Mechanisms regulating amphipod population density within macroalgal communities with low predator impact*

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SUMMARY: In eight mesocosms (land based basins) macroalgae communities with associated fauna were transplanted from the sea and established during two years. Then, different doses of nutrients (N and P) were added to the basins throughout the following three years. During the period of nutrient addition, macroinvertebrate grazers showed seasonal fluctuations with densities usually between 500,000 and 1 million individuals per mesocosm during summer and to a level of about 100,000 during winter. The macroinvertebrate grazers mainly consisted of about 10 species of amphipods and isopods, among which the amphipod *Gammarus locusta* dominated strongly by biomass. Although the number of predators was very low, the grazer populations never reached a density where considerable grazing impact could be found on the macroalgae. No increase in grazer density was found in the basins with improved nutrient conditions. Thus food quality may be insufficient for further population growth, or density dependant regulation mechanisms may have prevented the grazers from flourishing and overgrazing the system. In aquarium experiments we showed that *G. locusta* could grow and reproduce on *Fucus serratus, Ulva lactuca*, periphyton and detritus, and that cannibalism by adult *G. locusta* on juveniles may have great impact on the population growth. The basins were run with a water flow through system. Nets were placed in front of the inflow and outflow tubes to measure immigration and emigration. Only few individuals (and no *Gammarus* sp.) were recorded in the inflowing water, while high numbers of both amphipods and isopods were found in the outflowing water. Emigration reached peak values during night-time, and it was then two to three times as high as during day-time. Emigration of mobile grazers from the basins amounted to 1-2% of the standing stock daily. These mechanisms that regulate grazers do contribute to maintenance of the seaweed dominance and thus the stability of the seaweed community.

Key words: Mesocosm, macroalgae, grazers, *Gammarus locusta*, population regulation, eutrophication.

RESUMEN: MECANISMOS QUE REGULAN LA DENSIDAD DE POBLACIONES DE ANFÍPODOS EN COMUNIDADES DE MACROALGAS CON BAJO IMPACTO DE DEPREDACIÓN. – En ocho mesocosmos (depósitos situados en tierra) se trasplantaron comunidades de macroalgas con fauna asociada procedentes del mar y se establecieron durante dos años. Posteriormente se añadieron diferentes dosis de nutrientes (N y P) a los depósitos a lo largo de los tres años siguientes. Durante el período de adición de nutrientes, los macroinvertebrados herbívoros mostraron fluctuaciones estacionales con densidades que por lo general se encontraban entre 500.000 y 1 millón de individuos por mesocosmos durante el verano y hasta un nivel de unos 100.000 ind. en invierno. Los macroinvertebrados herbívoros eran principalmente unas 10 especies de anfípodos e isópodos, entre los cuales el anfípodo *Gammarus locusta* dominaba mucho por la biomasa. Aunque el número de depredadores fue muy bajo, las poblaciones de herbívoros no alcanzaron nunca una densidad que pudiera producir un efecto considerable de ramoneo sobre las macroalgas. No se encontró ningún aumento en la densidad de herbívoros en los depósitos con condiciones de mejora de los nutrientes. Así, la calidad del alimento puede ser insuficiente para un incremento ulterior de la población, o bien mecanismos de regulación dependientes de la densidad pudieron haber evitado que los herbívoros medraran y ramonearan en exceso el sistema. En experimentos de acuario demostramos que *G. locusta* puede crecer y reproducirse sobre *Fucus serratus, Ulva lactuca*, perifiton y detritos, y que el canibalismo de *G. locusta* adultos sobre los juveniles puede tener un gran impacto sobre el crecimiento de la población. Los depósitos funcionaban con un flujo de agua continuo; se colocaron redes frente a los tubos de entrada y de salida para medir la inmigración y la emigración. Sólo se registraron unos pocos

individuos (que no fueron *Gammarus* sp.) en el agua de entrada, mientras que en la de salida se encontró un número elevado de individuos, tanto de anfípodos como de isópodos. La emigración alcanzó valores elevados durante la noche, y entonces fue de dos a tres veces más alta que durante el día. La emigración de herbívoros móviles desde los depósitos supuso el 1-2% de la biomasa diaria. Estos mecanismos que regulan a los herbívoros contribuyen al mantenimiento de la dominancia de las algas y con ello a la estabilidad de la comunidad de algas.

Palabras clave: mesocosmos, macroalgas, herbívoros, *Gammarus locusta*, regulación de la población, eutrofización.

INTRODUCTION

Macroalgal associations dominate the biota on rocky coasts of temperate waters (Mann 1982, Denton and Chapman 1991), and may seem persistent with respect to their spatial and temporal occupancy. However, the persistence of these communities may be short, especially when exposed to high density of grazers. Important grazers responsible for changing these systems include sea urchins (Lawrence, 1975; Dayton, 1985; Harrold and Pearce, 1987; Elner and Vadas, 1990), periwinkles (Lein, 1984) and limpets (Hawkins *et al.*, 1992). Also, mobile crustacean macroinvertebrate grazers (amphipods and isopods) are often abundant components of the macrophytic habitat (Hagerman, 1966; Moore, 1972, 1973; Duffy, 1990; Schultze *et al.*, 1990; Christie *et al.*, 1998; Pavia *et al.*, 1999). However, the influence of these crustaceans on the algal community has been reported merely as structural change rather than destructive grazing (see Karez *et al.*, 2000; Worm *et al.*, 2000).

Hawkins *et al.* (1992) stated that little of the macroalgal production in the north-east Atlantic flows through herbivores. One reason for limited herbivore impact may be grazer resistance due to phlorotannins or other chemical components making the algae unpalatable (Denton and Chapman, 1991). In addition, grazer population growth may be retarded because of low quality food by feeding on algae only (Cruz-Riveira and Hay, 2000a, b). The grazer population may also be limited by predation, mainly by fish (Nelson, 1979; Kennelly, 1983, 1991; Holmlund *et al.*, 1990; Nordeide and Fosså, 1992; Fjøsne and Gjøsæter, 1996).

In a mesocosm experiment macroalgal communities were established successfully in 1996 and different doses of nutrients were added during 1998-2000. An overall conclusion from running these mesocosms for 5 years was that community structure did not change much, neither throughout time nor due to differences in nutrient supply (Bokn *et al.*, 2002, 2003; Kraufvelin *et al.*, 2002). The macroalgal assemblages in all basins were dominat-ed by *Fucus vesiculosus* and *F. serratus*, while a few species of green algae (mainly *Ulva lactuca*) and seasonal red algae were common. More than 10 species of macroinvertebrate grazers were common, and *Gammarus locusta* was the most abundant one and dominant concerning biomass. Few predators established themselves in the basins. In spite of low predator abundance, and despite a high potential of many grazer populations (e.g. *G. locusta*, *Idotea* spp.) to respond rapidly to the nutrient conditions among algae, the grazers never increased to densities where macroalgal beds were destructively affected (Kraufvelin *et al.*, 2002).

Edgar (1990) postulated that grazing macroinvertebrates in seagrass ecosystems were exposed to food limitation, and that food availability regulated these mobile epifauna populations. Fucoids have not been observed to be eaten by amphipods by Vassallo and Steele (1980), but a majority of common seaweeds are found to serve as food for grazers in other studies (Denton and Chapman, 1991; Costa and Costa, 1999; Cruz-Riveira and Hay, 2000a, b). Norderhaug *et al.* (2002) suggested that grazer populations most probably were space limited rather than food limited. If so, density dependent regulation mechanisms may be important. High mobility or dispersal rates may lead to migration out of the macroalgal beds when grazer population density is high (see Virnstein and Curran, 1986). In addition to predation by fish, cannibalism (adults eating smaller conspecifics) and intra-guild predation have also been found to occur among amphipods and isopods, and more frequently so at high densities (Leonardsson, 1991; Otto, 1998; MacNeil and Prenter, 2000).

In this study we have focused on the macroinvertebrate grazers. More specifically why *G. locusta* in the absence of its major predators did not reach high population densities and why the macroalgal beds did not become heavily grazed. One aim of the study has been to test if the algae do provide proper food for amphipod population growth. Further we have investigated if density-dependant factors regulate the macroinvertebrate grazer populations. Thus we

have performed experiments to test: (1) if the algae were proper for grazer population growth, (2) if cannibalism could act as a regulating mechanism, and (3) if animals emigrated out of the system.

MATERIAL AND METHODS

The rocky littoral mesocosms

The mesocosm facility is situated at the Marine Research Station Solbergstrand by the Oslofjord (59°37'N, 10°40'E), south-east Norway. The Solbergstrand mesocosm and the main methods have previously been described by Bakke (1990), Bokn et al. (1998, 2001, 2002) and Kraufvelin et al. (2002), but some information relevant to this paper are given below.

Eight concrete land-based mesocosms were set up in early summer 1996. These mesocosms have a water volume of 7-13 m^3 each, depending on tide level, and they are fed with water from 1 m depth in the Oslofjord. The mean water residence time was about 3 hours. A tidal regime (with amplitude 36 cm) was maintained, and waves were generated at a rate of 18 strokes per minute. To monitor the physical and chemical properties in the mesocosms, oxygen concentration, temperature and salinity was recorded continuously and nutrients on weekly basis both in the incoming water and in the outflow water (Bokn et al., 2001). The plant and animal communities were established by transplantation of small boulders with attached macroalgae and associated animals from the Oslofjord. Nutrients were added in a mixture consisting of 14.3 mol N as NH_4NO_3 and 0.9 mol P as H_3PO_4 (the N/P mol ratio was 16/1) along a geometrical gradient corresponding to 1, 2, 4, 8, 16 and 32 μmol l^{-1} N above background levels. Two basins served as controls without extra nutrient addition (concentration 0). Since nutrient addition started in May 1998, the total experimental period consisted of 2 background years and 2.5 years with elevated nutrient levels at the final sampling in August 2000.

The transplanted macroalgal community covered in 1996 4.2 m^2, and subsequently algal cover spread to bare surface on bottom, the walls of the basin and the wave-generating bar, altogether estimated to ca 8 m^2, similar for all eight basins.

The abundance and biomass of animals in each basin were usually investigated at three campaigns each year (spring, summer and autumn). The number of large motile and all sessile animals was esti-

mated by counting inside a frame (grid) system. Small mobile animals were estimated by collection from artificial substrates. We developed a type of artificial substrate consisting of three ropes and one stone in a petri-dish, tied closely together. Four + four replicate artificial substrates at two different depths (one intertidal and one subtidal depth) were exposed for two days in each basin. Three artificial substrates from each depth were analysed for fauna content non-destructively (animals returned alive), whereas one artificial substrate from each depth was sampled destructively for more detailed analysis of animal diversity. The number of individuals per basin could be estimated by extrapolation from artificial substrates to algal communities with knowledge of the total amount of algae and previous information about the distribution of animals among the major algal groups as well as in the artificial substrates (Kraufvelin et al., 2002). Animal biomasses (wet weight) were estimated from standardised masses of the different species.

The export of animals was investigated twice a year in 1999 and 2000 by placing a fine net over the outlet pipes of each mesocosm for one hour at daytime (12 till 1 p.m.) and one hour at night (00 till 1 a.m.) at high tide when the tide started to go down. Simultaneously, nets were also placed on the inlet pipes to the mesocosms to get a measure of animal import through the incoming fjord water. These procedures were always done twice (they were repeated the following day and night). After one hour of sampling, all the nets were collected and the animals were sorted out and preserved in 4% formalin for later taxonomic and numeric analyses. To get an estimate of the annual emigration of animals we extrapolated the values between the seasons (spring, summer and autumn) while taking the day/night differences and different day lengths into consideration. To be taken by the outlet flow, the animals had to leave the algal bed and swim up to the tube at the surface close to the south wall in the basins.

Aquarium experiments

To get more detailed information about the food conditions in the basins, i.e. if the major algal food could be readily exploited, an aquarium experiment was conducted during two months from June to August 1999. Twelve flow-through aquaria (6 litres) with surface water from the fjord and a water exchange rate of approximately 3-4 h were used. Gammarus locusta were used as test organisms since

they were the most abundant grazer occurring at all habitats and at all vertical levels in the basins. Newly hatched (47 individuals 1.3 mm length) juveniles of *G. locusta* amphipods were placed in each aquarium together with one of the four potential food items; *Fucus serratus, Ulva lactuca*, periphyton and algal based detritus. Thus we had four treatments with three replicates of each. The algal food was sampled from a low nutrient dose basin. Clean parts of *F. serratus* and *U. lactuca* were cut and washed gently in fresh water to exclude associated organisms (epiphytes). Periphyton (also washed gently in fresh water) was supplied on ceramic chips (5x5 cm) exposed in the same basin for about 2 weeks. Detritus was made by fine grain seaweed (mainly *Ascophyllum nodosum*) flour mixed with sediment from the basin and degraded for about 2 weeks before adding to the aquaria. Food was always in excess, regularly supplied when old food were grazed. The aquaria were cleaned on two occasions. The juvenile survival was counted after 28 days. After 62 days, the experiment was terminated and all individuals were counted and their total length was measured with an eyepiece micrometer.

In a second aquarium experiment in September 1999 we studied the effect of cannibalism on juvenile mortality. In this experiment, 20 juvenile (ca 1.5-2 mm) specimens of *G. locusta* were introduced to each of twelve aquaria. Three aquaria were kept as controls and to the remaining nine aquaria also five adult (about 10 mm total length) *G. locusta* specimens were introduced. The controls were given one piece of both *Fucus serratus* and *Ulva lactuca* each, and out of the nine aquaria where adults were present a piece of both *F. serratus* and *U. lactuca* were added to three, a piece of *F. serratus* and *U. lactuca* plus three small stones and a chip with periphyton were added to another three, whereas three aquaria got no substrate or food at all. Since there were no significant differences in juvenile mortality between the aquaria with food, with food and substrate (hiding places), and the aquaria without food and substrate, all treatments were pooled in the statistical analysis of differences in juvenile survival in the presence and absence of adult specimens.

RESULTS

The total abundance and total biomass of macroinvertebrate grazers through the experimental period 1997-2000 for each basin are presented in Figure 1. The seasonal fluctuations were large with highest values during summer and lowest during spring (the mid winter was not investigated). Large differences in estimates were found between the basins on each sampling date, but no systematic effects of the nutrient addition (from basin 0 to 32 in Fig. 1) could be observed (tested by Kraufvelin *et al.*, 2002). Grazer abundance values were generally in the range 500,000-1,000,000 individuals per basin, which corresponded to a biomass of 4-8 kg of fresh weight. On average, *G. locusta* contributed to approximately 20% of the abundance values (with an high value of 40% in the autumn 1997 and an extreme low value of 6% in the autumn 1999) and 70% of the biomass (with extremes at 89% in the summer 1998 and 54% in the spring 1998). The average contribution of *G. locusta* to the total abundance and biomass of mesograzers is indicated by a bold line in Figure 1.

In addition to *G. locusta*, *Hyale nilssoni* and members of Ischyroceridae, Aoridae, Calliopiidae, Corophiidae and Stenothoidae were common among the amphipods. Among the isopods, *Jaera* spp. was abundant, while *Idotea* spp. was common. The species reaching high densities next to *G. locusta* were *Hyale nilssoni* and *Jaera* spp., both occurring only in the uppermost intertidal zone, while *G. locusta* were abundant all over the basin. *Carcinus maenas* and *Asterias rubens* were both common predators. Among predators of the amphipods and isopods, only a few fish (labrids and gobids) were occasionally observed.

G. locusta survived, grew and reproduced when fed all the four different food items *Fucus serratus*, *Ulva lactuca*, periphyton and detritus (Table 1). After 4 weeks the implanted juveniles reached adult size (approximately >8 mm), formed precopula positions, and females started to carry eggs. Next generation of juveniles were seen in the aquaria after 6 weeks. The number of individuals counted in each aquarium after 4 weeks reflected the juvenile survival up to adult size (between 55 and 75% survival). The 9 week figures in Table 1 make up a combination of adult survival, reproductive success, and juvenile survival of the next generation. The average length of adults and the size of the biggest individual were also measured after 9 weeks to give a measure of the length growth (Table 1). The tests shown in Table 1 did not reveal any differences in survival of juvenile gammarids or ability to grow to reproductive size or to reproduce effectively when fed the four food items (one-way ANOVA, df = 3,
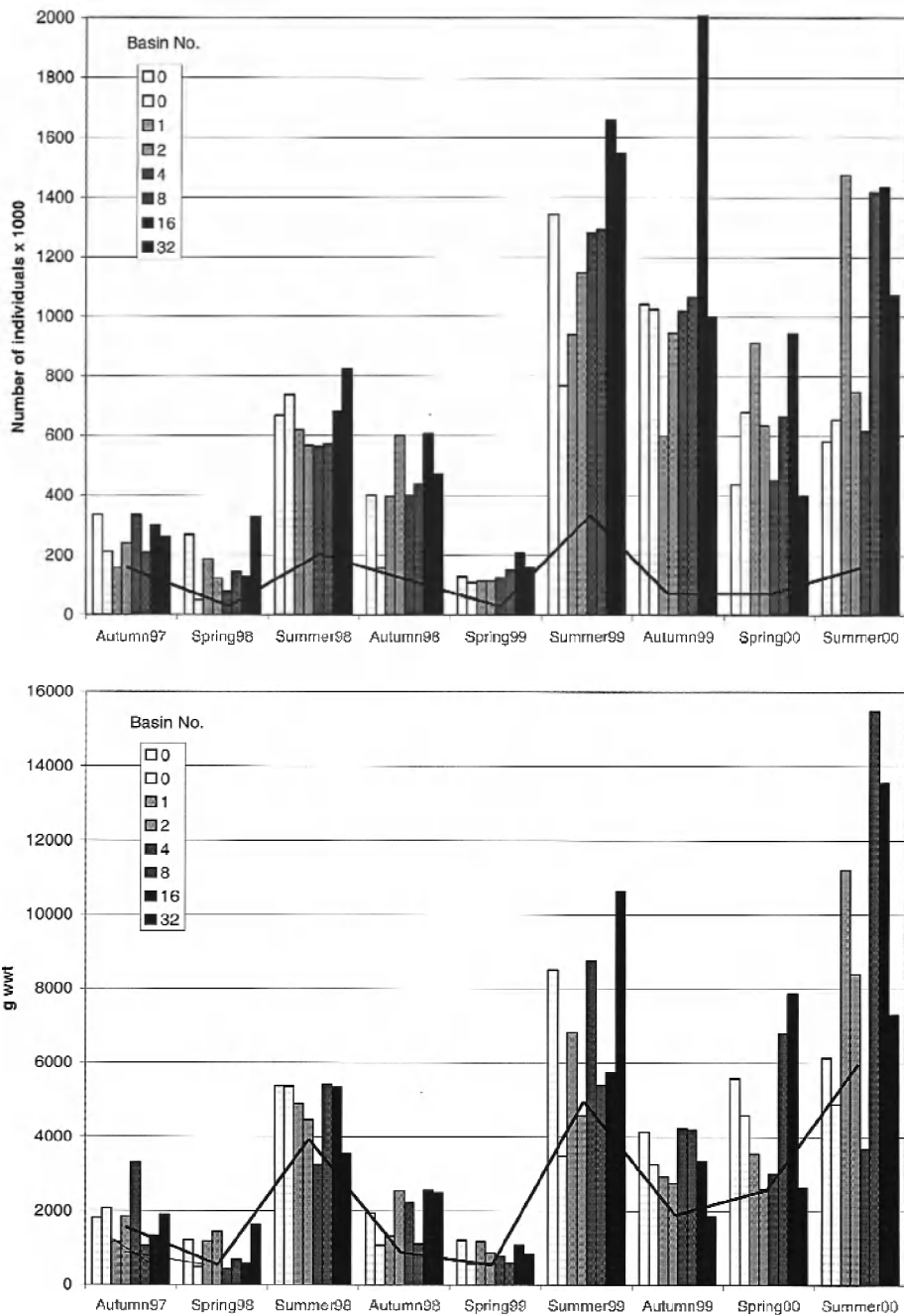
FIG. 1. – Total abundance (a) and total biomass in wet weight (b) of mesograzers per basin throughout the experimental period, 1997-2000. Basin enumeration refers to the amount of excessive nitrogen added from spring 1998 on (see Methods). The thick line indicates the average contribution of *Gammarus locusta* to the total abundance and biomass, respectively.

8). However, the size frequency distribution of *G. locusta* at all four food items indicate that juvenile production was favoured in the aquaria fed with *Ulva lactuca* and periphyton compared to those fed with *Fucus* and detritus (Fig. 2).

Cannibalism (adults eating juveniles) was shown to be a very important population regulating mechanism in the aquaria. In the aquaria to which no adults had been added, more than 98% (59 out of 60) of the

juveniles survived for five days, whereas in those containing adults (5 from the start, 1-5 left after five days), less than 50% of the juveniles remained after five days. An unbalanced one-way ANOVA (df = 1, 10) gave a p-value of 0.004 for differences in juvenile survival between aquaria containing adults and aquaria that just contained juveniles. In the aquaria where three or more adults survived during the experiment, an average mortality of 62% was found

TABLE 1. – Survival, growth and reproductive success of *Gammarus locusta* given as mean number of individuals per aquarium (mean ± SD) after 4 and 9 weeks when fed four different food items. The initial number of juvenile *G. locusta* was 47 in all aquaria. After 9 weeks we distinguished between adults and juveniles, and then the mean length of adults and length of biggest individual from each aquarium within each treatment are given. Results from a one-way ANOVA on overall differences in gammarid variables among the four food items are presented in the right column (d.f. 3, 8), ns = non-significant.

|	*Fucus*	*Ulva*	Periphyton	Detritus	F	significance
No of inds. aquarium^{-1}						
Number 4 weeks	35.3 ± 5.9	30.3 ± 9.3	29.7 ± 5.1	26.0 ± 5.0	1.0	0.430 ns
Number 9 weeks	29.7 ± 21.5	96.7 ± 106.9	102.0 ± 26.0	12.7 ± 7.2	2.0	0.195 ns
Juveniles < 8 mm	20.7 ± 22.7	89.7 ± 102.9	89.7 ± 20.0	10.0 ± 6.9	1.9	0.203 ns
Adults > 8 mm	9.0 ± 1.7	7.0 ± 4.6	12.3 ± 7.0	2.7 ± 0.6	2.7	0.119 ns
Length						
Adult length, mm	10.8 ± 1.1	11.3 ± 0.5	12.9 ± 1.0	13.1 ± 1.6	3.3	0.078 ns
Biggest ind., mm	12.4 ± 0.5	14.9 ± 1.7	16.1 ± 0.8	15.6 ± 2.3	3.5	0.071 ns
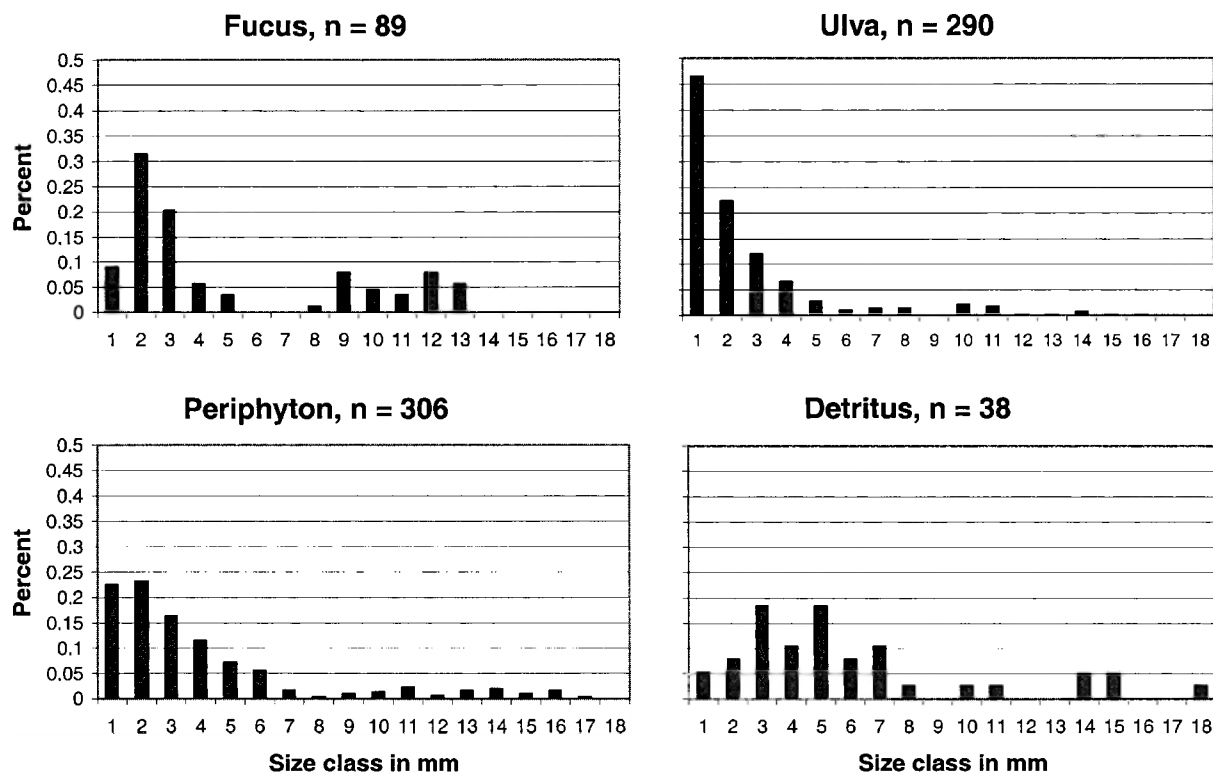
FIG. 2. – Size frequency distribution (percent) for *Gammarus locusta* in aquaria (3 pooled replicates of each) fed four different food items (*Fucus serratus, Ulva lactuca*, periphyton, detritus) for nine weeks.

(no more than 8 out of 20 juveniles survived in any of these aquaria during the five days).

A considerable fraction of the macroinvertebrate grazer populations was exported through the outlets of the basins. The estimated daily mean biomass (g wwt) of isopods and amphipods leaving the mesocosms during four periods is presented in Figure 3. There were large seasonal differences in the export of animals, with highest export when density and biomass were highest in the summer. The daily export of amphipods was estimated to be about 1% of the standing stock of amphipods, while corre-sponding value for the isopod *Idotea* spp. reached 2%. While all the common amphipods were export-ed, mainly *Idotea* spp. were found among isopods in the outlet samples. The export was higher at night than during day. An average of 550 amphipod indi-viduals were collected per hour from the outlets at night in the summer 1999, while only 50 were col-lected at 1 h at noon. For the isopods the corre-sponding values reached 130 and 20 respectively. In the summer 2000 the corresponding figures were 250 and 140 for amphipods, and 115 and 40 for isopods respectively. In addition to amphipods and
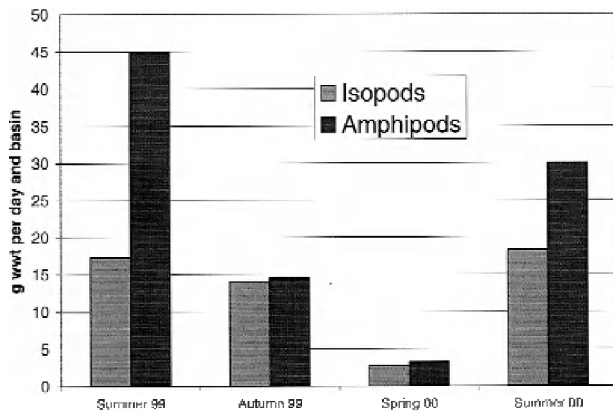
FIG. 3. – Export of animal biomass (g wwt) through the outlets of the basins (means of all eight basins during four sampling events 1999-2000).

isopods, juvenile *Mytilus edulis* were found in relative high numbers in the outlets. No significant differences in export rate between the basins (due to the nutrient addition) could be noted in these data sets (linear regression analyses, df = 7, p always > 0.166).

Some animals were found to enter the basins through the water supply, but the vast majority of the imported animals consisted of zooplankton (copepods and cladocerans). Some times the density of zooplankton reached far beyond 1000 individuals per hour. Macroinvertebrate grazers were rare in the inlet samples (usually <5 amphipods and isopods combined per h). Small amphipods of the family Calliopiidae made an exception once (a maximum of 150 individuals per hour at night in August 2000).

DISCUSSION

The macroalgae in the basins formed a proper food supply for the crustacean macroinvertebrate grazers present. Our aquarium experiment demonstrated that gammarids could grow and reproduce successfully on the major algal food items offered. Our results revealed especially high survival of juveniles and rapid growth to adult and reproductive size of the first generation. However, there were indications of differences between the aquaria with respect to density of the next generation. Moreover, this may not necessarily be a result of food quality, but the property of the food type as substrate for the newborn to hide themselves to avoid cannibalism. The detritus, which provided no substrate for hiding, showed high survival of the first batch of juveniles, but low survival of the next generation compared to

the food items offering hiding places. This result supports the idea of the importance of substrate for hiding for the survival of the newborn.

Although many types of macroalgae have been reported to be suboptimal as food for amphipods (Vassallo and Steele, 1980; Cruz-Riveira and Hay, 2000a,b), other studies (Karez *et al.*, 2000; Worm *et al.*, 2000, and some results in Cruz-Riveira and Hay, 2000a,b) support the results from our experiment that macroalgal beds including Fucoids supply the food for grazer species. Additional food of better quality (microorganisms, zooplankton) may have been introduced by the incoming water during the experiment, but the high number of amphipods per aquarium and the low amount of inflowing water insure that other supplies must be negligible compared with the food item given to each aquarium. The observed grazing (disappearance of food item or grazer marks) of each food type showed that *Fucus* sp., *Ulva lactuca*, periphyton and detritus all were eaten.

With surplus food, a generation time of 4-6 weeks, and a number of offspring in the range of 30-120 (cf. Costa and Costa, 1999), *G. locusta* and probably other amphipods and isopods have the potential to develop enormous densities in macroalgal habitats during the summer season as indicated by the annual summer peak (Fig. 1). As long as the macroalgal community persisted in all the basins, annual grazing could not exceed annual macroalgae production. Further, any grazing preferences could not be detected as long as algal species composition did not undergo dramatic changes throughout the years (Bokn *et al.*, 2002, 2003). With high food abundance and high temperatures, other factors may be responsible for the decreasing grazer abundance starting in late summer each year. In the absence of fish predators, and with grazer reproduction taking place almost throughout the year (Tully and O Ceidigh, 1986), increasing densities should be expected throughout late summer and autumn. Thus the grazer populations seemed to be limited by internal density dependant regulating mechanisms, like cannibalism and increased mobility leading to dispersal out of the system.

Cannibalism was found for *G. locusta* in aquaria regardless if sufficient food in terms of macroalgae and periphyton was available or not. *Gammarus* species and other amphipods are found to enhance fitness when given animal food in addition to plant diet, and when given algae only a compensatory feeding ensure growth and reproduction (Cruz-

Riveira and Hay, 2000a,b). Thus *Gammarus* sp. will probably include smaller crustaceans in their diet although sufficient (sufficient both in terms of biomass and quality) algae are present. The impact of adult cannibalism on juveniles in the aquarium test was at a rate that may affect the recruitment rate severely, and may contribute to regulation of *G. locusta* population size. Both cannibalism and intraguild predation have been described among both amphipods and isopods (Leonardsson, 1991; Otto, 1998; MacNeil and Prenter, 2000), and this type of predation has been found more common at high population densities. Cannibalism and predation within the crustacean mesograzer populations may thus be important regulation factors. In our basins, mainly *G. locusta* due to its size and abundance, but also to some extent *Idotea granulosa* and *Hyale nilssoni* can probably be predators of influence to mesograzer recruitment.

Emigration out of the system may be an important factor regulating density of mobile species. Among invertebrate grazers, a high degree of mobility seems to be common (Virnstein and Curran, 1986; Franz and Mohamed, 1989; Martel and Diefenbach, 1993; Duffy and Hay, 1994; Pavia *et al.*, 1999) and active dispersal out of macrophyte systems has been found (Virnstein and Curran, 1986, and personal observations from kelp forests). Frequent mobility has been found to be a favourable strategy to provide a high population density when space is short (Winder, 1990), and an elevated export of animals during summer should be due to higher population densities and probably also higher locomotory activity. In our experiment the macroinvertebrate grazers could emigrate through the water outlets. In order to do that the amphipods and isopods must swim out of the macroalgal bed to the outlet tube.

In natural macrophyte systems fish predation may be important in regulating macroinvertebrate densities (Nelson, 1979; Kennelly, 1983, 1991; Holmlund *et al.*, 1990; Nordeide and Fosså, 1992; Fjøsne and Gjøsæter, 1996), thus exploiting a high secondary production. According to the P/B ratios given by Alongi (1990) and Brey (1990), a secondary production of more than 30 kg wet weight may be estimated for each basin per year. With a total basin area of about 15 m², a macroinvertebrate production of 2 kg ww per m² per year is realistic as it makes about 10% of the macroalgal production reported by Bokn *et al.* (2003). Considering our estimate that about 8 m² per basin are fouled by macroalgae, the production esti-

mate per unit area will be almost twice that amount. The emigration data through the outlets lead to an estimate of animals being exported at a rate of 10 kg wwt per year per basin. Considering cannibalism, predation and degradation within the basins, and the fact that some benthic consumers (*Jaera* spp., *Littorina* spp.) are not exported through the outlets, the emigration from these basins may be considerably lower than the total secondary production. As found here, macroalgal associations often have high primary production (Mann, 1982). The system exports both plant biomass (see Bokn *et al.*, 2002, 2003, personal observations) and a considerable amount of animals, and the system must be a net exporter of energy (see Hawkins *et al.*, 1992). This high production and export may therefore be important for adjacent systems.

Only few significant effects due to the differences in nutrient addition between the basins were detected at the community level (Bokn *et al.*, 2002, 2003; Kraufvelin *et al.*, 2002). Slightly higher abundance values were obtained in the small isopod *Jaera* spp. in some of the highest nutrient doses while a consistent stimulation was found for the common periwinkle, *Littorina littorea* (Kraufvelin *et al.*, 2002). As a curiosity, it may be mentioned that both *Jaera* and *L. littorea* belonged to the few grazing species that did not leave the system through the outlets. The lack of clear responses to the nutrient addition on algal species composition may be due to modulating effects from grazing (cf. Worm *et al.*, 2000). Cannibalism and emigration may act as regulating factors hiding any further effects in the secondary production. Differences in emigration between the basins (if any) were impossible to detect due to high temporal variability.

As a conclusion, cannibalism and emigration seemed to limit population growth of the crustacean grazers. These factors should be important for the stability properties of communities dominated by macroalgae as both habitat and food.

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