C. strictum	11,67	0,33	0,00	0,00
Porphyra sp.	0,00	0,33	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	5,00	30,00	0,67	11,67
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	100,00
B. improvisus	6,67	6,67	1,00	0,33
P. ciliata	5,00	5,33	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	3,33	0,00	0,00	3,33
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	46,67	20,00	20,00	3,33
unidentified green alga	0,00	0,00	0,00	0,00
Ectocarpus sp.	5,00	23,33	0,00	0,00
chironomids	0,00	0,00	0,00	0,33
total cover	188,67	191,00	135,33	120,67
Shannon index	0,99	0,96	0,48	0,50
species number	8,00	8,00	5,00	6,00
evenness	0,48	0,46	0,30	0,28

12 mo old communities in 2000 after 4 wk of experimental duration. 24x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	3,67	11,67	2,33	16,67
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	20,00	16,67	16,67	0,00
P. elongata	0,00	0,00	0,00	0,00
C. strictum	3,67	5,00	6,67	25,00
Porphyra sp.	0,00	0,00	0,00	1,67
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	3,33	13,33	1,67	1,67
C. multicornis	0,00	1,67	0,33	0,00
M. edulis	100,00	100,00	100,00	100,00
B. improvisus	3,33	10,33	0,33	0,00
P. ciliata	7,00	2,00	3,33	2,00
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	23,33	0,00
unidentified green alga	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	3,67
Ectocarpus sp.	0,00	1,67	0,00	0,00
total cover	141,00	162,33	154,67	150,67
Shannon index	0,76	1,08	0,64	0,97
species number	7,00	9,00	8,00	6,00
evenness	0,39	0,49	0,31	0,54

12 mo old communities in 2000 after 4 wk of experimental duration. 48x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	8,67	8,67	2,33	13,67
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	0,00	3,33	1,67	3,67
P. elongata	0,00	0,00	0,00	0,00
C. strictum	7,00	6,67	2,00	3,33
Porphyra sp.	0,33	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	1,67	0,00	0,33	0,00
C. multicornis	1,67	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	100,00
B. improvisus	3,33	6,67	18,33	0,00
P. ciliata	0,67	2,00	2,00	2,33
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	60,00	15,00	0,00	73,33
unidentified green alga	0,00	0,00	0,00	0,00
Ectocarpus sp.	0,00	0,00	0,00	0,00
chironomids	0,00	0,33	0,00	0,00
total cover	183,33	142,67	126,67	196,33
Shannon index	0,79	0,77	0,69	0,65
species number	8,00	7,00	7,00	5,00
evenness	0,38	0,39	0,35	0,40

12 mo old communities in 2000 after 4 wk of experimental duration. 1h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	3,33	0,00	5,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	13,33	10,00	11,67	8,33
P. elongata	0,00	0,00	0,00	0,00
C. strictum	5,33	6,67	13,33	0,33
Porphyra sp.	0,00	0,00	0,00	1,67
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	36,67	1,67	18,67	2,00
C. multicornis	1,67	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	100,00
B. improvisus	10,33	8,33	0,33	1,67
P. ciliata	2,00	5,00	0,33	3,33
C. volutator	0,00	0,33	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	1,67	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	3,33	18,33	43,33
unidentified green alga	0,00	0,00	0,00	0,00
Ectocarpus sp.	0,00	0,00	0,00	0,00
total cover	171,00	138,67	162,67	165,67
Shannon index	1,06	0,83	0,78	0,65
species number	8,00	8,00	6,00	8,00
evenness	0,51	0,40	0,43	0,31

12 mo old communities in 2000 after 4 wk of experimental duration. 2 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5
Enteromorpha sp.	0,00	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	6,67	6,67	13,33	18,33
P. elongata	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00	0,00
Porphyra sp.	0,33	0,00	0,00	1,67	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	3,67	3,67	0,00	13,33
C. multicornis	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	100,00	100,00
B. improvisus	6,67	16,67	16,67	20,00	0,00
P. ciliata	0,00	0,00	0,00	0,00	0,33
C. volutator	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	1,67
Fucus sp.	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	10,00
unidentified green alga	0,00	0,00	0,00	5,00	0,00
total cover	107,00	127,00	127,00	140,00	143,67
Shannon index	0,25	0,56	0,56	0,57	0,54
species number	3,00	4,00	4,00	5,00	5,00
evenness	0,23	0,40	0,40	0,35	0,33

12 mo old communities in 2000 after 4 wk of experimental duration. 6 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	1,67	0,00	0,67	0,00
Ulva sp.	0,00	0,00	0,00	10,00
Melosira sp.	0,00	0,00	1,67	0,00
P. elongata	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	2,00	0,33	5,00
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	100,00
B. improvisus	3,33	6,67	10,00	3,33
P. ciliata	0,00	0,00	0,33	0,00
C. volutator	0,00	0,00	0,33	0,00
C. tortuosa	0,00	2,00	2,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
unidentified green alga	1,67	0,00	5,33	0,00
total cover	106,67	110,67	120,67	118,33
Shannon index	0,23	0,41	0,51	0,59
species number	4,00	4,00	9,00	4,00
evenness	0,17	0,29	0,23	0,42

12 mo old communities in 2000 after 4 wk of experimental duration. 12 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5
Enteromorpha sp.	0,00	0,33	0,33	2,00	0,00
Ulva sp.	0,00	0,00	0,00	40,00	0,00
Melosira sp.	0,00	0,00	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,00	0,00	0,67	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	41,67	100,00
B. improvisus	10,00	8,33	8,33	10,00	3,33
P. ciliata	0,00	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00	0,00
C. tortuosa	43,33	5,00	5,00	3,67	1,67
M. membranacea	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	33,33	33,33	0,00	15,00
total cover	153,33	147,00	147,00	98,00	120,00
Shannon index	0,81	0,55	0,55	1,20	0,31
species number	3,00	5,00	5,00	6,00	4,00
evenness	0,74	0,34	0,34	0,67	0,22

12 mo old communities in 2000 after 4 wk of experimental duration. controls

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	6,67	0,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	10,00	3,33	10,00	0,00
P. elongata	0,00	0,00	0,00	0,00
C. strictum	83,33	25,00	13,33	63,33
Porphyra sp.	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	20,00	33,33	26,67	10,00
C. multicornis	1,67	0,00	0,00	0,00
M. edulis	100,00	100,00	100,00	100,00
B. improvisus	6,67	13,33	0,00	1,67
P. ciliata	0,33	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	6,67	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00
total cover	222,00	181,67	156,67	175,00
Shannon index	1,10	1,23	0,93	0,90
species number	7,00	6,00	5,00	4,00
evenness	0,56	0,68	0,58	0,65

12 mo old communities in 2000 after 4 wk of experimental duration. recruitment panels

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,33	0,33	2,00	0,33	0,33	2,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	0,00	0,33	0,00	0,00	0,33
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,33	0,00	1,00	7,00	0,33	0,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,33	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	0,67	5,00	5,00	6,67	5,00	8,33
B. improvisus	3,67	0,33	3,33	1,67	3,33	1,67
P. ciliata	0,00	0,00	0,00	0,00	0,00	0,00
C. volutator	3,67	20,00	3,33	11,67	20,00	0,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	96,67	0,00	0,00	26,67	0,00	0,00
unidentified green alga	1,67	0,00	0,00	0,00	0,00	0,00
Ectocarpus sp.	7,00	40,00	23,33	20,00	30,00	20,00
total cover	114,00	65,67	38,33	74,00	59,33	33,33
Shannon index	0,29	0,61	0,94	0,84	0,82	0,77
species number	8,00	5,00	9,00	8,00	9,00	7,00
evenness	0,14	0,38	0,43	0,40	0,38	0,40

Emersion 2000 **8th wk**

12 mo old communities in 2000 after 8 wk of experimental duration. 1x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	2,5	2,5	0	0,5
Ulva sp.	0	0	0	0
Melosira sp.	17,5	5	3	5
P. elongata	0	0	0	0
C. strictum	5	5	20	0,5
Porphyra sp.	0	0	0	0
P. litoralis	0	12,5	0	0
L. flexuosa	0	2,5	0,5	0,5
C. multicornis	0	0	0	0
M. edulis	140	120	125	155
B. improvisus	3	1	7,5	2,5
P. ciliata	7,5	5	0,5	12,5
C. volutator	0,5	0	0	2,5
C. tortuosa	0	0	0	0
M. membranacea	0	2,5	0	0
Fucus sp.	0	0	0	0
diatoms other than Melosira sp.	10	25	0	15
unidentified green alga	0	0	0	0
total cover	186,00	181,00	156,50	194,00
Shannon index	0,58	0,86	0,62	0,51
species number	7,00	9,00	6,00	8,00
evenness	0,30	0,39	0,35	0,25

12 mo old communities in 2000 after 8 wk of experimental duration. 4x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	2,5	0,5	0,5	0,5
Ulva sp.	0	0	0	0
Melosira sp.	0,5	1	5,5	5,5
P. elongata	0	0	0	0
C. strictum	10	0,5	0	5,5
Porphyra sp.	2,5	0	0	0
P. litoralis	2,5	10	0,5	0
L. flexuosa	0	7,5	3	10
C. multicornis	3	0	0	0
M. edulis	120	107,5	112,5	115
B. improvisus	20	7,5	7,5	7,5
P. ciliata	3	2,5	1	5
C. volutator	0	0	0	0
C. tortuosa	0	0	0	0
M. membranacea	0	0	0	0
Fucus sp.	0	0	0	0
diatoms other than Melosira sp.	10	30	0	0
unidentified green alga	10	0	0	0
chironomids	0	0	1	0
total cover	184,00	167,00	131,50	149,00
Shannon index	0,99	0,83	0,46	0,79
species number	10,00	8,00	8,00	7,00
evenness	0,43	0,40	0,22	0,40

12 mo old communities in 2000 after 8 wk of experimental duration. 8x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,50	20,00	0,00	55,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	5,00	7,50	0,50	7,50
P. elongata	0,00	0,00	0,00	0,00
C. strictum	2,50	5,50	0,00	0,50
Porphyra sp.	0,00	5,00	0,00	0,00
P. litoralis	2,50	0,00	2,50	5,00
L. flexuosa	0,50	15,00	7,50	2,50
C. multicornis	5,00	7,50	0,00	0,50
M. edulis	130,00	120,00	140,00	130,00
B. improvisus	20,00	10,00	5,00	3,00
P. ciliata	12,50	5,50	0,50	2,50
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	15,00	0,00
unidentified green alga	5,00	0,00	0,00	0,00
chironomids	0,50	0,00	0,00	0,00
total cover	184,00	196,00	171,00	206,50
Shannon index	0,92	1,30	0,48	0,93
species number	11,00	9,00	6,00	9,00
evenness	0,38	0,59	0,27	0,42

12 mo old communities in 2000 after 8 wk of experimental duration. 24x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	15,00	12,50	0,00	5,50
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	2,50	0,50	1,00	0,00
P. elongata	0,00	0,00	0,00	0,00
C. strictum	10,50	0,00	0,00	0,50
Porphyra sp.	3,00	0,50	0,00	5,00
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	0,50	0,00	7,50	0,00
C. multicornis	1,00	0,00	0,00	0,00
M. edulis	107,50	112,50	120,00	110,00
B. improvisus	15,00	5,00	0,50	5,00
P. ciliata	1,00	0,50	3,00	0,00
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	30,00	22,50	10,00
unidentified green alga	0,00	0,00	0,00	0,00
total cover	156,00	161,50	154,50	136,00
Shannon index	1,05	0,59	0,44	0,56
species number	9,00	6,00	5,00	5,00
evenness	0,48	0,33	0,27	0,35

12 mo old communities in 2000 after 8 wk of experimental duration. 48x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5
Enteromorpha sp.	35,00	35,00	5,50	20,00	15,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	0,00	0,50	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00
C. strictum	5,00	0,50	0,00	0,00	0,00
Porphyra sp.	7,50	3,00	3,00	5,00	2,50
P. litoralis	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00
C. multicornis	2,50	0,00	0,00	0,00	0,00
M. edulis	107,50	105,50	103,00	5,00	101,00
B. improvisus	20,00	10,00	10,00	5,00	0,00
P. ciliata	0,00	0,50	0,00	0,50	1,00
C. volutator	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	2,50	0,00	15,00	2,50
Fucus sp.	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00
chironomids	0,50	0,00	0,00	0,00	0,00
total cover	178,00	157,00	122,00	50,50	122,00
Shannon index	1,16	0,96	0,58	1,46	0,61
species number	7,00	7,00	5,00	6,00	5,00
evenness	0,60	0,49	0,36	0,81	0,38

12 mo old communities in 2000 after 8 wk of experimental duration. 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5
Enteromorpha sp.	0,50	0,50	5,50	0,00	2,50
Ulva sp.	0,00	0,00	0,00	0,00	0,00
Melosira sp.	15,00	30,00	0,00	0,50	0,50
P. elongata	0,00	5,00	0,00	0,00	0,00
C. strictum	0,50	0,00	0,50	3,00	0,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00
P. litoralis	10,00	2,50	0,50	5,00	0,00
L. flexuosa	5,50	2,00	0,50	5,00	7,50
C. multicornis	5,00	0,00	0,00	0,00	2,50
M. edulis	15,00	107,50	130,00	115,00	125,00
B. improvisus	10,00	2,50	5,00	5,00	5,00
P. ciliata	0,00	0,50	5,50	0,00	2,50
C. volutator	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	2,50	35,00	30,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00
total cover	61,50	153,00	182,50	163,50	145,50
Shannon index	1,43	0,48	0,60	0,64	0,61
species number	8,00	8,00	7,00	6,00	7,00
evenness	0,69	0,23	0,31	0,36	0,31

12 mo old communities in 2000 after 8 wk of experimental duration. 2 h treatment

Arten	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	15	1	3	0
Ulva sp.	0	0	0	0
Melosira sp.	0	0	0	0
P. elongata	0	0	0	0
C. strictum	0	0	0	0
Porphyra sp.	0	0	2,5	0
P. litoralis	0	0	0	0
L. flexuosa	5	0	0	0
C. multicornis	0	0	0	0
M. edulis	105	122,5	105,5	135
B. improvisus	2,5	5	17,5	0,5
P. ciliata	0	0	0	0,5
C. volutator	0	0	0	0
C. tortuosa	0	0	0	0
M. membranacea	0	0	0	0
Fucus sp.	0	0	0	0
diatoms other than Melosira sp.	0	20	0	0
unidentified green alga	20	0	7,5	0
total cover	147,50	148,50	136,00	136,00
Shannon index	0,66	0,31	0,62	0,05
species number	5,00	3,00	5,00	3,00
evenness	0,41	0,28	0,38	0,04

12 mo old communities in 2000 after 8 wk of experimental duration. 6 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	7,50	2,50	3,00	5,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	0,00	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,00	0,50	0,00
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	110,00	100,50	100,00	101,00
B. improvisus	0,00	0,00	7,50	10,00
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	2,50	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	25,00	0,00	25,00
unidentified green alga	55,00	0,00	0,00	0,00
total cover	172,50	128,00	113,50	141,00
Shannon index	0,42	0,27	0,50	0,55
species number	3,00	3,00	5,00	2,00
evenness	0,39	0,24	0,31	0,79

12 mo old communities in 2000 after 8 wk of experimental duration. 12 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	20,00	12,50	65,00	5,00
Ulva sp.	0,00	7,50	10,00	0,00
Melosira sp.	0,00	0,00	0,50	0,00
P. elongata	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00
Porphyra sp.	7,50	7,50	5,00	3,00
P. litoralis	0,00	2,50	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	100,00	110,00	20,50	100,50
B. improvisus	7,50	7,50	5,00	0,00
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	2,50	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
unidentified green alga	25,00	65,00	0,00	12,50
total cover	162,50	212,50	106,00	121,00
Shannon index	0,90	0,91	1,13	0,38
species number	6,00	7,00	6,00	4,00
evenness	0,50	0,47	0,63	0,27

12 mo old communities in 2000 after 8 wk of experimental duration.

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	2,50	0,00	0,00	2,50
P. elongata	0,00	0,00	0,00	0,00
C. strictum	12,50	25,00	37,50	25,00
Porphyra sp.	0,00	0,00	0,00	0,00
P. litoralis	2,50	2,50	0,00	20,00
L. flexuosa	45,00	20,00	35,00	15,00
C. multicornis	0,50	0,00	2,50	0,00
M. edulis	120,00	120,00	145,00	130,00
B. improvisus	5,50	2,50	7,50	15,00
P. ciliata	2,50	5,00	1,00	3,00
C. volutator	0,00	0,00	2,50	2,50
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	2,50	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00
Vorticella sp.	0,00	0,00	20,00	0,00
total cover	191,00	177,50	251,00	213,00
Shannon index	1,04	1,01	1,09	1,26
species number	8,00	6,00	8,00	8,00
evenness	0,50	0,56	0,53	0,61

12 mo old communities in 2000 after 8 wk of experimental duration.

					recruitment panels	
species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	1,00	5,00	0,50	3,00	5,00	1,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	3,00	1,00	3,00	0,50	0,50	3,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,50	1,00	1,00	1,00	5,00	3,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,50	0,00
P. litoralis	0,00	0,00	40,00	7,50	0,00	5,00
L. flexuosa	7,50	25,00	2,50	0,50	25,00	20,00
C. multicornis	0,00	0,50	0,00	0,00	0,00	0,00
M. edulis	45,00	15,00	5,00	10,00	25,00	15,00
B. improvisus	10,00	10,00	2,50	1,00	3,00	20,00
P. ciliata	0,50	2,50	10,00	10,00	3,00	1,00
C. volutator	0,50	5,00	1,00	1,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
chironomids	0,00	1,00	0,00	3,00	3,00	0,00
total cover	68,00	66,00	65,50	37,50	70,00	68,00
Shannon index	0,97	1,61	1,20	1,58	1,42	1,51
species number	8,00	10,00	9,00	10,00	9,00	8,00
evenness	0,47	0,70	0,55	0,68	0,65	0,72

Emersion 2000 **12th wk**

12 mo old communities in 2000 after 12 wk of experimental duration. 1x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	5,00	3,33	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	3,00	13,33	1,67	0,00
P. elongata	0,00	0,00	0,00	0,00
C. strictum	0,00	8,33	3,67	0,00
Porphyra sp.	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	100,00	176,67	180,00	180,00
B. improvisus	0,00	3,33	4,00	10,00
P. ciliata	7,50	16,67	16,67	5,00
C. volutator	0,50	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	3,33	0,00
unidentified green alga	0,00	0,00	0,00	0,00
total cover	116,00	221,67	209,33	195,00
Shannon index	0,46	0,62	0,48	0,32
species number	5,00	6,00	5,00	3,00
evenness	0,29	0,35	0,30	0,29

12 mo old communities in 2000 after 12 wk of experimental duration. 4x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,33	0,00	0,33	3,33
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	1,67	38,33	23,33	30,00
P. elongata	3,33	1,67	0,00	0,00
C. strictum	5,00	1,67	1,67	0,00
Porphyra sp.	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	100,00	130,00	136,67	160,00
B. improvisus	15,00	3,67	10,00	10,00
P. ciliata	6,67	23,33	16,67	23,33
C. volutator	0,00	0,33	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
unidentified green alga	3,33	0,00	0,00	0,00
total cover	135,33	199,00	188,67	226,67
Shannon index	0,75	0,65	0,66	0,68
species number	8,00	7,00	6,00	5,00
evenness	0,36	0,34	0,37	0,42

12 mo old communities in 2000 after 12 wk of experimental duration. 8x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	5,00	13,33	6,67	1,67
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	5,00	18,33	3,33	36,67
P. elongata	0,00	0,00	0,00	0,00
C. strictum	0,00	5,00	3,33	0,00
Porphyra sp.	0,00	0,00	0,00	0,00
P. litoralis	0,00	1,67	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
C. multicornis	0,00	3,33	0,00	1,67
M. edulis	105,00	80,00	173,33	126,67
B. improvisus	10,00	8,33	8,33	26,67
P. ciliata	25,00	40,00	8,33	16,67
C. volutator	0,00	0,33	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	1,67
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	11,67	0,00	0,00
unidentified green alga	2,50	0,00	0,00	0,00
total cover	152,50	182,00	203,33	211,67
Shannon index	0,84	1,25	0,58	0,88
species number	6,00	9,00	6,00	7,00
evenness	0,47	0,57	0,32	0,45

12 mo old communities in 2000 after 12 wk of experimental duration. 24x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	10,00	14,00	7,50	5,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	5,00	1,67	2,50	0,00
P. elongata	0,00	0,33	0,00	0,00
C. strictum	0,00	5,33	0,00	0,33
Porphyra sp.	1,67	0,00	0,00	0,00
P. litoralis	0,00	3,33	2,50	0,00
L. flexuosa	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,33	0,00	0,00
M. edulis	143,33	153,33	180,00	136,67
B. improvisus	6,67	8,33	7,50	3,67
P. ciliata	10,00	15,00	10,50	0,67
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	1,67
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
unidentified green alga	26,67	0,00	15,00	10,00
chironomids	0,33	0,00	0,00	0,00
total cover	203,67	201,67	225,50	158,00
Shannon index	0,69	0,89	0,60	0,41
species number	8,00	9,00	7,00	7,00
evenness	0,33	0,41	0,31	0,21

12 mo old communities in 2000 after 12 wk of experimental duration. 48x15 min treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5
Enteromorpha sp.	30,00	50,00	25,00	36,67	20,00
Ulva sp.	0,00	0,00	6,67	0,00	15,00
Melosira sp.	3,00	8,67	0,33	3,33	0,00
P. elongata	0,00	0,00	0,00	0,33	0,00
C. strictum	1,00	0,00	0,00	0,00	0,00
Porphyra sp.	0,50	0,00	0,00	1,67	0,50
P. litoralis	0,00	1,67	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,50	0,00	0,00	0,00	0,50
M. edulis	115,00	91,67	116,67	107,33	60,00
B. improvisus	15,00	13,33	20,00	3,67	12,50
P. ciliata	5,00	1,00	4,00	0,67	12,50
C. volutator	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	6,67	0,00	0,00	7,50
Fucus sp.	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	55,00	16,67	10,00	0,00	0,00
unidentified green alga	0,00	0,00	1,67	0,00	25,00
chironomids	0,00	0,00	0,00	1,67	0,00
total cover	225,00	189,67	184,33	155,33	153,50
Shannon index	0,93	1,08	1,00	0,76	1,45
species number	8,00	7,00	7,00	8,00	9,00
evenness	0,45	0,55	0,52	0,36	0,66

12 mo old communities in 2000 after 12 wk of experimental duration. 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5
Enteromorpha sp.	0,00	1,67	1,67	0,33	13,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00
Melosira sp.	23,33	46,67	3,67	16,67	40,00
P. elongata	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	3,67	10,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00
M. edulis	190,00	163,33	170,00	160,00	173,33
B. improvisus	0,00	0,00	3,67	5,00	5,00
P. ciliata	16,67	8,33	16,67	11,67	10,00
C. volutator	0,33	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	3,33	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00
Achnanthes sp.	0,00	0,00	3,33	0,00	0,00
total cover	230,33	223,33	199,00	197,33	251,67
Shannon index	0,36	0,45	0,46	0,52	0,75
species number	4,00	5,00	6,00	5,00	6,00
evenness	0,26	0,28	0,25	0,32	0,42

12 mo old communities in 2000 after 12 wk of experimental duration. 2 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	0,00	8,33	0,00	0,33
P. elongata	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	133,33	133,33	133,33	80,00
B. improvisus	8,33	8,33	6,67	2,00
P. ciliata	0,00	1,67	3,33	8,67
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
unidentified green alga	6,67	0,00	6,67	0,00
total cover	148,33	151,67	150,00	91,00
Shannon index	0,26	0,32	0,33	0,42
species number	3,00	4,00	4,00	4,00
evenness	0,23	0,23	0,24	0,30

12 mo old communities in 2000 after 12 wk of experimental duration. 6 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	2,50	0,00	2,00	0,00
Ulva sp.	2,50	0,00	0,33	3,33
Melosira sp.	0,00	1,00	0,33	0,67
P. elongata	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,50	0,33	1,67
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	103,00	105,00	123,67	133,33
B. improvisus	0,00	10,00	10,33	0,00
P. ciliata	0,50	17,50	1,00	2,00
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,33	0,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00
unidentified green alga	0,00	45,00	0,00	6,67
total cover	108,50	179,00	138,33	147,67
Shannon index	0,25	0,72	0,43	0,29
species number	4,00	6,00	8,00	6,00
evenness	0,18	0,40	0,21	0,16

12 mo old communities in 2000 after 12 wk of experimental duration. 12 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	5,33	10,00	3,67	5,00
Ulva sp.	10,00	13,33	40,00	25,00
Melosira sp.	0,00	0,33	0,67	0,50
P. elongata	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,00	0,00
Porphyra sp.	3,67	0,33	2,33	0,50
P. litoralis	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	113,33	106,67	103,33	15,50
B. improvisus	10,00	13,33	0,00	0,00
P. ciliata	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00
C. tortuosa	0,00	13,33	7,33	1,00
M. membranacea	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	46,67	63,33	0,00	95,00
unidentified green alga	0,00	0,00	53,33	0,00
total cover	189,00	220,67	210,67	142,50
Shannon index	0,79	1,01	0,90	0,72
species number	5,00	7,00	7,00	6,00
evenness	0,49	0,52	0,46	0,40

12 mo old communities in 2000 after 12 wk of experimental duration. controls

species	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,67
Ulva sp.	0,00	0,00	0,00	0,00
Melosira sp.	1,67	3,67	2,00	3,33
P. elongata	0,00	0,00	0,00	0,00
C. strictum	11,67	30,00	5,00	33,33
Porphyra sp.	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,33	0,00	0,00
L. flexuosa	5,00	0,33	1,67	1,67
C. multicornis	0,00	0,00	0,00	0,00
M. edulis	146,67	130,00	153,33	110,00
B. improvisus	11,67	10,00	31,67	17,00
P. ciliata	13,33	11,67	16,67	33,33
C. volutator	0,00	0,00	0,33	0,33
C. tortuosa	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	3,33	0,00
Fucus sp.	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	1,67
unidentified green alga	0,00	0,00	0,00	0,00
Zoothamnion sp.	6,67	0,00	0,00	0,00
total cover	196,67	186,00	214,00	201,33
Shannon index	0,83	0,90	0,92	1,20
species number	7,00	7,00	8,00	8,00
evenness	0,43	0,46	0,44	0,58

12 mo old communities in 2000 after 12 wk of experimental duration. recruitment panels

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,33	6,67	30,00	20,33	36,67	8,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	40,00	20,00	5,33	11,67	16,67	8,33
P. elongata	0,00	0,00	3,33	20,00	0,00	0,00
C. strictum	2,00	6,67	2,33	26,67	5,00	6,67
Porphyra sp.	1,67	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	3,33	0,00	0,00	0,33
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	13,33	40,00	10,00	30,00	30,00	26,67
B. improvisus	31,67	25,00	11,67	13,33	20,00	16,67
P. ciliata	15,00	16,67	16,67	8,33	13,33	16,67
C. volutator	1,67	3,33	1,67	10,00	0,33	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
A. aurita	0,00	1,67	0,00	0,00	0,00	0,00
E. gemmipara	0,00	0,00	10,00	0,00	0,00	0,00
Zoothamnion sp.	0,00	0,00	0,00	0,00	0,00	0,33
total cover	105,67	120,00	94,33	140,33	122,00	84,33
Shannon index	1,12	1,39	1,45	1,50	1,39	1,46
species number	8,00	8,00	10,00	9,00	7,00	8,00
evenness	0,54	0,67	0,63	0,68	0,72	0,70

UVBR exposure **3 mo old communities**

start communities (data are percent cover values)

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6	replicate 7	replicate 8
Enteromorpha sp.	3,33	0,00	0,00	0,33	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	2,00	0,00	0,00	0,00	0,67	0,00	0,00	0,00
P. elongata	0,00	5,00	10,00	2,00	13,33	0,00	3,67	23,33
C. strictum	10,00	8,33	20,00	28,33	36,67	33,33	26,67	1,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	1,67	0,00	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	43,33	83,33	80,00	43,33	18,33	76,67	33,33	76,67
B. improvisus	6,67	0,00	1,67	5,00	11,67	2,33	0,00	2,00
P. ciliata	40,00	11,67	10,00	13,33	16,67	23,33	8,33	7,00
C. volutator	6,67	3,33	0,00	11,67	2,00	3,33	1,67	1,67
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	13,33	55,00	10,00	0,00	13,33	18,33	20,00	20,33
Gammarus sp.	0,00	0,00	0,00	0,00	0,33	0,00	3,33	0,00
total cover	127,00	166,67	131,67	104,00	113,00	157,33	97,00	132,67
Shannon index	1,39	0,76	0,84	1,39	1,25	1,11	1,00	0,65
species richness	9,00	6,00	6,00	7,00	9,00	6,00	7,00	7,00
evenness	0,63	0,42	0,47	0,72	0,57	0,62	0,52	0,33

UVBR exposure **6th wk**

3 mo old communities after 6 wk of experimental duration. 0.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	2,00	0,67	0,00	0,67	2,00	1,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	2,00	2,33	50,00	23,33	30,00	2,00
P. elongata	13,33	30,00	20,00	11,67	26,67	3,33
C. strictum	36,67	30,00	16,67	16,67	3,67	46,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,33	0,00
P. litoralis	3,33	0,00	5,00	1,67	0,00	0,00
L. flexuosa	3,33	0,00	0,00	18,33	20,00	16,67
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	3,33	2,33	2,00	3,33	5,00	21,67
B. improvisus	16,67	11,67	27,00	33,33	13,33	23,33
P. ciliata	33,33	36,67	60,00	46,67	20,00	33,33
C. volutator	1,67	0,00	0,33	0,00	3,33	0,00
C. tortuosa	0,00	0,00	0,00	1,67	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,33	0,00	0,00	0,33	0,33
diatoms other than Melosira sp. or A	33,33	0,00	40,00	53,33	0,00	0,00
unidentified green alga	10,00	0,00	0,00	0,00	36,67	0,00
Achnanthes sp.	0,00	1,67	0,00	0,00	3,33	0,00
unidentified red alga	0,00	0,00	0,00	0,00	0,00	13,33
total cover	159,00	115,67	221,00	210,67	164,67	162,33
Shannon index	1,25	1,05	0,94	1,20	1,05	1,51
species richness	11,00	9,00	8,00	10,00	13,00	10,00
evenness	0,52	0,48	0,45	0,52	0,41	0,66

3 mo old communities after 6 wk of experimental duration. 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	1,00	0,33	5,00	3,33	0,00	3,67
Ulva sp.	0,00	0,00	1,67	0,00	0,00	0,00
Melosira sp.	18,33	20,33	20,00	33,33	43,33	3,67
P. elongata	16,67	10,00	23,33	15,00	6,67	0,33
C. strictum	23,33	18,33	10,00	16,67	6,67	0,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	1,67	0,00	0,00	3,33	0,00	1,67
L. flexuosa	0,67	0,00	0,00	0,33	1,67	35,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	0,00	0,33	0,67	1,00	5,00	2,00
B. improvisus	0,33	8,33	16,67	5,00	10,00	3,33
P. ciliata	23,33	40,00	36,67	26,67	33,33	43,33
C. volutator	0,00	0,00	3,33	0,33	0,00	0,00
C. tortuosa	0,33	0,00	0,00	7,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	2,00	0,33	0,00	0,00	0,00
diatoms other than Melosira sp.	30,00	5,33	0,00	50,00	0,00	3,33
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
unidentified red alga	0,00	0,00	6,67	13,33	0,00	0,00
Achnanthes sp.	0,00	0,00	13,33	0,00	0,00	0,00
total cover	115,67	105,00	137,67	175,33	106,67	96,67
Shannon index	0,81	0,91	1,09	0,94	0,97	1,14
species richness	9,00	8,00	12,00	12,00	7,00	9,00
evenness	0,37	0,44	0,44	0,38	0,50	0,52

3 mo old communities after 6 wk of experimental duration. 2h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	0,00	2,00	10,00	0,33	1,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	11,67	2,00	18,33	3,67	0,00	0,00
P. elongata	10,00	6,67	18,33	0,00	0,00	0,00
C. strictum	16,67	11,67	13,33	0,00	0,33	1,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,33	0,00
P. litoralis	1,67	1,67	1,67	0,00	0,00	0,00
L. flexuosa	3,33	8,33	1,67	1,67	0,00	0,00
C. multicornis	1,67	0,00	0,00	0,00	0,00	0,00
M. edulis	6,67	11,67	2,00	2,00	101,67	90,00
B. improvisus	31,67	13,33	1,67	8,33	3,33	6,67
P. ciliata	43,33	13,33	50,00	26,67	3,33	13,33
C. volutator	1,67	0,00	1,67	1,67	0,00	0,00
C. tortuosa	0,00	0,00	26,67	16,67	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp. or A	0,00	0,00	0,00	26,67	0,00	0,00
unidentified green alga	18,33	53,33	16,67	21,67	0,00	0,00
unidentified red alga	36,67	0,00	0,00	0,00	0,00	0,00
Gammarus sp.	0,00	6,67	0,00	0,00	0,00	0,00
Achnanthes sp.	0,00	0,00	13,33	0,00	0,00	0,00
total cover	183,33	128,67	167,33	119,00	109,33	113,33
Shannon index	1,18	1,14	1,14	1,19	0,33	0,73
species richness	12,00	10,00	13,00	9,00	6,00	5,00
evenness	0,48	0,49	0,45	0,54	0,19	0,45

3 mo old communities after 6 wk of experimental duration. 4 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	20,00	0,33	2,33	3,33	8,33	0,33
Ulva sp.	1,67	0,00	0,00	0,33	0,00	0,00
Melosira sp.	1,00	0,33	0,67	10,00	0,67	0,33
P. elongata	3,33	1,67	5,00	33,33	7,00	0,33
C. strictum	8,67	0,33	1,00	15,00	0,67	0,33
Porphyra sp.	0,00	0,00	0,00	1,67	0,00	0,00
P. litoralis	0,00	0,00	1,67	1,67	0,00	10,00
L. flexuosa	0,00	0,00	1,67	5,00	6,67	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	0,67	4,00	1,67	4,00	0,33	55,00
B. improvisus	0,00	0,00	3,33	10,33	20,00	20,00
P. ciliata	43,33	46,67	40,00	43,33	23,33	11,67
C. volutator	1,67	0,00	0,00	0,00	0,33	1,67
C. tortuosa	36,67	1,67	60,00	21,67	63,33	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,33	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	43,33	3,33	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
Achnanthes sp.	0,00	0,00	0,00	3,33	3,33	0,00
total cover	117,00	55,33	160,67	156,33	134,00	99,67
Shannon index	1,38	0,50	1,03	1,43	1,32	1,24
species richness	9,00	8,00	10,00	13,00	11,00	9,00
evenness	0,63	0,24	0,45	0,56	0,55	0,56

3 mo old communities after 6 wk of experimental duration. 8 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	2,33	2,00	6,67	5,00	2,33	2,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	3,33
Melosira sp.	2,33	0,33	0,33	0,00	0,33	0,67
P. elongata	1,67	0,00	0,00	0,00	0,00	0,00
C. strictum	7,00	0,00	2,00	0,00	0,00	0,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	10,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	1,67	5,00	3,67	5,00	6,67	3,33
B. improvisus	0,33	0,33	5,00	0,00	5,00	1,67
P. ciliata	20,00	40,00	20,00	25,00	6,67	10,00
C. volutator	0,00	0,00	0,00	0,33	1,67	1,67
C. tortuosa	8,33	23,33	41,67	0,00	53,33	43,33
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,33	0,00	0,00	0,00	1,67	0,00
diatoms other than Melosira sp.	43,33	0,00	30,00	76,67	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
total cover	97,33	71,00	109,33	112,00	77,67	66,33
Shannon index	1,14	1,00	1,18	0,63	1,04	1,18
species richness	10,00	6,00	7,00	4,00	8,00	9,00
evenness	0,49	0,56	0,60	0,45	0,50	0,54

3 mo old communities after 6 wk of experimental duration. controls

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,33	0,67	2,00	0,67	2,00	0,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	3,33	0,67	0,33	26,67	36,67	2,33
P. elongata	1,67	5,00	11,67	5,00	7,00	0,33
C. strictum	50,00	53,33	23,33	26,67	13,33	1,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	1,67	1,67	3,33	1,67	0,00
L. flexuosa	0,00	1,67	3,33	5,33	0,00	0,00
C. multicornis	0,33	0,00	0,00	0,00	0,00	0,00
M. edulis	3,67	3,33	2,00	5,33	0,33	0,33
B. improvisus	1,67	33,33	0,67	14,00	25,00	0,00
P. ciliata	50,00	36,67	43,33	36,67	23,33	10,00
C. volutator	3,33	5,00	2,00	4,00	1,67	1,67
C. tortuosa	0,00	0,00	11,67	0,00	0,33	53,33
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	2,00	0,00
diatoms other than Melosira sp.	0,00	0,00	43,33	30,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
total cover	114,33	141,33	145,33	157,67	113,33	70,33
Shannon index	1,03	1,40	1,20	1,28	1,14	0,73
species richness	9,00	10,00	11,00	10,00	11,00	8,00
evenness	0,47	0,61	0,50	0,56	0,48	0,35

3 mo old communities after 6 wk of experimental duration. procedural controls treatment

species	replicate 1	replicate 2	replicate 3
Enteromorpha sp.	2,33	0,00	5,33
Ulva sp.	0,00	0,00	0,00
Melosira sp.	0,33	20,00	11,67
P. elongata	0,00	8,67	13,33
C. strictum	5,00	20,00	6,67
Porphyra sp.	0,00	0,00	0,00
P. litoralis	1,67	0,33	0,00
L. flexuosa	0,00	2,00	0,33
C. multicornis	0,00	0,00	0,00
M. edulis	20,00	10,00	3,67
B. improvisus	26,67	6,67	16,67
P. ciliata	43,33	30,00	56,67
C. volutator	1,67	2,00	0,00
C. tortuosa	3,33	0,00	0,00
M. membranacea	0,00	0,00	0,00
Fucus sp.	1,67	1,67	6,67
diatoms other than Melosira sp.	0,00	16,67	16,67
unidentified green alga	0,00	30,00	0,00
total cover	106,00	148,00	137,67
Shannon index	1,49	1,05	1,00
species richness	10,00	11,00	9,00
evenness	0,65	0,44	0,46

UVBR exposure **7 mo**

3 mo old communities after 7 mo of experimental duration. 0.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	10,00	0,00	16,67	10,00	40,00	3,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	3,33	0,00	0,00	1,67	26,67	1,67
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	3,67	0,00	0,00	3,33	3,33	6,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
tubedwelling diatoms	21,67	43,33	6,67	3,33	43,33	33,33
L. flexuosa	13,67	0,00	0,00	2,00	5,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	3,33	0,00	0,00	0,00	0,00	40,00
B. improvisus	6,67	0,00	3,33	3,33	0,00	3,33
P. ciliata	10,67	5,00	10,00	7,33	5,00	7,00
C. volutator	0,00	1,67	0,00	0,00	2,00	0,00
C. tortuosa	0,00	23,33	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Laminaria sp.	20,00	0,00	0,00	0,00	0,00	0,00
other diatoms	93,33	60,00	60,00	60,00	100,00	63,33
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
total cover	186,33	133,33	96,67	91,00	225,33	158,67
Shannon index	1,03	0,85	0,84	0,89	0,90	1,11
species richness	9,00	4,00	4,00	7,00	7,00	7,00
evenness	0,47	0,61	0,60	0,46	0,46	0,57

3 mo old communities after 7 mo of experimental duration. 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	10,00	3,33	5,00	8,67	3,67	33,33
Ulva sp.	3,33	0,00	0,00	0,00	1,67	0,00
Melosira sp.	0,00	10,00	6,67	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	3,33	0,00	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
tubedwelling diatoms	1,67	5,00	8,33	0,00	6,67	3,33
L. flexuosa	1,67	0,00	1,67	0,33	3,33	3,33
C. multicornis	0,00	0,00	0,00	0,00	0,33	0,00
M. edulis	0,00	0,00	0,00	0,00	0,00	0,00
B. improvisus	0,00	0,00	6,67	3,33	10,00	3,33
P. ciliata	1,67	3,33	3,33	0,00	0,00	0,33
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Laminaria sp.	3,33	3,33	0,00	6,67	0,00	13,33
other diatoms	93,33	66,67	100,00	100,00	83,33	90,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
Achnanthes sp.	1,67	0,00	0,00	0,00	0,00	0,00
total cover	120,00	91,67	131,67	119,00	109,00	147,00
Shannon index	0,58	0,40	0,60	0,31	0,69	0,61
species richness	8,00	5,00	6,00	4,00	6,00	6,00
evenness	0,28	0,25	0,33	0,22	0,39	0,34

3 mo old communities after 7 mo of experimental duration. 2 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,33	0,00	3,67	5,00	1,67	missing
Ulva sp.	0,00	0,00	0,00	0,00	0,00	missing
Melosira sp.	2,00	8,67	3,33	3,33	0,00	missing
P. elongata	0,00	0,00	0,00	0,00	0,00	missing
C. strictum	5,00	0,00	0,00	0,00	0,00	missing
Porphyra sp.	0,00	0,00	3,33	0,00	1,67	missing
tubedwelling diatoms	60,00	16,67	3,33	3,33	11,67	missing
L. flexuosa	13,33	6,67	1,67	0,00	0,00	missing
C. multicornis	0,00	0,00	0,00	0,00	0,00	missing
M. edulis	0,00	0,00	3,33	100,00	100,00	missing
B. improvisus	10,00	3,33	6,67	0,00	0,00	missing
P. ciliata	0,00	6,67	3,33	3,33	0,00	missing
C. volutator	0,00	0,00	0,00	0,00	0,00	missing
C. tortuosa	0,00	0,00	0,00	0,00	0,00	missing
M. membranacea	0,00	0,00	0,00	0,00	0,00	missing
Laminaria sp.	0,00	0,00	0,00	0,00	0,00	missing
other diatoms	23,67	56,67	91,67	180,00	96,67	missing
unidentified green alga	0,00	0,00	0,00	0,00	0,00	missing
P. litoralis	0,00	0,00	0,00	3,33	0,00	missing
total cover	114,33	98,67	120,33	298,33	211,67	missing
Shannon index	0,96	0,78	0,72	0,54	0,59	missing
species richness	6,00	5,00	8,00	6,00	4,00	missing
evenness	0,53	0,48	0,35	0,30	0,43	missing

3 mo old communities after 7 mo of experimental duration. 4 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	missing	missing	11,67	1,67	13,33	5,33
Ulva sp.	missing	missing	0,33	0,00	0,00	0,00
Melosira sp.	missing	missing	0,00	15,00	6,67	0,00
P. elongata	missing	missing	0,00	0,00	0,00	0,00
C. strictum	missing	missing	0,00	0,00	0,00	0,00
Porphyra sp.	missing	missing	0,00	0,00	0,00	0,00
tubedwelling diatoms	missing	missing	3,33	1,67	3,33	1,67
L. flexuosa	missing	missing	0,00	1,67	0,00	0,00
C. multicornis	missing	missing	0,00	0,00	0,00	0,00
M. edulis	missing	missing	0,00	0,00	0,00	61,67
B. improvisus	missing	missing	0,00	3,33	10,00	0,00
P. ciliata	missing	missing	0,00	11,67	2,00	1,67
C. volutator	missing	missing	0,00	0,00	0,00	0,00
C. tortuosa	missing	missing	0,00	0,00	0,00	0,00
M. membranacea	missing	missing	0,00	0,00	0,00	0,00
Laminaria sp.	missing	missing	0,00	0,00	53,33	5,00
other diatoms	missing	missing	100,00	33,33	100,00	33,33
unidentified green alga	missing	missing	0,00	13,33	0,00	13,33
P. litoralis	missing	missing	0,00	0,00	16,67	0,00
total cover	missing	missing	115,33	81,67	205,33	122,00
Shannon index	missing	missing	0,35	0,65	0,44	0,60
species richness	missing	missing	3,00	7,00	7,00	6,00
evenness	missing	missing	0,32	0,33	0,22	0,33

3 mo old communities after 7 mo of experimental duration. 8 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	20,00	36,67	2,33	13,33	26,67	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	10,00
Melosira sp.	33,33	43,33	1,67	20,00	53,33	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,33	0,00	0,00	0,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
tubedwelling diatoms	0,00	0,00	46,67	0,00	0,00	20,00
L. flexuosa	0,00	0,00	5,00	0,00	3,33	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	0,00	0,00	0,00	0,00	0,00	0,00
B. improvisus	0,00	3,33	3,33	0,00	0,00	3,33
P. ciliata	7,00	0,00	3,33	0,00	0,33	0,00
C. volutator	0,00	0,00	0,33	0,00	0,00	0,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Laminaria sp.	3,33	3,33	0,00	0,00	5,00	0,00
other diatoms	60,00	60,00	66,67	100,00	0,00	83,33
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
total cover	123,67	146,67	129,67	133,33	88,67	117,00
Shannon index	0,46	0,43	0,78	0,23	0,51	0,63
species richness	4,00	4,00	8,00	2,00	5,00	4,00
evenness	0,33	0,31	0,38	0,33	0,31	0,45

3 mo old communities after 7 mo of experimental duration.

controls

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	3,33	15,00	2,33	36,67	5,00	5,33
Ulva sp.	0,00	0,00	0,00	5,00	0,00	20,00
Melosira sp.	0,00	50,00	1,67	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	0,33	0,00	1,67	0,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
tubedwelling diatoms	33,33	0,00	46,67	10,00	96,67	0,00
L. flexuosa	0,00	3,33	5,00	0,00	1,67	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	0,00	0,00	0,00	0,00	0,00	0,00
B. improvisus	0,00	15,00	3,33	6,67	6,67	3,33
P. ciliata	0,00	2,00	3,33	0,00	0,00	0,00
C. volutator	0,00	0,00	0,33	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Laminaria sp.	13,33	0,00	0,00	6,67	0,00	6,67
other diatoms	96,67	66,67	66,67	73,33	100,00	53,33
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
total cover	146,67	152,00	129,67	138,33	211,67	88,67
Shannon index	0,42	0,60	0,78	0,81	0,63	0,63
species richness	3,00	5,00	8,00	5,00	5,00	4,00
evenness	0,38	0,37	0,38	0,50	0,39	0,45

3 mo old communities after 7 mo of experimental duration.

Procedural controls

species	replicate 1	replicate 2	replicate 3
Enteromorpha sp.	0,33	0,00	0,00
Ulva sp.	0,00	0,00	0,00
Melosira sp.	76,67	0,00	0,00
P. elongata	0,00	0,00	0,00
C. strictum	0,00	0,00	1,67
Porphyra sp.	0,00	0,00	0,00
tubedwelling diatoms	16,67	30,00	10,00
L. flexuosa	1,67	2,00	63,33
C. multicornis	0,00	6,67	0,00
M. edulis	0,00	0,00	0,00
B. improvisus	0,00	3,33	6,67
P. ciliata	0,00	0,33	3,33
C. volutator	3,33	0,00	0,00
C. tortuosa	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00
Laminaria sp.	0,00	13,33	20,00
other diatoms	13,33	73,33	63,33
unidentified green alga	0,00	0,00	0,00
total cover	112,00	129,00	168,33
Shannon index	0,47	0,67	0,79
species richness	5,00	6,00	6,00
evenness	0,29	0,37	0,44

UVBR exposure **12 mo old communities**

start communities (data are percent cover values)

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6	replicate 7	replicate 8
Enteromorpha sp.	0,00	0,33	0,33	1,67	0,00	0,00	0,33	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	5,00	3,33	6,67	0,00	0,00	5,00	8,33
P. elongata	0,00	0,00	0,00	1,67	0,00	0,00	0,00	0,00
C. strictum	93,33	36,67	36,67	40,00	56,67	43,33	30,00	43,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	6,67	2,00	6,67	0,33	8,33	5,00	0,00	13,33
C. multicornis	0,00	0,00	0,00	6,67	0,00	0,00	0,00	0,00
M. edulis	2,33	2,33	5,00	5,00	3,67	4,00	5,33	3,67
B. improvisus	0,00	16,67	23,33	3,33	0,00	10,00	6,67	0,00
P. ciliata	11,67	8,33	16,67	2,33	20,00	13,33	60,00	36,67
C. volutator	0,00	3,33	1,67	2,33	6,67	3,33	3,33	0,67
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	1,67	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	6,67	6,67	0,00	0,00
total cover	114,00	74,67	93,67	70,00	102,00	85,67	112,33	106,00
Shannon index	0,64	1,30	1,46	1,22	1,15	1,32	1,18	1,14
species richness	5,00	4,00	7,00	6,00	7,00	4,00	5,00	8,00
evenness	0,40	0,94	0,75	0,68	0,59	0,95	0,74	0,55

UVBR exposure **4th wk**

12 mo old communities after 4 wk of experimental duration 0.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	5,50	1,67	3,67	0,67	0,00	1,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	1,00	2,00	0,33	0,67	0,33	1,67
P. elongata	2,50	3,33	11,67	0,00	0,00	0,00
C. strictum	45,00	80,00	30,00	66,67	86,67	66,67
Porphyra sp.	0,50	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	15,00	10,00	26,67	17,00	15,00	27,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	5,00	11,67	6,67	41,67	50,00	16,67
B. improvisus	20,00	13,33	0,00	21,67	16,67	6,67
P. ciliata	1,00	0,00	0,00	0,00	1,67	0,00
C. volutator	0,00	6,67	3,33	3,33	8,33	13,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	6,67	0,00	0,00	0,00	1,67
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	10,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	20,00
Ectocarpus sp.	7,50	0,00	0,00	3,33	0,00	0,00
A. aurita	0,50	0,00	0,00	0,00	0,00	0,00
chironomids	0,00	1,67	0,00	0,00	0,00	1,67
total cover	103,50	137,00	82,33	155,00	188,67	157,00
Shannon index	1,33	1,29	1,20	1,34	1,30	1,34
species richness	11,00	10,00	7,00	8,00	7,00	10,00
evenness	0,56	0,56	0,62	0,64	0,67	0,58

12 mo old communities after 4 wk of experimental duration 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	0,33	0,33	5,00	8,33	20,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	3,33
Melosira sp.	0,33	0,67	0,00	0,67	2,00	2,00
P. elongata	0,00	6,67	3,33	0,00	0,00	0,00
C. strictum	96,67	33,33	56,67	20,00	33,33	36,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	16,67	26,67	26,67	10,00	6,67
C. multicornis	0,00	0,00	0,00	0,33	3,67	1,67
M. edulis	0,67	18,33	13,33	15,00	8,33	3,67
B. improvisus	10,00	33,33	0,00	3,33	13,67	0,00
P. ciliata	0,00	2,00	0,00	0,33	0,33	0,33
C. volutator	1,67	3,33	3,33	1,67	3,67	0,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	6,67	10,00	6,67	0,00	1,67
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	23,33	23,33	23,33	73,33
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
Ectocarpus sp.	0,00	0,00	0,00	5,00	11,67	5,00
chironomids	0,00	0,00	0,00	0,00	1,67	0,00
total cover	109,33	121,33	137,00	108,00	120,00	154,67
Shannon index	0,42	1,61	1,21	1,45	1,41	1,04
species richness	5,00	10,00	7,00	11,00	11,00	11,00
evenness	0,26	0,70	0,62	0,61	0,59	0,43

12 mo old communities after 4 wk of experimental duration 2 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	2,00	3,67	26,67	3,33	3,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	0,33	0,33	0,33	2,00	3,33
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	100,00	30,00	80,00	36,67	76,67	70,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,67
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	30,00	28,33	15,00	15,00	11,67	5,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	10,00	8,33	5,33	6,67	13,33	15,00
B. improvisus	3,33	0,00	0,00	3,33	40,00	3,33
P. ciliata	0,00	0,33	0,00	0,00	0,33	0,00
C. volutator	0,33	2,00	1,67	1,67	6,67	2,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	10,00	0,00	0,00	0,00	0,00	6,67
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	66,67	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
Ectocarpus sp.	0,00	11,67	1,67	6,67	0,00	0,00
chironomids	0,00	0,00	0,00	0,00	1,67	0,00
total cover	153,67	83,00	174,33	97,00	155,67	109,67
Shannon index	1,05	1,17	0,80	1,38	1,33	1,20
species richness	6,00	8,00	7,00	8,00	9,00	9,00
evenness	0,59	0,56	0,41	0,66	0,61	0,54

12 mo old communities after 4 wk of experimental duration 4 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	20,00	6,67	8,33	5,33	30,00	28,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,67	3,67	0,33	1,67	0,67	0,33
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	8,33	53,33	25,00	21,67	76,67	46,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,33	23,67	60,00	0,00	1,67
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	5,00	13,33	2,33	6,67	6,67	20,00
B. improvisus	10,00	26,67	3,33	10,00	13,33	5,00
P. ciliata	2,00	0,33	0,33	0,00	0,00	3,67
C. volutator	5,00	8,33	3,33	0,00	6,67	11,67
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	13,33	50,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
Ectocarpus sp.	3,33	0,00	46,67	21,67	0,00	0,00
chironomids	0,33	0,67	0,00	1,67	1,67	0,00
total cover	54,67	113,33	126,67	178,67	135,67	117,33
Shannon index	1,52	1,34	1,09	1,01	1,18	1,54
species richness	9,00	9,00	9,00	8,00	7,00	8,00
evenness	0,69	0,61	0,50	0,49	0,61	0,74

12 mo old communities after 4 wk of experimental duration 8 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	21,67	0,00	3,67	30,00	90,00	86,67
Ulva sp.	0,00	0,33	0,00	0,00	0,00	0,00
Melosira sp.	0,67	0,33	0,00	0,00	5,00	0,33
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	26,67	66,67	96,67	66,67	40,00	10,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	1,67	0,00	0,33	0,00	11,67	3,33
C. multicornis	0,00	0,67	0,00	0,00	0,00	0,00
M. edulis	10,00	11,67	5,00	10,00	30,00	40,00
B. improvisus	0,00	16,67	16,67	0,00	13,33	0,33
P. ciliata	0,67	2,00	0,33	0,00	0,33	0,00
C. volutator	5,00	6,67	1,67	6,67	5,00	6,67
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	3,33
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00	0,33	2,00
total cover	66,33	105,00	124,33	113,33	195,67	153,00
Shannon index	1,35	1,13	0,79	1,04	1,42	1,17
species richness	7,00	8,00	7,00	4,00	9,00	9,00
evenness	0,69	0,54	0,40	0,75	0,65	0,53

12 mo old communities after 4 wk of experimental duration controls

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	5,00	3,67	10,00	0,00	2,00	8,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,33	0,67	0,67	0,00	3,67	3,67
P. elongata	0,00	0,00	0,00	0,00	0,00	10,00
C. strictum	26,67	23,67	10,00	90,00	21,67	11,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	16,67	2,33	1,67	11,67	23,33
C. multicornis	3,33	0,00	0,00	0,00	0,00	0,00
M. edulis	5,00	3,67	6,67	8,33	6,67	16,67
B. improvisus	3,33	3,33	6,67	16,67	0,00	16,67
P. ciliata	0,67	0,00	1,67	0,00	0,67	3,33
C. volutator	8,33	6,67	5,33	13,33	6,67	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	3,33	2,00	1,67	0,00	3,33	3,33
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	30,00	25,00	0,00	11,67	20,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
Ectocarpus sp.	0,33	1,67	5,33	0,00	13,33	1,67
chironomids	1,67	0,00	0,00	0,00	0,00	2,00
total cover	58,00	92,00	75,33	130,00	81,33	120,67
Shannon index	1,60	1,31	1,43	0,98	1,30	1,47
species richness	11,00	9,00	10,00	5,00	9,00	11,00
evenness	0,67	0,60	0,62	0,61	0,59	0,61

12 mo old communities after 4 wk of experimental duration procedural controls

species	replicate 1	replicate 2	replicate 3
Enteromorpha sp.	2,00	1,67	0,33
Ulva sp.	0,00	0,00	0,00
Melosira sp.	3,67	2,33	4,00
P. elongata	0,00	0,00	0,00
C. strictum	46,67	15,00	46,67
Porphyra sp.	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00
L. flexuosa	36,67	20,00	11,67
C. multicornis	0,00	0,00	0,00
M. edulis	8,33	8,33	25,00
B. improvisus	1,67	36,67	13,33
P. ciliata	1,67	6,67	1,67
C. volutator	0,00	2,00	1,67
C. tortuosa	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00
diatoms other than Melosira sp.	10,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00
chironomids	0,33	0,00	0,00
Ectocarpus sp.	0,00	8,33	0,00
total cover	111,00	101,00	104,33
Shannon index	1,12	1,50	1,36
species richness	8,00	9,00	8,00
evenness	0,54	0,68	0,65

UVBR exposure **8th wk**

12 mo old communities after 8 wk of experimental duration 0.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	100,00	8,67	13,33	23,33	5,33	18,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	2,50	2,33	5,00	3,33	8,33	6,67
P. elongata	0,00	0,00	1,67	0,00	0,00	0,00
C. strictum	25,00	50,00	33,33	35,00	0,67	50,00
Porphyra sp.	7,50	1,67	0,00	0,00	0,00	0,33
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	15,00	8,33	16,67	5,33	3,33	0,00
C. multicornis	0,50	0,00	11,67	0,33	6,67	0,00
M. edulis	55,00	30,00	20,00	73,33	6,67	63,33
B. improvisus	25,00	13,33	23,33	13,33	0,33	6,67
P. ciliata	17,50	8,33	8,33	10,00	3,67	13,33
C. volutator	2,50	6,67	0,33	5,00	6,67	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	10,33
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	15,00	8,33	16,67	16,67	5,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
Achnanthes sp.	0,00	0,00	0,00	3,33	0,00	0,00
chironomids	0,00	0,00	0,00	0,00	1,67	0,00
total cover	265,50	137,67	150,33	189,00	48,33	169,33
Shannon index	1,64	1,64	1,72	1,49	1,54	1,48
species richness	10,00	9,00	10,00	10,00	10,00	8,00
evenness	0,71	0,75	0,75	0,65	0,67	0,71

12 mo old communities after 8 wk of experimental duration 1 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	10,50	10,33	11,67	53,33	30,00	20,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	3,33
Melosira sp.	10,00	3,33	0,33	6,67	10,00	20,00
P. elongata	0,00	5,00	43,33	0,00	0,00	0,00
C. strictum	35,00	40,00	25,00	30,00	5,33	0,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	2,00	0,00	0,00	0,00
L. flexuosa	2,50	7,00	3,33	13,33	2,00	0,00
C. multicornis	0,00	0,00	0,00	1,00	2,00	6,67
M. edulis	65,00	33,33	20,00	36,67	18,33	15,00
B. improvisus	25,00	23,33	5,00	2,00	15,33	10,00
P. ciliata	15,00	6,67	3,67	7,00	20,00	13,33
C. volutator	1,00	6,67	3,67	3,33	2,00	1,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	3,33	20,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	5,00	5,00	16,67	13,33	2,00	13,67
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00	1,67	0,00
total cover	169,00	140,67	138,00	186,67	108,67	103,33
Shannon index	1,46	1,63	1,35	1,67	1,61	1,44
species richness	8,00	9,00	11,00	10,00	10,00	9,00
evenness	0,70	0,74	0,56	0,73	0,70	0,66

12 mo old communities after 8 wk of experimental duration 2 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	15,00	30,00	6,67	3,67	3,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	5,00	0,67	5,00	11,67	3,67	11,67
P. elongata	0,00	0,00	1,67	0,00	0,00	0,00
C. strictum	35,00	20,00	27,00	10,67	30,00	20,00
Porphyra sp.	0,00	0,33	0,00	0,00	0,00	1,67
P. litoralis	5,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	7,50	11,67	11,67	0,33	0,00	0,33
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	45,00	30,00	33,33	13,33	66,67	33,33
B. improvisus	20,00	13,33	0,67	1,67	16,67	13,33
P. ciliata	10,00	6,67	6,67	5,00	16,67	13,33
C. volutator	3,00	3,33	1,67	0,33	3,33	5,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	5,00	0,00	3,33	0,00	0,00	30,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	20,00	5,00	11,67	30,00	3,33	1,67
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,33	3,33	1,67
total cover	155,50	106,00	132,67	80,00	147,33	135,33
Shannon index	1,58	1,75	1,55	1,07	1,35	1,70
species richness	9,00	9,00	10,00	9,00	8,00	11,00
evenness	0,72	0,80	0,67	0,49	0,65	0,71

12 mo old communities after 8 wk of experimental duration 4 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	40,00	86,67	20,00	50,00	0,00	0,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	7,50	3,33	2,00	8,33	8,33	3,67
P. elongata	0,00	0,00	0,00	0,00	0,00	13,33
C. strictum	25,00	30,00	46,67	13,33	30,00	30,00
Porphyra sp.	2,50	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	7,50	1,67	6,67	3,67	1,67	0,00
C. multicornis	0,50	0,00	0,00	0,00	0,00	0,00
M. edulis	50,00	46,67	20,00	23,33	46,67	46,67
B. improvisus	25,00	10,00	0,33	2,00	13,33	6,67
P. ciliata	30,00	6,67	10,00	16,67	16,67	10,00
C. volutator	0,00	5,00	3,33	5,00	5,00	5,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	1,67	5,00	0,00	1,67
unidentified green alga	0,00	0,00	3,33	23,33	0,00	0,00
chironomids	0,00	0,00	5,00	1,67	0,00	0,00
total cover	188,00	190,00	119,00	152,33	121,67	117,33
Shannon index	1,71	1,40	1,45	1,37	1,42	1,24
species richness	9,00	8,00	10,00	10,00	7,00	8,00
evenness	0,78	0,68	0,63	0,59	0,73	0,60

12 mo old communities after 8 wk of experimental duration 8 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	13,33	80,00	0,67	66,67	30,00	11,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	3,33	3,33	1,67	3,67	23,33	2,33
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	26,67	10,00	40,00	20,33	3,67	5,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	6,67	0,00	0,00	0,00
L. flexuosa	2,00	0,33	0,00	0,00	2,00	0,33
C. multicornis	0,00	0,33	0,00	0,00	0,00	0,00
M. edulis	30,00	53,33	53,33	16,67	40,00	16,67
B. improvisus	3,67	16,67	33,33	0,00	10,00	0,00
P. ciliata	8,33	13,33	10,00	23,33	10,00	5,00
C. volutator	5,00	5,00	3,33	6,67	3,33	0,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	3,33	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	1,67
diatoms other than Melosira sp.	5,00	0,00	10,00	0,00	5,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	1,67	0,33	0,00
total cover	97,33	182,33	159,00	142,33	127,67	43,00
Shannon index	1,56	1,41	1,45	1,41	1,37	1,30
species richness	8,00	9,00	8,00	8,00	9,00	8,00
evenness	0,75	0,64	0,70	0,68	0,62	0,62

12 mo old communities after 8 wk of experimental duration controls

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	33,33	40,00	13,33	23,33	3,33	6,67
Ulva sp.	6,67	23,33	0,00	0,00	0,00	0,00
Melosira sp.	5,33	3,67	0,67	0,67	10,00	23,33
P. elongata	1,67	0,00	0,00	8,33	0,00	0,00
C. strictum	26,67	30,00	5,33	63,33	15,00	13,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	8,67	3,33	2,00	3,67	6,67	1,00
C. multicornis	3,33	0,00	0,33	0,33	0,00	0,00
M. edulis	43,33	30,00	33,33	30,00	50,00	23,33
B. improvisus	5,00	3,33	23,67	20,00	10,33	5,00
P. ciliata	11,67	20,00	6,67	7,00	13,33	5,00
C. volutator	5,00	6,67	5,00	5,33	0,33	2,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	3,33	20,00	13,33	0,00	3,67	11,67
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	5,00	8,33	0,00
unidentified green alga	0,00	6,67	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00	0,00	1,67
B. plumosa	0,00	0,00	0,00	0,00	0,00	1,67
total cover	154,00	187,00	103,67	167,00	121,00	94,67
Shannon index	1,87	1,92	1,80	1,54	1,46	1,51
species richness	12,00	11,00	10,00	10,00	9,00	11,00
evenness	0,75	0,80	0,78	0,67	0,66	0,63

12 mo old communities after 8 wk of experimental duration procedural controls

species	replicate 1	replicate 2	replicate 3
Enteromorpha sp.	7,33	8,33	16,67
Ulva sp.	3,33	0,00	0,00
Melosira sp.	50,00	0,67	2,00
P. elongata	0,00	0,00	0,00
C. strictum	3,33	6,67	30,00
Porphyra sp.	0,00	0,00	0,00
P. litoralis	3,33	0,00	0,00
L. flexuosa	3,67	0,33	0,67
C. multicornis	3,33	0,00	1,00
M. edulis	23,33	80,00	53,33
B. improvisus	2,00	23,33	20,00
P. ciliata	4,33	23,33	5,33
C. volutator	2,00	2,00	2,00
C. tortuosa	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00
diatoms other than Melosira sp.	8,33	0,00	0,00
unidentified green alga	0,00	0,00	0,00
total cover	114,33	144,67	131,00
Shannon index	1,29	1,30	1,51
species richness	12,00	8,00	9,00
evenness	0,52	0,62	0,69

UVBR exposure **12th wk**

12 mo old communities after 12 wk of experimental duration 0.5 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	2,00	2,00	15,00	10,00	5,00	2,00
Ulva sp.	0,00	0,00	0,00	0,00	5,00	0,00
Melosira sp.	5,33	2,00	3,33	0,67	18,33	10,67
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	76,67	100,00	36,67	46,67	50,00	43,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	2,00	2,00	1,67	0,33	0,00	1,67
C. multicornis	0,00	0,00	5,00	0,00	0,00	0,00
M. edulis	28,33	20,00	33,33	86,67	11,67	53,33
B. improvisus	8,33	6,67	16,67	7,00	16,67	3,67
P. ciliata	23,33	13,33	30,00	20,00	11,67	18,33
C. volutator	1,67	3,33	0,00	1,67	0,00	1,67
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	10,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	13,33	0,00	23,33	15,00
unidentified green alga	0,00	10,00	16,67	3,33	0,00	16,67
Chironomiden	0,00	0,00	0,00	1,67	0,00	0,00
Nereis sp.	0,00	0,00	0,00	0,00	3,33	0,00
Gammarus sp.	0,00	0,00	0,00	0,00	5,00	0,00
total cover	147,67	159,33	171,67	178,00	150,00	176,33
Shannon index	1,28	1,08	1,54	1,29	1,23	1,32
species richness	8,00	9,00	9,00	10,00	9,00	10,00
evenness	0,61	0,49	0,70	0,56	0,56	0,58

12 mo old communities after 12 wk of experimental duration					1 h treatment	
species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	5,33	0,00	2,00	20,00	30,00	5,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	6,67
Melosira sp.	8,67	3,67	2,00	8,33	8,67	36,67
P. elongata	0,00	2,00	70,00	0,00	0,00	3,33
C. strictum	60,00	53,33	6,67	73,33	46,67	33,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	10,00	6,67	5,33	0,00	1,67	0,00
C. multicornis	0,00	0,00	0,33	0,00	1,67	0,00
M. edulis	21,67	28,33	10,00	16,67	5,00	17,00
B. improvisus	32,00	23,67	15,00	8,33	6,67	7,00
P. ciliata	10,00	10,00	18,33	20,00	16,67	26,67
C. volutator	0,00	0,33	0,33	1,67	3,33	2,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	6,67	3,33	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	0,00	10,00	8,33	3,33
unidentified green alga	0,00	0,00	0,00	0,00	0,00	3,33
Gammarus sp.	3,33	0,00	0,00	0,00	0,00	0,00
B. plumosa	0,00	0,00	0,00	0,00	13,33	0,00
total cover	151,00	128,00	130,00	165,00	145,33	144,33
Shannon index	1,45	1,38	1,10	1,43	1,47	1,37
species richness	8,00	8,00	10,00	8,00	11,00	10,00
evenness	0,70	0,66	0,48	0,69	0,61	0,59

12 mo old communities after 12 wk of experimental duration					2 h treatment	
species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	1,67	10,00	10,33	33,33	6,67	3,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	16,67	0,33	3,67	16,67	6,67	10,33
P. elongata	0,00	0,00	0,00	3,33	0,00	0,00
C. strictum	70,00	100,00	73,33	13,33	33,33	36,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	20,00	2,33	0,00	0,00	0,00	0,33
C. multicornis	1,67	0,00	0,00	0,00	0,00	0,00
M. edulis	15,00	10,00	10,00	15,00	96,67	50,00
B. improvisus	15,00	0,33	3,67	7,00	10,00	12,33
P. ciliata	16,67	10,00	20,00	13,33	8,33	20,00
C. volutator	2,00	0,00	2,00	3,33	0,33	3,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	13,33	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	1,67
diatoms other than Melosira sp.	18,33	0,00	20,00	0,00	3,33	5,00
unidentified green alga	0,00	3,33	0,00	0,00	0,00	0,00
Gammarus sp.	0,00	6,67	0,00	0,00	0,00	0,00
total cover	190,33	143,00	143,00	105,33	165,33	143,00
Shannon index	1,54	0,89	1,15	1,45	1,10	1,39
species richness	10,00	9,00	7,00	8,00	7,00	9,00
evenness	0,67	0,40	0,59	0,70	0,56	0,63

12 mo old communities after 12 wk of experimental duration 4 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	2,33	2,00	23,67	40,00	4,00	7,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	8,33	0,67	3,67	8,33	11,67	23,33
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	60,00	76,67	70,00	26,67	43,33	36,67
Porphyra sp.	1,67	0,00	0,00	0,00	0,00	1,67
P. litoralis	0,00	1,67	1,67	1,67	0,00	0,00
L. flexuosa	5,00	0,00	0,00	2,00	0,33	0,33
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	30,00	46,67	5,33	1,00	23,33	23,33
B. improvisus	17,00	16,67	2,33	0,33	13,33	7,00
P. ciliata	20,00	26,67	23,33	30,00	16,67	13,33
C. volutator	3,33	1,67	0,00	6,67	1,67	0,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	3,33	0,00	0,00	1,67	0,00
diatoms other than Melosira sp.	3,33	0,00	30,00	20,00	0,00	16,67
unidentified green alga	3,33	3,33	3,33	0,00	0,00	11,67
total cover	154,33	179,33	163,33	136,67	116,00	141,33
Shannon index	1,50	1,35	1,14	1,32	1,41	1,25
species richness	10,00	10,00	8,00	9,00	9,00	10,00
evenness	0,65	0,59	0,55	0,60	0,64	0,54

12 mo old communities after 12 wk of experimental duration 8 h treatment

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,67	43,33	20,33	50,00	8,33	53,33
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	3,67	2,00	3,33	3,67	16,67	3,33
P. elongata	0,00	0,00	1,67	0,00	0,00	0,00
C. strictum	73,33	63,33	33,33	16,67	36,67	0,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	1,67	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	1,67	0,67	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	10,00	53,33	83,33	2,00	53,33	23,33
B. improvisus	12,33	14,33	6,67	0,67	12,00	0,67
P. ciliata	16,67	13,33	20,00	20,00	20,00	31,67
C. volutator	0,33	2,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	2,00	0,00	0,00	0,00	10,00
diatoms other than Melosira sp.	3,33	1,67	25,00	43,33	0,00	0,00
unidentified green alga	0,00	0,00	6,67	10,00	10,00	3,33
Gammarus sp.	10,00	0,00	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00	0,00	1,67
total cover	130,33	195,33	202,00	148,00	157,67	127,33
Shannon index	1,05	1,48	1,27	1,02	1,34	1,05
species richness	8,00	8,00	9,00	8,00	8,00	8,00
evenness	0,50	0,71	0,58	0,49	0,65	0,50

12 mo old communities after 12 wk of experimental duration controls

species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 5	replicate 6
Enteromorpha sp.	0,00	23,33	5,33	0,00	0,00	0,67
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,33	3,33	2,00	5,00	20,00	53,33
P. elongata	0,00	0,00	23,33	0,00	0,00	0,00
C. strictum	100,00	46,67	43,33	20,00	26,67	30,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	1,67	0,00	1,67	0,00	0,00
L. flexuosa	0,00	0,33	8,33	0,00	5,00	1,67
C. multicornis	0,67	0,00	1,67	0,00	0,00	0,00
M. edulis	30,00	6,67	13,67	46,67	60,00	17,00
B. improvisus	0,67	0,33	26,67	33,33	3,33	7,33
P. ciliata	13,33	23,33	23,33	30,00	23,33	8,33
C. volutator	1,67	5,00	3,33	3,33	0,33	1,67
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	40,00	0,00	3,33	6,67	16,67
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than Melosira sp.	0,00	0,00	13,67	0,00	11,67	6,67
unidentified green alga	0,00	10,00	0,00	0,00	0,00	0,00
Gammarus sp.	3,33	5,00	0,00	0,00	0,00	0,00
total cover	150,00	165,67	164,67	143,33	157,00	143,33
Shannon index	0,91	1,56	1,52	1,53	1,29	1,28
species richness	8,00	12,00	10,00	8,00	8,00	9,00
evenness	0,44	0,63	0,66	0,74	0,62	0,58

12 mo old communities after 12 wk of experimental duration procedural controls

species	replicate 1	replicate 2	replicate 3
Enteromorpha sp.	2,00	0,00	missing
Ulva sp.	3,33	0,00	missing
Melosira sp.	36,67	1,00	missing
P. elongata	0,00	0,00	missing
C. strictum	16,67	53,33	missing
Porphyra sp.	0,00	0,00	missing
P. litoralis	0,00	0,00	missing
L. flexuosa	0,00	2,00	missing
C. multicornis	0,00	1,67	missing
M. edulis	10,33	28,33	missing
B. improvisus	3,67	16,67	missing
P. ciliata	13,33	10,00	missing
C. volutator	0,00	5,00	missing
C. tortuosa	0,00	0,00	missing
M. membranacea	0,00	0,00	missing
Fucus sp.	0,00	1,67	missing
diatoms other than Melosira sp.	33,33	0,00	missing
unidentified green alga	0,00	0,00	missing
B. plumosa	3,33	0,00	missing
total cover	122,67	119,67	missing
Shannon index	0,99	1,44	missing
species richness	9,00	9,00	missing
evenness	0,45	0,66	missing

Succession panels **2000-2001**

Succession on undisturbed panels in 2000. 6th wk.

At each position one panel was randomly chosen from four replicates.
Positions were evenly distributed within the bay.

species	position 1	position 2	position 3	postion 4	position 5	position 6	postion 7	position 8
Enteromorpha sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	13,33	0,00	0,00	0,00
Melosira sp.	0,00	0,67	0,00	0,67	0,00	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	16,67	2,33	6,67	2,00	10,00	13,33	15,00	8,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	100,00	70,00	63,33	60,00	66,67	40,00	40,00	56,67
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	8,33	5,00	15,00	8,33	20,00	10,00	8,33	13,33
B. improvisus	2,00	4,00	7,00	0,00	0,00	1,67	2,00	0,00
P. ciliata	0,00	0,33	0,00	0,00	0,00	0,00	0,00	0,00
C. volutator	3,33	5,00	6,67	3,33	0,00	3,33	3,33	1,67
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than *Melosira sp.*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ectocarpus sp.	16,67	5,00	7,00	8,33	13,33	20,00	5,00	10,00
chironomids	0,00	0,00	0,00	0,00	0,00	0,00	3,33	0,00
total cover	147,00	92,33	105,67	82,67	123,33	88,33	77,00	90,33
Shannon index	0,82	0,77	1,11	0,68	1,07	1,09	1,13	0,87
species number	6,00	8,00	6,00	6,00	5,00	6,00	7,00	5,00
evenness	0,46	0,37	0,62	0,38	0,67	0,61	0,58	0,54

Succession on undisturbed panels in 2000. 8th wk.

species	position 1	position 2	position 3	postion 4	position 5	position 6	postion 7	position 8
Enteromorpha sp.	0,00	30,00	0,00	0,00	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	6,67	0,33	0,00	0,67	0,67	0,67	0,00	0,33
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	13,67	26,67	16,67	15,00	36,67	10,00	86,67	50,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	90,00	76,67	80,00	66,67	53,33	70,00	16,67	43,33
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,33	0,00
M. edulis	30,00	33,33	33,33	26,67	23,33	40,00	30,00	30,00
B. improvisus	3,33	0,00	6,67	3,33	1,67	6,67	0,33	3,33
P. ciliata	0,33	0,00	0,33	0,00	0,00	0,00	0,00	0,00
C. volutator	3,33	5,00	5,00	13,67	13,33	8,33	3,33	5,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than *Melosira sp.*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ectocarpus sp.	1,67	1,67	3,33	0,33	10,00	3,33	0,00	0,00
chironomids	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
total cover	149,00	173,67	145,33	126,33	139,00	139,00	137,33	132,00
Shannon index	1,03	1,37	1,19	1,26	1,30	1,21	1,00	1,29
species number	8,00	7,00	7,00	7,00	7,00	7,00	6,00	6,00
evenness	0,50	0,70	0,61	0,65	0,67	0,62	0,56	0,72

Succession on undisturbed panels in 2000. 10th wk.

species	position 1	position 2	position 3	postion 4	position 5	position 6	postion 7	position 8
Enteromorpha sp.	0,00	10,00	0,00	0,00	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	3,33	0,67	1,67	2,33	0,00	2,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	13,33	28,33	15,00	15,00	30,00	6,67	70,00	18,33
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	63,33	60,00	70,00	40,00	30,00	66,67	36,67	23,33
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	23,33	40,00	36,67	53,33	26,67	43,33	40,00	16,67
B. improvisus	0,33	3,33	5,00	3,33	0,00	5,33	6,67	3,67
P. ciliata	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. volutator	0,00	5,00	5,33	3,33	11,67	3,67	5,00	3,33
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than *Melosira sp.*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ectocarpus sp.	0,00	0,00	40,00	1,67	0,00	20,00	1,67	3,33
chironomids	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
total cover	103,67	147,33	173,67	119,00	98,33	147,67	160,00	68,67
Shannon index	0,92	1,42	1,12	1,19	1,33	1,07	1,29	1,37
species number	5,00	7,00	7,00	7,00	4,00	7,00	6,00	6,00
evenness	0,57	0,73	0,57	0,61	0,96	0,55	0,72	0,76

Succession on undisturbed panels in 2000. 12th wk.

species	position 1	position 2	position 3	postion 4	position 5	position 6	postion 7	position 8
Enteromorpha sp.	0	0	0	0	0	0	0	0,5
Ulva sp.	0	0	0	0	0	0	0	0
Melosira sp.	0,5	5,5	0	30	0	0,5	0	0
P. elongata	0	0	0	0	25	0	0	10
C. strictum	7,5	10	7,5	7,5	20	25	25	25
Porphyra sp.	0	0	0	0	0	0	0	0
P. litoralis	0	0	0	0	0	0	0	0
L. flexuosa	0	0	20	0	0	0	0	0
C. multicornis	0	0	0	0	0	0	0	0
M. edulis	100	80	100	80	45	100	95	90
B. improvisus	10	5	10	20	15	0	0	5,5
P. ciliata	0	2,5	0	3	3	0	0,5	0
C. volutator	0	0	0	0	2,5	0	0	0
C. tortuosa	0	0	0	0	0	0	0	0
M. membranacea	0	0	0	0	0	0	0	0
Fucus sp.	0	0	0	0	0	0	0	0
diatoms other than *Melosira sp.*	0	0	0	0	0	0	0	0
unidentified green alga	0	0	0	0	0	0	0	0
Ectocarpus sp.	0	0	0	0	0	0	0	0
chironomids	0	0	0	0	0	0	0	0
total cover	118,00	103,00	137,50	140,50	110,50	125,50	120,50	131,00
Shannon index	0,52	0,66	0,86	0,84	1,13	0,50	0,54	0,73
species number	4,00	5,00	4,00	5,00	6,00	3,00	3,00	5,00
evenness	0,38	0,41	0,62	0,52	0,63	0,46	0,49	0,45

Succession on undisturbed panels in 2000. 14th wk.

species	position 1	position 2	position 3	postion 4	position 5	position 6	postion 7	position 8
Enteromorpha sp.	0,00	0,00	0,00	0,00	0,00	0,33	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	13,67	1,67	0,00	0,33	8,33	4,00	0,33
P. elongata	0,00	0,00	0,00	26,67	0,00	3,33	0,00	0,00
C. strictum	0,00	6,67	0,00	15,00	10,00	4,00	4,00	3,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,33	0,00	0,00	0,00	0,33	0,00	0,00
C. multicornis	0,00	1,67	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	60,00	100,00	100,00	86,67	60,00	100,00	96,67
B. improvisus	0,00	23,33	0,00	1,67	5,33	23,33	0,00	3,33
P. ciliata	3,33	13,33	0,00	0,00	8,33	10,00	0,00	1,67
C. volutator	0,00	1,67	0,00	0,00	3,33	3,67	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	3,33	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than *Melosira sp.*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Zoothamnion sp.	0,00	8,33	0,00	0,00	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
total cover	103,33	132,33	101,67	143,33	114,00	113,33	108,00	105,67
Shannon index	0,14	1,26	0,02	0,54	0,86	1,14	0,19	0,37
species number	2,00	10,00	2,00	4,00	6,00	9,00	3,00	5,00
evenness	0,21	0,55	0,02	0,39	0,48	0,52	0,18	0,23

Succession on undisturbed panels in 2000. 16th wk.

species	position 1	position 2	position 3	postion 4	position 5	position 6	postion 7	position 8
Enteromorpha sp.	0,00	0,00	10,00	0,00	0,00	0,33	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	1,67	0,00	0,67	3,67	0,00	0,00	1,67
P. elongata	1,67	3,33	0,00	0,00	5,00	0,00	0,00	0,00
C. strictum	1,67	46,67	6,67	26,67	16,67	3,33	3,33	26,67
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,33	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	93,33	100,00	100,00	76,67	100,00	100,00	100,00
B. improvisus	0,67	6,67	0,00	0,00	13,33	0,33	0,00	0,00
P. ciliata	2,00	8,33	3,33	3,33	10,33	1,67	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00	1,67	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than *Melosira sp.*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Vorticella sp.	3,33	0,00	0,00	0,00	0,00	0,00	1,67	0,00
chironomids	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
total cover	109,33	160,00	120,00	130,67	127,67	105,67	105,00	128,33
Shannon index	0,25	0,96	0,62	0,62	1,08	0,26	0,16	0,52
species number	6,00	6,00	4,00	4,00	8,00	5,00	3,00	3,00
evenness	0,14	0,54	0,45	0,45	0,52	0,16	0,14	0,47

Succession on undisturbed panels in 2000. 18th wk.

species	position 1	position 2	position 3	postion 4	position 5	position 6	postion 7	position 8
Enteromorpha sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	2,33	0,00	0,00	0,33	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	6,67	0,00	0,00	5,00
C. strictum	0,00	23,33	0,00	0,00	1,67	0,00	0,00	5,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	93,33	100,00	100,00	86,67	100,00	100,00	100,00
B. improvisus	0,00	10,00	0,33	0,00	13,33	0,00	0,00	3,33
P. ciliata	0,00	6,67	0,00	0,33	11,67	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	1,67	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than *Melosira sp.*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	1,67	0,00	0,00	0,00
Ectocarpus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
total cover	100,00	135,67	100,33	100,33	122,00	100,00	101,67	113,33
Shannon index	0,00	0,90	0,02	0,02	0,77	0,00	0,08	0,35
species number	1,00	5,00	2,00	2,00	7,00	1,00	2,00	4,00
evenness	0,00	0,56	0,03	0,03	0,39	0,00	0,12	0,25

Succession on undisturbed panels in 2000. 20th wk.

species	position 1	position 2	position 3	postion 4	position 5	position 6	postion 7	position 8
Enteromorpha sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ulva sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Melosira sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. strictum	0,00	0,00	5,00	0,00	16,67	0,00	0,00	10,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
L. flexuosa	0,00	11,67	0,00	0,00	1,67	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	100,00	86,67	100,00	100,00	93,33	100,00	100,00	100,00
B. improvisus	0,00	0,00	1,67	0,00	8,33	3,33	0,00	1,67
P. ciliata	0,33	0,00	3,33	0,00	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms other than *Melosira sp.*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ectocarpus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
chironomids	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
total cover	102,00	98,33	110,00	100,00	120,00	103,33	103,33	111,67
Shannon index	0,04	0,36	0,40	0,00	0,71	0,14	0,03	0,38
species number	3,00	2,00	4,00	1,00	4,00	2,00	2,00	3,00
evenness	0,03	0,53	0,29	0,00	0,52	0,21	0,05	0,34

Succession on undisturbed panels in 2000. 52nd wk.

Each position contained four replicate panels. Values shown in the results are averaged over replicates and positions.

	Position 1				Position 2			
species	replicate 1	replicate 2	replicate 3	replicate 4	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms	10,00	10,00	13,34	13,34	10,00	13,34	23,34	13,34
C. strictum	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. ciliata	4,00	0,00	2,00	0,00	0,34	2,34	1,00	2,00
L. flexuosa	0,00	0,00	0,00	0,00	0,00	0,00	1,67	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	75,00	50,00	53,34	116,67	126,67	120,00	116,67	113,34
B. improvisus	11,67	5,00	0,00	2,00	0,00	2,00	3,34	1,67
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ephelota gemmipara	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Laminaria sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Zoothamnion sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Vorticella sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
total cover	100,67	65,00	68,68	132,01	137,01	137,68	146,02	130,35
Shannon index	0,56	0,3	0,155	0,085	0,018	0,17	0,24	0,16
species number	3	2	2	2	2	3	4	3
evenness	0,51	0,44	0,22	0,12	0,027	0,16	0,17	0,15

	Position 3				Position 4			
	replicate 1	replicate 2	replicate 3	replicate 4	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	missing	1,67	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
diatoms	13,34	3,34	6,67	missing	53,34	5,00	56,67	10,00
C. strictum	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
Porphyra sp.	3,34	0,00	0,00	missing	0,00	0,00	0,00	0,00
P. ciliata	1,67	2,00	1,67	missing	0,34	0,67	0,34	0,34
L. flexuosa	0,00	0,00	0,00	missing	10,00	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
M. edulis	126,67	133,33	126,67	missing	76,67	100,00	100,00	100,00
B. improvisus	0,34	0,00	3,34	missing	0,00	3,34	0,00	3,34
Fucus sp.	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
Ephelota gemmipara	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
Laminaria sp.	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
Zoothamnion sp.	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
Vorticella sp.	0,00	0,00	0,00	missing	0,00	0,00	0,00	0,00
total cover	145,36	138,67	138,35	missing	142,02	109,01	157,01	113,68
Shannon index	0,2	0,077	0,18	missing	0,46	0,18	0,022	0,16
species number	4	2	3	missing	4	3	2	3
evenness	0,15	0,11	0,17	missing	0,34	0,16	0,032	0,15

	Position 5				Position 6			
	replicate 1	replicate 2	replicate 3	replicate 4	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms	20,00	3,34	43,34	83,34	83,34	96,67	16,67	16,67
C. strictum	0,00	46,67	0,00	0,00	0,00	0,00	0,00	0,34
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. ciliata	0,67	0,67	2,34	0,67	0,00	0,00	0,34	0,34
L. flexuosa	0,00	56,67	0,00	10,00	0,00	10,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. edulis	101,67	41,67	100,00	5,00	0,00	0,00	100,00	100,00
B. improvisus	0,00	8,34	6,67	20,00	3,34	15,00	1,67	1,67
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ephelota gemmipara	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Laminaria sp.	20,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Zoothamnion sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Vorticella sp.	0,00	0,00	0,00	3,34	0,00	0,00	6,67	0,00
total cover	142,34	157,36	152,35	122,35	86,68	121,67	125,35	119,02
Shannon index	0,47	1,26	0,33	1,23	0	0,67	0,33	0,13
species number	3	5	3	5	1	2	4	4
evenness	0,43	0,78	0,3	0,77	error	0,97	0,24	0,092

	Position 7				Position 8			
	replicate 1	replicate 2	replicate 3	replicate 4	replicate 1	replicate 2	replicate 3	replicate 4
Enteromorpha sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
C. tortuosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. litoralis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
diatoms	11,67	1,67	23,34	20,00	53,34	63,34	30,00	40,00
C. strictum	1,67	0,00	25,00	10,00	6,67	30,00	0,00	0,00
Porphyra sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. ciliata	0,34	0,34	3,67	0,34	0,67	0,00	2,00	1,00
L. flexuosa	0,00	0,00	0,00	0,00	3,34	0,00	0,00	0,00
C. multicornis	0,00	0,00	0,00	0,00	1,67	0,00	0,00	0,00
M. edulis	115,00	0,00	116,67	103,34	100,00	100,00	100,00	53,34
B. improvisus	6,67	1,67	10,00	0,00	1,67	3,34	0,00	0,00
Fucus sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
unidentified green alga	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ephelota gemmipara	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Laminaria sp.	0,00	0,00	0,00	6,67	0,00	0,00	0,00	3,34
C. volutator	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,67
M. membranacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Callithamnion sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
P. elongata	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Zoothamnion sp.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Vorticella sp.	0,00	1,67	0,00	0,00	0,00	0,00	0,00	0,00
total cover	135,35	5,35	178,68	140,35	167,36	196,68	132,00	99,35
Shannon index	0,29	0,94	0,77	0,51	0,54	0,64	0,096	0,43
species number	4	3	4	4	6	3	2	4
evenness	0,22	0,85	0,56	0,37	0,3	0,58	0,14	0,31

Ultraviolet radiation (unweighted: ambient + enhanced UVBR) measured at the study site using a LiCor UW-1800 spectroradiometer. 30.06.1999 at local noon.
Ambient radiation (W m-2)

	Water depth				
Wavelength	10 cm	20 cm	30 cm	40 cm	50 cm
300	0,00325	0,001625	0,00125	0,001125	-0,25
302	0,00625	0,003375	0,001375	0,0005	0,25
304	0,01137	0,005	0,002	0,000875	0,75
306	0,02024	0,009374	0,002875	0,002125	0,875
308	0,03312	0,0155	0,00525	0,0025	0,875
310	0,05087	0,02287	0,0075	0,00325	1,625
312	0,07099	0,03249	0,01124	0,0045	2,125
314	0,09399	0,04337	0,01587	0,0065	3,375
316	0,1192	0,056	0,02024	0,008749	5,124
318	0,1463	0,06862	0,02587	0,01124	5,624
320	0,1739	0,08312	0,03212	0,0135	7,5
322	0,2086	0,1	0,04	0,01737	9,624
324	0,2519	0,1231	0,05012	0,02124	12
326	0,2982	0,1476	0,06	0,02662	15
328	0,3385	0,1716	0,07024	0,03112	17,62
330	0,3719	0,1916	0,07949	0,03549	20,74
332	0,3901	0,2047	0,08662	0,03937	23,12
334	0,4032	0,2158	0,09261	0,04287	24,87
336	0,4145	0,2313	0,09761	0,046	27,24
338	0,4299	0,2471	0,1031	0,04912	30,49
340	0,445	0,2597	0,1112	0,05349	33,24
342	0,4552	0,272	0,12	0,05762	36,62
344	0,4652	0,2821	0,1262	0,06049	38,62
346	0,471	0,2949	0,1319	0,06387	41,24
348	0,4854	0,3064	0,1387	0,06774	44,49
350	0,5559	0,3608	0,1686	0,08236	55,62
352	0,5878	0,384	0,1823	0,08986	62,24
354	0,6265	0,4064	0,1938	0,09699	67,24
356	0,6573	0,4276	0,2072	0,1027	71,62
358	0,6964	0,4514	0,2199	0,1108	77,24
360	0,7546	0,4899	0,2438	0,124	86,87
362	0,8393	0,5518	0,2771	0,1417	99,74
364	0,9481	0,6256	0,3189	0,1629	116,4
366	1,07	0,6974	0,3593	0,1861	133,8
368	1,149	0,7587	0,3937	0,2058	149,3
370	1,214	0,8035	0,4207	0,2202	160,2
372	1,27	0,8383	0,4416	0,2336	168,7
374	1,33	0,8739	0,4683	0,2491	180,7
376	1,402	0,9257	0,504	0,2673	195,8
378	1,455	0,9663	0,53	0,2832	209,2
380	1,479	1,001	0,5406	0,2918	215,3
382	1,485	1,011	0,5422	0,2941	217,9
384	1,475	1,022	0,5513	0,3011	224,3
386	1,549	1,067	0,583	0,3213	240,4
388	1,649	1,15	0,6294	0,3479	260,6
390	1,749	1,25	0,6801	0,3791	281,3
392	1,834	1,319	0,72	0,4009	298,9
394	1,969	1,402	0,78	0,4362	326,5
396	2,277	1,61	0,8939	0,508	377
398	2,711	1,936	1,058	0,6112	453,4
400	3,118	2,277	1,244	0,7222	542,9

Enhanced UVR (W m-2)

	Water depth				
Wavelength	10 cm	20 cm	30 cm	40 cm	50 cm
300	0,02174	0,007374	0,003	0,0015	0,0005
302	0,03037	0,01062	0,00425	0,001125	0,000625
304	0,04149	0,0145	0,00575	0,002625	0,0005
306	0,05549	0,02062	0,008249	0,00375	0,001375
308	0,07374	0,02887	0,012	0,005	0,001625
310	0,09462	0,03837	0,016	0,006624	0,002
312	0,1162	0,04874	0,02049	0,008624	0,00325
314	0,1381	0,06062	0,02687	0,01074	0,004
316	0,1577	0,07299	0,03274	0,01362	0,005374
318	0,1799	0,08512	0,03824	0,01662	0,006374
320	0,2023	0,09836	0,04587	0,02024	0,008124
322	0,2261	0,1147	0,05287	0,02424	0,01087
324	0,2572	0,1331	0,06349	0,029	0,013
326	0,2898	0,1556	0,07499	0,03424	0,016
328	0,3152	0,1769	0,08486	0,04012	0,02012
330	0,3317	0,1942	0,09462	0,04499	0,02374
332	0,3413	0,2086	0,1031	0,04987	0,02662
334	0,3447	0,2178	0,1106	0,05412	0,029
336	0,3507	0,2278	0,1182	0,05774	0,03249
338	0,3573	0,2392	0,1253	0,06187	0,03637
340	0,3674	0,2544	0,1336	0,06724	0,04024
342	0,3767	0,2669	0,1388	0,07162	0,04387
344	0,3757	0,2754	0,144	0,07624	0,04824
346	0,3741	0,2824	0,1527	0,08061	0,05274
348	0,3732	0,2938	0,1623	0,08624	0,05787
350	0,4211	0,3516	0,1957	0,1058	0,07412
352	0,4436	0,3749	0,2129	0,1169	0,08249
354	0,4578	0,3984	0,2289	0,1266	0,09012
356	0,4662	0,423	0,2434	0,1348	0,09862
358	0,4828	0,4464	0,2604	0,1444	0,1076
360	0,535	0,4876	0,2921	0,1628	0,1226
362	0,6135	0,5483	0,3397	0,1893	0,144
364	0,6964	0,6315	0,3937	0,2206	0,1706
366	0,769	0,7188	0,4427	0,2529	0,1977
368	0,8186	0,7763	0,4785	0,2784	0,2186
370	0,8441	0,8051	0,5056	0,2976	0,2337
372	0,867	0,8291	0,53	0,3139	0,2502
374	0,9164	0,8652	0,5652	0,3343	0,2709
376	0,9722	0,9264	0,6135	0,3616	0,2999
378	1,015	0,9846	0,657	0,3868	0,3263
380	1,035	1,015	0,6769	0,4058	0,3444
382	1,037	1,014	0,6942	0,4174	0,3544
384	1,033	1,012	0,7074	0,4292	0,3662
386	1,064	1,07	0,7464	0,4593	0,3959
388	1,112	1,155	0,7997	0,5016	0,4362
390	1,212	1,251	0,8652	0,5475	0,4814
392	1,28	1,327	0,9238	0,5887	0,5212
394	1,395	1,425	1	0,6463	0,5784
396	1,6	1,621	1,152	0,7495	0,6835
398	1,892	1,941	1,394	0,9036	0,8372
400	2,272	2,336	1,667	1,087	1,007

Ambient UVBR (280-315 nm) in 10 cm water depth.

Data were recorded with the RM 12 pocket spectroradiometer at the study site ±15 min around local noon.
Daily data were averaged for analysis.
UVBR levels that were >10 times smaller than the value recorded with the LiCor UW-1800 spectroradiometer
in 10 cm water depth on 30.06.1999 (0.73 W m-2) were rejected.

date	time	UVBR (mW	daily mean
01.06.2000	13:06:40	0,02584	0,0098283
	13:12:40	0,01358	
	13:18:40	0,00648	
	13:24:40	0,00111	
	13:30:40	0,00428	
	13:36:40	0,00768	
02.06.2000	13:06:40	0,02959	0,0292417
	13:12:40	0,02384	
	13:18:40	0,03367	
	13:24:40	0,04427	
	13:30:40	0,02507	
	13:36:40	0,01901	
03.06.2000	13:06:40	0,03812	0,034495
	13:12:40	0,03925	
	13:18:40	0,02518	
	13:24:40	0,04142	
	13:30:40	0,03565	
	13:36:40	0,02735	
04.06.2000	13:07:51	-0,0017	-0,0006983
	13:13:51	0,00121	
	13:19:51	-0,0021	
	13:25:51	0,0008	
	13:31:51	-0,0009	
	13:37:51	-0,0015	
05.06.2000	13:05:02	0,03364	0,03497
	13:11:02	0,03078	
	13:17:02	0,0397	
	13:23:02	0,03805	
	13:29:02	0,04088	
	13:35:02	0,02677	
06.06.2000	13:05:02	-0,0026	-0,00185
	13:11:02	-0,0021	
	13:17:02	-0,0029	
	13:23:02	-0,0039	
	13:29:02	-0,0025	
	13:35:02	0,0029	
07.06.2000	13:05:02	0,01063	0,013585
	13:11:02	0,02318	
	13:17:02	0,02617	
	13:23:02	0,00672	
	13:29:02	-0,001	
	13:35:02	0,01581	
08.06.2000	13:05:27	0,04174	0,037905
	13:11:27	0,06	
	13:17:27	0,03052	
	13:23:28	0,01999	
	13:29:27	0,03564	
	13:35:27	0,03954	
09.06.2000	13:05:27	0,04373	0,03977
	13:11:27	0,04501	
	13:17:27	0,02464	
	13:23:27	0,0323	
	13:29:28	0,05345	
	13:35:27	0,03949	
10.06.2000	13:05:30	0,04013	0,0439983
	13:11:30	0,04581	
	13:17:30	0,04217	
	13:23:30	0,04501	

01.06.2000	0,0098283
02.06.2000	0,0292417
03.06.2000	0,034495
04.06.2000	-0,0006983
05.06.2000	0,03497
06.06.2000	-0,00185
07.06.2000	0,013585
08.06.2000	0,037905
09.06.2000	0,03977
10.06.2000	0,0439983
11.06.2000	0,0442217
12.06.2000	0,0202133
13.06.2000	missing
14.06.2000	0,0254
15.06.2000	0,024385
16.06.2000	0,0313767
17.06.2000	0,0385167
18.06.2000	0,0343417
19.06.2000	0,0368183
20.06.2000	0,0320533
21.06.2000	0,033155
22.06.2000	0,030395
23.06.2000	missing
24.06.2000	0,01192
25.06.2000	0,0009783
26.06.2000	0,0127533
27.06.2000	0,0089667
28.06.2000	0,015615
29.06.2000	0,0112233
30.06.2000	0,013435
01.07.2000	0,0066167
02.07.2000	0,0176083
03.07.2000	0,0367983
04.07.2000	0,0342667
05.07.2000	0,0310233
06.07.2000	0,0129767
07.07.2000	0,0224883
08.07.2000	0,0095833
09.07.2000	0,007385
10.07.2000	missing
11.07.2000	missing
12.07.2000	0,01809
13.07.2000	0,030335
14.07.2000	0,0061633
15.07.2000	0,012255
16.07.2000	0,02983
17.07.2000	missing
08.09.2000	0,0004583
09.09.2000	0,0171467
10.09.2000	0,0112083
11.09.2000	0,0220733
12.09.2000	0,014365
13.09.2000	0,0009517
14.09.2000	0,0142033
15.09.2000	0,0009733
16.09.2000	0,6742833
17.09.2000	0,6988333

	13:29:30	0,04581	
	13:35:30	0,04506	
11.06.2000	13:05:30	0,04844	0,0442217
	13:11:30	0,04304	
	13:17:30	0,04491	
	13:23:30	0,04737	
	13:29:30	0,04334	
	13:35:30	0,03823	
12.06.2000	13:05:30	0,0111	0,0202133
	13:11:30	0,01067	
	13:17:30	0,0052	
	13:23:30	0,02293	
	13:29:30	0,05064	
	13:35:30	0,02074	
13.06.2000		missing	
14.06.2000	13:08:44	0,01612	0,0254
	13:14:44	0,02476	
	13:20:44	0,0288	
	13:26:44	0,02991	
	13:32:44	0,02859	
	13:38:44	0,02422	
15.06.2000	13:08:44	0,04496	0,024385
	13:14:44	0,00802	
	13:20:44	0,01357	
	13:26:44	0,01404	
	13:32:44	0,02292	
	13:38:44	0,0428	
16.06.2000	13:08:44	0,04534	0,0313767
	13:14:44	0,02775	
	13:20:44	0,01463	
	13:26:44	0,01248	
	13:32:44	0,03947	
	13:38:44	0,04859	
17.06.2000	13:08:44	0,0429	0,0385167
	13:14:44	0,04875	
	13:20:44	0,03498	
	13:26:44	0,0351	
	13:32:44	0,03731	
	13:38:44	0,03206	
18.06.2000	13:07:01	0,02992	0,0343417
	13:13:00	0,04185	
	13:19:00	0,03027	
	13:25:00	0,03736	
	13:31:00	0,03478	
	13:37:00	0,03187	
19.06.2000	13:09:58	0,03263	0,0368183
	13:15:58	0,03895	
	13:21:58	0,03739	
	13:27:58	0,04075	
	13:33:58	0,04032	
	13:39:58	0,03087	
20.06.2000	13:09:58	0,03757	0,0320533
	13:15:58	0,03301	
	13:21:58	0,0393	
	13:27:58	0,02541	
	13:33:58	0,01869	
	13:39:58	0,03834	
21.06.2000	13:05:55	0,03531	0,033155
	13:11:55	0,03725	
	13:17:55	0,03076	
	13:23:55	0,03569	
	13:29:55	0,03301	
	13:35:55	0,02691	
22.06.2000	13:09:39	0,03555	0,030395
	13:15:38	0,03177	

18.09.2000	0,62045
19.09.2000	0,7765167
20.09.2000	1,2065
21.09.2000	0,6841667
22.09.2000	missing
23.09.2000	0,30695
24.09.2000	0,3518667
25.09.2000	0,2542833
26.09.2000	0,1768833
27.09.2000	0,1390833
28.09.2000	0,1345833
29.09.2000	0,1668333
30.09.2000	0,1395
01.10.2000	0,14645
02.10.2000	0,11905
03.10.2000	0,1134833
04.10.2000	0,14035
05.10.2000	0,1115167
06.10.2000	missing
07.10.2000	missing
08.10.2000	0,17245
09.10.2000	0,1157833
10.10.2000	0,1031433

	13:21:38	0,03114	
	13:27:38	0,02307	
	13:33:38	0,02324	
	13:39:38	0,0376	
23.06.2000	missing	missing	
24.06.2000	13:05:03	0,00941	0,01192
	13:11:03	0,01246	
	13:17:03	0,00743	
	13:23:03	0,01014	
	13:29:03	0,0129	
	13:35:03	0,01918	
25.06.2000	13:05:03	-0,0032	0,0009783
	13:11:03	-0,0028	
	13:17:03	-0,0027	
	13:23:03	0,00098	
	13:29:03	0,00865	
	13:35:03	0,00494	
26.06.2000	13:05:40	0,00937	0,0127533
	13:11:39	0,01445	
	13:17:39	0,01436	
	13:23:39	0,02024	
	13:29:39	0,01565	
	13:35:39	0,00245	
27.06.2000	13:08:12	0,0086	0,0089667
	13:14:12	0,01448	
	13:20:13	0,01685	
	13:26:12	0,0084	
	13:32:12	0,00113	
	13:38:12	0,00434	
28.06.2000	13:08:12	0,02459	0,015615
	13:14:12	0,0191	
	13:20:12	0,01375	
	13:26:13	0,01202	
	13:32:12	0,00996	
	13:38:12	0,01427	
29.06.2000	13:08:12	0,02041	0,0112233
	13:14:12	0,01278	
	13:20:12	0,01033	
	13:26:12	0,00733	
	13:32:12	0,0042	
	13:38:12	0,01229	
30.06.2000	13:06:43	0,0051	0,013435
	13:12:43	0,02583	
	13:18:43	0,014	
	13:24:43	0,01438	
	13:30:43	0,0129	
	13:36:43	0,0084	
01.07.2000	13:09:39	0,00654	0,0066167
	13:15:39	0,00402	
	13:21:39	0,0107	
	13:27:39	0,01	
	13:33:39	0,00486	
	13:39:39	0,00358	
02.07.2000	13:09:39	0,01508	0,0176083
	13:15:39	0,01935	
	13:21:39	0,01247	
	13:27:39	0,02045	
	13:33:39	0,02053	
	13:39:39	0,01777	
03.07.2000	13:09:39	0,03857	0,0367983
	13:15:39	0,0399	
	13:21:39	0,03809	
	13:27:39	0,03606	
	13:33:39	0,03343	
	13:39:39	0,03474	

04.07.2000	13:05:07	0,03399	0,0342667
	13:11:07	0,04097	
	13:17:07	0,03964	
	13:23:07	0,03266	
	13:29:07	0,02747	
	13:35:07	0,03087	
05.07.2000	13:06:36	0,02413	0,0310233
	13:12:36	0,02497	
	13:18:36	0,0325	
	13:24:36	0,03345	
	13:30:36	0,03639	
	13:36:36	0,0347	
06.07.2000	13:06:36	0,02257	0,0129767
	13:12:36	0,00918	
	13:18:37	0,00948	
	13:24:36	0,01589	
	13:30:36	0,01112	
	13:36:36	0,00962	
07.07.2000	13:06:36	0,02379	0,0224883
	13:12:36	0,01618	
	13:18:36	0,01807	
	13:24:37	0,01662	
	13:30:36	0,04409	
	13:36:36	0,01618	
08.07.2000	13:09:08	0,01609	0,0095833
	13:15:08	0,01987	
	13:21:08	0,01117	
	13:27:08	0,01016	
	13:33:08	0,00281	
	13:39:08	-0,0026	
09.07.2000	13:09:08	0,00727	0,007385
	13:15:08	0,0111	
	13:21:08	0,01052	
	13:27:08	0,004	
	13:33:08	0,00309	
	13:39:08	0,00833	
10.07.2000	missing	missing	
11.07.2000	missing	missing	
12.07.2000	13:04:31	0,01371	0,01809
	13:10:31	0,02468	
	13:16:31	0,02378	
	13:22:31	0,01647	
	13:28:31	0,02028	
	13:34:31	0,00962	
13.07.2000	13:04:31	0,01502	0,030335
	13:10:31	0,0399	
	13:16:31	0,03927	
	13:22:31	0,04112	
	13:28:31	0,03654	
	13:34:31	0,01016	
14.07.2000	13:06:50	0,00854	0,0061633
	13:12:51	0,01883	
	13:18:50	0,00772	
	13:24:50	0,00168	
	13:30:50	0,00381	
	13:36:50	-0,0036	
15.07.2000	13:04:57	0,01524	0,012255
	13:10:57	0,00624	
	13:16:57	0,01579	
	13:22:57	0,0165	
	13:28:57	0,01279	
	13:34:57	0,00697	
16.07.2000	13:04:57	0,01212	0,02983
	13:10:57	0,01434	

	13:16:57	0,04058	
	13:22:57	0,03511	
	13:28:57	0,03828	
	13:34:57	0,03855	
17.07.2000	missing	missing	
	missing	missing	
07.09.2000	missing	missing	
08.09.2000	13:09:33	0,00035	0,0004583
	13:15:33	0,0016	
	13:21:33	0,00202	
	13:27:33	-0,0002	
	13:33:33	0,00038	
	13:39:33	-0,0014	
09.09.2000	13:09:33	0,01764	0,0171467
	13:15:33	0,02295	
	13:21:33	0,01597	
	13:27:33	0,01185	
	13:33:33	0,01828	
	13:39:33	0,01619	
10.09.2000	13:09:33	0,01488	0,0112083
	13:15:33	0,01873	
	13:21:33	0,01351	
	13:27:33	0,00815	
	13:33:33	0,00437	
	13:39:33	0,00761	
11.09.2000	13:04:04	0,02321	0,0220733
	13:10:04	0,02486	
	13:16:04	0,01534	
	13:22:04	0,02297	
	13:28:04	0,02393	
	13:34:04	0,02213	
12.09.2000	13:04:04	0,01429	0,014365
	13:10:04	0,01283	
	13:16:04	0,01335	
	13:22:04	0,01481	
	13:28:04	0,01621	
	13:34:04	0,0147	
13.09.2000	13:04:04	0,0001	0,0009517
	13:10:04	0,00863	
	13:16:04	-0,0004	
	13:22:04	0,00028	
	13:28:04	-0,0012	
	13:34:04	-0,0017	
14.09.2000	13:08:18	0,00831	0,0142033
	13:14:18	0,00809	
	13:20:18	0,02039	
	13:26:18	0,01918	
	13:32:18	0,01481	
	13:38:19	0,01444	
15.09.2000	13:06:09	0,00045	0,0009733
	13:12:09	0,00106	
	13:18:09	0,00063	
	13:24:09	0,00126	
	13:30:09	0,00204	
	13:36:09	0,0004	
16.09.2000	13:06:09	0,6526	0,6742833
	13:12:09	0,6551	
	13:18:09	0,6535	
	13:24:09	0,7161	
	13:30:09	0,708	
	13:36:09	0,6604	
17.09.2000	13:06:09	0,7	0,6988333
	13:12:09	0,6939	
	13:18:09	0,6954	
	13:24:09	0,71	

	13:30:09	0,6929	
	13:36:09	0,7008	
18.09.2000	13:04:05	0,6214	0,62045
	13:10:05	0,619	
	13:16:05	0,6237	
	13:22:05	0,6206	
	13:28:05	0,6215	
	13:34:05	0,6165	
19.09.2000	13:04:05	0,7723	0,7765167
	13:10:05	0,7752	
	13:16:05	0,7727	
	13:22:05	0,7833	
	13:28:05	0,7727	
	13:34:05	0,7829	
20.09.2000	13:04:05	1,161	1,2065
	13:10:05	1,112	
	13:16:05	1,211	
	13:22:05	1,244	
	13:28:05	1,268	
	13:34:05	1,243	
21.09.2000	13:09:19	0,6693	0,6841667
	13:15:19	0,6802	
	13:21:19	0,6782	
	13:27:19	0,6623	
	13:33:19	0,7352	
	13:39:19	0,6798	
22.09.2000	missing	missing	
23.09.2000	13:09:20	0,2838	0,30695
	13:15:21	0,3088	
	13:21:20	0,2854	
	13:27:20	0,3291	
	13:33:20	0,3289	
	13:39:20	0,3057	
24.09.2000	13:09:20	0,3413	0,3518667
	13:15:20	0,3531	
	13:21:21	0,3562	
	13:27:20	0,3824	
	13:33:20	0,3593	
	13:39:20	0,3189	
25.09.2000	13:05:19	0,2504	0,2542833
	13:11:19	0,2514	
	13:17:19	0,2577	
	13:23:19	0,2554	
	13:29:19	0,2578	
	13:35:19	0,253	
26.09.2000	13:05:19	0,1951	0,1768833
	13:11:19	0,1692	
	13:17:19	0,2072	
	13:23:19	0,1781	
	13:29:19	0,1558	
	13:35:19	0,1559	
27.09.2000	13:08:40	0,1428	0,1390833
	13:14:40	0,1397	
	13:20:40	0,1421	
	13:26:40	0,1285	
	13:32:40	0,1466	
	13:38:40	0,1348	
28.09.2000	13:08:40	0,1366	0,1345833
	13:14:40	0,1303	
	13:20:40	0,1274	
	13:26:40	0,1367	
	13:32:40	0,1381	
	13:38:40	0,1384	
29.09.2000	13:08:41	0,1493	0,1668333
	13:14:40	0,1369	

	13:20:40	0,2025	
	13:26:40	0,1875	
	13:32:40	0,1559	
	13:38:40	0,1689	
30.09.2000	13:08:40	0,1357	0,1395
	13:14:41	0,1382	
	13:20:40	0,1406	
	13:26:40	0,1438	
	13:32:40	0,1395	
	13:38:40	0,1392	
01.10.2000	13:08:40	0,1424	0,14645
	13:14:40	0,1497	
	13:20:41	0,146	
	13:26:40	0,1469	
	13:32:40	0,151	
	13:38:40	0,1427	
02.10.2000	13:07:04	0,1112	0,11905
	13:13:04	0,1147	
	13:19:04	0,1208	
	13:25:04	0,1232	
	13:31:04	0,1219	
	13:37:04	0,1225	
03.10.2000	13:07:04	0,112	0,1134833
	13:13:04	0,1089	
	13:19:04	0,1129	
	13:25:04	0,113	
	13:31:05	0,1193	
	13:37:04	0,1148	
04.10.2000	13:07:04	0,1414	0,14035
	13:13:04	0,1387	
	13:19:04	0,1405	
	13:25:04	0,1429	
	13:31:04	0,1395	
	13:37:05	0,1391	
05.10.2000	13:07:04	0,107	0,1115167
	13:13:04	0,1093	
	13:19:04	0,1148	
	13:25:04	0,1113	
	13:31:04	0,1129	
	13:37:04	0,1138	
06.10.2000	missing	missing	
07.10.2000	missing	missing	
08.10.2000	13:04:10	0,1711	0,17245
	13:10:09	0,1716	
	13:16:09	0,1725	
	13:22:09	0,173	
	13:28:09	0,173	
	13:34:09	0,1735	
09.10.2000	13:04:09	0,1176	0,1157833
	13:10:09	0,1146	
	13:16:09	0,1151	
	13:22:09	0,113	
	13:28:09	0,1185	
	13:34:09	0,1159	
10.10.2000	13:04:09	0,09926	0,1031433
	13:10:09	0,1026	
	13:16:09	0,1014	
	13:22:09	0,1037	
	13:28:09	0,1023	
	13:34:09	0,1096	

Air temperature at noon from August 1 to November 30 in 1999 and 2000. Data were acquired from the Institute for Marine Research, Kiel

day	Aug 99	Aug 00	Sep 99	Sep 00	October 1999	October 200	Nov 99	Nov 00
1	27	23	19	20	14,5	17	13,3	9
2	25,5	21	21	17	18	16	13,3	6,5
3	25	20,5	22,5	14	13,5	14,5	11,9	9,5
4	26	22	24	17	14,5	18	11,8	10
5	28	19	25	16	15	14	6,3	7,8
6	24	21	23	16	13,5	14	11,8	7
7	25	18	24	19,5	13,5	12	9	10,4
8	23	18	23	17,5	13	13	9,8	10,4
9	23	19,5	27	19	14,5	11,5	8,6	9,8
10	22,5	20	20	18	16	11,5	9	8,3
11	18	18	27	17	15	11,5	9,5	8,7
12	19	21	27	20	14,5	14,5	8	9
13	19,5	20	25	18	14	14	9,5	10
14	19	27,5	24	18,5	14	14	7	9
15	18	21	23	16	12	14,5	5,1	8,3
16	19,5	20	18	13	10	16	1,8	9
17	19	21,5	17,5	13	9	15	6,2	6,1
18	20	22	17	14	9	11	3,1	5,5
19	17	20	19	12	9	11	4,8	8,1
20	20,5	20,5	23	12	8	12	3,5	8,5
21	16	19	20	16	7,5	14	2,8	6,8
22	18	19	21	17	9	15	2,3	9,5
23	17	18	18,5	18	10	17	3	8,2
24	18	17	21	15	14	13	8	8,8
25	22	20	20	15	15	12	8,9	6,8
26	20	21	17,5	13,5	13	11	10,5	7
27	22	23,5	18	19	14	11,5	7,2	7
28	20	20	18	18	12	14	10,1	12
29	21	19	16	22	11	12	9	12,5
30	22	20	17	18	12	13	9	11,1
31	20	17,5			13	11		

Daily precipitation (mm)

Month	day	1999	2000
September	1	0	0
	2	0	3,33
	3	0	6,12
	4	0	8,41
	5	0	0
	6	0	0
	7	0	1,32
	8	0	0,55
	9	0	0,39
	10	0	4,31
	11	0	0
	12	0	2,36
	13	0	0
	14	0	1,51
	15	0	0,24
	16	0	0,31
	17	0,36	24,54
	18	5,4	0,34
	19	0	0
	20	0	0
	21	14,89	0
	22	0	0
	23	3,15	0
	24	0,44	0
	25	7,58	0
	26	1,75	0,49

	27	0,1	0,92
	28	2,97	4,13
	29	15,79	7,5
	30	0,93	0
October	1	6,06	0
	2	6,22	0
	3	0,25	19,4
	4	2,93	0
	5	0,02	0
	6	0	0,13
	7	0,38	0,9
	8	6,35	0
	9	1,58	0,2
	10	2,04	4,2
	11	1,06	0,11
	12	0,56	2,81
	13	0	0
	14	0,3	0,34
	15	0	0
	16	0	0
	17	0	0,07
	18	0,48	0
	19	0	0,22
	20	0	0
	21	0	0
	22	1,12	0
	23	3,08	0
	24	0,18	4,65
	25	0,98	2,93
	26	4,18	2,73
	27	1,37	6,92
	28	0,97	1,03
	29	0,22	1,23
	30	0	2,27
	31	2,42	0,13
November	1	0,5	0,36
	2	0	3,47
	3	0	0,88
	4	0	0
	5	0	0
	6	0,64	0
	7	4,9	3,97
	8	0	0,77
	9	0,14	0,36
	10	0	0,33
	11	0	2,75
	12	0,18	1,32
	13	0	0
	14	0	0
	15	0,65	0
	16	3,9	0
	17	3,23	3,96
	18	1,09	2,5
	19	0,13	0,67
	20	0	0,23
	21	0	0,07
	22	0	0,22
	23	5,47	0,02
	24	0	0,02
	25	1,67	0
	26	0	0
	27	1,69	0
	28	3,23	3
	29	missing	0
	30	missing	0

Solar radiation (W m-2) at noon from August 1 to November 30 in 1999 and 2000. Data were acquired from the Institute for Marine Research, Kiel

day	Aug 99	Aug 00	Sep 99	Sep 00	October 1999	October 200	Nov 99	Nov 00
1	900	840	750	600	660	480	355	298
2	825	900	690	810	510	460	250	398
3	800	900	700	170	510	350	325	240
4	800	910	740	830	630	500	310	350
5	800	660	690	650	500	240	320	140
6	790	900	660	390	590	540	310	145
7	830	920	640	730	510	260	210	310
8	760	900	660	430	250	520	150	300
9	830	870	620	700	550	130	270	105
10	830	750	600	560	260	250	140	55
11	690	660	600	690	550	450	295	70
12	890	860	640	650	490	500	295	170
13	900	800	640	450	500	490	70	280
14	700	730	580	550	250	440	340	275
15	710	350	580	190	530	410	295	225
16	920	750	460	100	530	550	350	270
17	850	750	410	250	550	250	380	50
18	700	830	350	210	550	450	110	100
19	350	610	640	760	500	290	80	200
20	750	810	610	320	460	140	50	250
21	790	750	550	610	410	260	55	180
22	750	890	600	620	400	280	210	240
23	790	880	390	630	150	370	100	240
24	800	500	570	600	450	400	110	70
25	870	900	650	580	470	70	30	240
26	350	740	410	360	230	280	70	150
27	840	730	630	500	250	200	50	100
28	690	630	500	280	210	350	100	90
29	850	740	300	500	370	400	90	220
30	710	850	400	500	270	130	140	240
31	790	750			220	160		

Water temperature at noon from September 1 to November 30 in 1999 and 2000. Data were acquired from the Institute for Marine Research, Kiel

day	month	1999	2000
1	September	19,5	16,8
2	September	19,2	17,1
3	September	19,8	17
4	September	19,8	16,9
5	September	20	16,3
6	September	19,1	16,4
7	September	18,8	16,8
8	September	18,2	16,3
9	September	19	16,8
10	September	19,2	18,1
11	September	19,8	17,9
12	September	19,8	17
13	September	19,2	16,8
14	September	19,1	17,1
15	September	19	16,9
16	September	18	15,8
17	September	17,7	15,2
18	September	19,1	14,9
19	September	17,6	14,9
20	September	17,7	14,5
21	September	17,9	14,6
22	September	18	14,5
23	September	17,6	14,5
24	September	17,5	14,2
25	September	17,5	14,1
26	September	17,1	14,1

27	September	17,1	14,7
28	September	16,5	14,8
29	September	16,2	15,9
30	September	16,2	15,2
1	Oktober	16	15,7
2	Oktober	15,5	14,9
3	Oktober	14,8	14,8
4	Oktober	14	14,9
5	Oktober	14	14,8
6	Oktober	13,9	14,5
7	Oktober	13,8	14,2
8	Oktober	13,9	14,2
9	Oktober	13,9	14
10	Oktober	13,8	14
11	Oktober	13,9	13,3
12	Oktober	14	13,6
13	Oktober	13,8	13,8
14	Oktober	14,6	13,8
15	Oktober	14	13,9
16	Oktober	14	13,9
17	Oktober	12,5	13,2
18	Oktober	12,1	13,1
19	Oktober	13	13
20	Oktober	12	13,1
21	Oktober	11,1	13
22	Oktober	10,8	13
23	Oktober	12	13,1
24	Oktober	13,1	12,8
25	Oktober	12,9	12,8
26	Oktober	12,1	12,5
27	Oktober	12,2	12,4
28	Oktober	12	12,7
29	Oktober	12	12,6
30	Oktober	10,8	12,3
31	Oktober	11,4	12,2
1	November	11,3	12
2	November	11,3	11,9
3	November	11,3	11,8
4	November	11,2	11,6
5	November	10,8	11,5
6	November	11,1	11
7	November	11,3	10,9
8	November	10,9	11
9	November	11	11
10	November	10,8	11
11	November	10	10,9
12	November	10,8	10,5
13	November	10,3	10,8
14	November	9,7	10,4
15	November	9,1	10
16	November	9,1	10,2
17	November	9,3	10
18	November	9,2	10,1
19	November	8,3	10,1
20	November	7,8	9,8
21	November	7,3	9,3
22	November	7,3	9,5
23	November	7,5	9,5
24	November	7,5	9,4
25	November	7,6	9
26	November	7,4	8,8
27	November	7,5	8,8
28	November	7	8,8
29	November	7,2	9
30	November	6,9	8,9