Density-dependent migration in an *Amphiura filiformis* (Amphiuridae, Echinodermata) infaunal population

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ABSTRACT: The hypothesis that the semi-mobile brittle star *Amphiura filiformis* may have density-dependent migratory behaviour and that their dispersion may be dependent on food availability was examined. Sediment with intact fauna dominated by *A. filiformis* (~2250 ind. m^{-2}) was brought to the laboratory in 0.22 m^2 plexiglass boxes. The experiment was a 2-factorial design with density (high or moderate) and food (fed in excess or starved) as factors. To investigate migration in the high and moderate densities, the abundance of *A. filiformis* was experimentally manipulated in the boxes at the start of the experiment to 'low' (100 ind. 0.11 m^{-2}) numbers in one-half of all boxes and to 'high' (350 ind. 0.11 m^{-2}) or 'moderate' (220 ind. 0.11 m^{-2}) numbers in the other half. The experiment was run for 63 d. At termination of the experiment, a mean number of 90 and 36 ind. box^{-1} had migrated into the low density side of the box from the high density and moderate density side, respectively. Significantly higher migration rates per individual were observed from the high density side compared to the moderate density side. The migration rate was estimated from a diffusion coefficient based on the 'Random Walk' theory. No significant differences in migration rates were observed between fed and starved boxes, indicating that dispersal was primarily density-dependent rather than food-dependent. Based on the diffusion coefficient, a total dispersal of all *A. filiformis* from the high density side was estimated at 47 m h^{-1}. Fed *A. filiformis* had a higher weight and larger gonads than starved brittle stars. A separate experiment was set up to study migratory behaviour. It appeared that *A. filiformis* can move both on the sediment surface and within the sediment. In conclusion, migration in *A. filiformis* may be a common feature, which may cause a more or less continuous displacement of sediment with significant ecological effects.

KEY WORDS: Food · Interaction · Competition · Dispersal Random walk

INTRODUCTION

In many habitats, animal density and biomass are limited by shortage of food. In areas where food is abundant, space may instead be a factor limiting population expansion. Thus, exploitation and interference competition are key factors for species distribution and animal community organization. According to a definition by Mayr (1977), competition evolves when 2 species simultaneously seek an essential resource that is limited in supply, such as food or a place to live. Any factor whose effect becomes more severe as population density increases is called a density-dependent factor. From an evolutionary perspective, competition may widen the spectrum of species functional behaviour and cause niches between species to diverge in order to reduce competition (Branch 1984).

Most experimental studies of density, predation and food availability as regulating factors in marine benthos have so far been restricted to shallow coastal and intertidal areas. Pioneering field studies were initiated in the 1950s on rocky bottom barnacle populations (Southward 1991), which were followed by experimental investigations in the 1960s and early 1970s (e.g. Paine & Vadas 1969, Connell 1974, Ebert 1977). In the 1970s, investigations into the structuring factors of marine soft-bottom communities were initiated, often

in manipulative field or laboratory experiments. In such a study, Woodin (1974) demonstrated that competition for space and food was not a significant factor between tube-building polychaetes or between tube builders and burrowing polychaetes. In an experiment with suspension-feeding bivalves, Peterson (1982) did not find any interspecific effect on growth, whereas strong intraspecific density effects on growth and gonad development were recorded. In another study performed in the same subtidal lagoon with other filter-feeding bivalves, Peterson & Andre (1980) found significant interspecific competition for space. Thus, interference and resource competition are important structuring factors for soft-bottom shallow water communities, but may be significantly different depending upon which species and which functional groups (e.g. suspension feeders, surface and sub-surface deposit feeders, and carnivores) are present in the sediment.

In the marine environment, strong spatial gradients occur from highly productive coastal and estuarine areas to offshore deep areas with poor food supply. In the food-abundant end of such a gradient, benthic communities are rich in numbers and biomass, whereas these attributes gradually decline towards the impoverished end-point (Pearson & Rosenberg 1987). Quantity and quality of food generally attenuate with depth, and, in most sublittoral sediments, deposit-feeding animals have to compete for limited food resources (Levinton 1979, Jumars & Wheatcroft 1989). Based on data from field samples, it has been suggested that over large sea areas, such as the North Sea, the Skagerrak and the Kattegat, sublittoral macrobenthic communities are limited by insufficient food supply (Josefson 1985, Rosenberg 1995). Temporarily, food may be abundant, for example, following a spring or autumn phytoplankton bloom. In shallow waters, however, suspension feeders may not experience any food limitation during seasons with high production of phytoplankton (Möller & Rosenberg 1983, Olafsson 1986).

In some localized parts of the North Sea and the Skagerrak, enhanced numbers and biomasses of benthic fauna have been recorded. For example, in an area with tidal fronts off the Dutch coast, high sedimentation supports a rich benthic infauna (Creutzberg et al. 1984). Similarly, off the Swedish west coast in the Deep Trench, advective near-bottom processes distribute enough food to support a rich benthic fauna with very large biomasses dominated by the brittle star *Amphiura filiformis* (Rosenberg 1995). Thus, species like *A. filiformis* appear to be more densely packed in the sediment when food occurs super-abundantly compared to when food is less common. Quantity and quality of food are fundamental factors underlying the structure, abundance and biomass of marine benthic communities (Pearson & Rosenberg 1987, Olafsson et al. 1994).

Amphiura filiformis is one of the dominant macrofaunal species on soft-bottoms in the north-east Atlantic at depths from about 15 m down to 100 m or more; it has shown long-term stability and a life span of 20 yr or, more (O'Connor et al. 1983, Künitzer et al. 1992, Sköld et al. 1994). This species is buried in the sediment with its disk at about 4 cm depth. One or 2 arms are stretched up above the sediment for feeding. *A. filiformis* can switch between suspension and deposit feeding depending on current speed and availability of food (Buchanan 1964). *A. filiformis* appears to be stationary for long periods, but has been observed to leave its position in the sediment during spawning (Woodley 1975) and when oxygen saturation declines below 13 % (Rosenberg et al. 1991). Thus, this species, which does not move daily in search of food, seems suitable for conservative assessments of density-dependent or space-dependent dispersal of a marine sublittoral population.

In this study, we address the question of whether benthic sublittoral infauna may show density-dependent migration and how this eventually may be related to availability of food. Samples of the dense *Amphiura filiformis* (about 2250 ind. m^{-2}) community from the Deep Trench in the Skagerrak were collected together with its intact sediment for laboratory experiments. *A. filiformis* were initially manipulated to form 1 high and 1 moderate density treatment, each able to migrate to a less densely populated portion of the sediment. Dispersive behaviour was examined. The animals in these treatments were either given food in super-abundance or were starved.

The measurement of dispersal in this study was analyzed as a 'Random Walk' from high to low density and from moderate to low density, respectively. Should the starved and crowded population of *Amphiura filiformis* migrate to the less densely populated part of the sediment, this would suggest density-dependent and/or starvation induced dispersion. Should the fed and crowded animals also migrate to the less crowded section of sediment, this would suggest that density-dependence is the primary factor for dispersion rather than competition for food.

MATERIAL AND METHODS

Sediment collection. Sediment with intact fauna was collected on the western slope of the Deep Trench (57° 54.63' N, 11° 13.98' S) in the southeast Skagerrak off the Swedish west coast at 86 m depth on 13 September 1995. The sampler was a USNEL spade-corer (~700 kg) inside which transparent plexiglass boxes

(47 × 47 cm, height 39 cm) were installed before each deployment (Berge et al. 1986). When on board, each of the 16 boxes for the experiment was closed at the bottom. One additional sample was taken and the animals retrieved on a 1 mm mesh were identified and counted. The sediment in the samples was ~25 cm high with ~15 cm of water above the sediment. The water in all boxes was aerated with air-stones until connected to a flow-through sea water system in a thermo-constant (10°C) experimental room at Kristineberg Marine Research Station. Each box was continuously flushed with 2 to 2.5 l min^{-1} sea water (13 to 6°C and 34 psu, similar to natural conditions) of an almost laminary flow of water (0.25 to 0.30 cm s^{-1}) close to the surface of the sediment. The water was pumped from 35 m water depth and generally contained very little seston. The animals in the boxes were acclimated until 2 October.

Experimental densities. A 2-factorial experimental design replicated 4 times (16 boxes) was used with food in 2 levels (fed or starved) and density at 2 levels (moderate or high; Fig. 1). Dispersal was measured as changes in abundance. To be able to manipulate the number of *Amphiura filiformis*, but with the rest of the benthic community and sediment intact, flushing of the boxes was cut off for 24 h. By means of this treatment, hypoxic conditions were produced and approximately half of the *A. filiformis* population and several other species appeared on the sediment surface within 24 h. Each box was divided into 2 halves with a cardboard barrier. All specimens of *A. filiformis* and *A. chiajei* with their disk visible on the sediment surface were removed from one side of each box, which is referred to as the side with 'low' density. On the other side of the box, 1 'high' or 1 'moderate' density level of *A. filiformis* was prepared. By counting the number of remaining brittle star arms visible at the sediment surface on the 'low' density side of each box (~160 arms, SD = 53), the number of amphiurids 'hidden' in the sediment was estimated to about 900 ind. m^{-2}. On the other sides of the boxes, a high density of *A. filiformis* was established in 8 boxes (350 ind. equal to ~3200 ind. m^{-2}, including the estimated number of burrowed specimens). Moderate densities were established in the other 8 boxes (220 ind. equal to ~2000 ind. m^{-2}, including the estimated number of burrowed specimens as above). Densities were manipulated during 1 d. *A. filiformis* and *A. chiajei* were not distinguished during this process. A few large sea urchins *Brissopsis lyrifera* emerged on the sediment surface during hypoxia; these were removed from the boxes. The high density treatment represents natural densities; numbers were only adjusted to be similar in all aquaria. All treatments were randomized in the boxes. As soon as treatments were finished, the boxes were flushed as

before, and all infauna buried into the sediment within 1 h. After 24 h, the cardboard barriers were removed. The vast majority of *A. filiformis* were adults with a mean oral width (Sköld et al. 1994) of 2.5 (SD = 0.11) mm, equal to a disk mean diameter of 8.0 mm.

Food treatment. Eight boxes, 4 with high and 4 with moderate densities in half of the boxes, were starved during the experiment (Fig. 1). Of the other 8 boxes, animals in the high density treatments were fed daily with 25 g frozen, chopped spinach (equal to 3.1 g C m^{-2}), and the boxes with moderate density with 10 g spinach (equal to 1.2 g C m^{-2}). The food was equally spread on the sediment surface in the whole box, i.e. also in the side with low density. Spinach has proven to be a high quality food for marine animals (Åkesson 1975). When food was introduced, *Amphiura filiformis* immediately became active and their arms dragged food into the sediment. In the areas with high or low density, almost all spinach had disappeared within an hour. Spinach left on the sediment surface after 2 h was removed. The amount of food suspended in the incoming and outgoing water of the boxes was measured in 3 randomly chosen boxes 8 times and no difference was found, which suggests that food supply via the flow-through water system was insignificant compared to the food added to the boxes. For the whole period (63 d) the amount of food given was 194 and 78 g C m^{-2}, respectively.

A crude estimate of food requirements of *Amphiura filiformis*, the dominant species in both abundance and biomass (see below), can be calculated based on an energy budget for *A. filiformis* in the Skagerrak. This budget gives an energy need of 0.29 mg C ind.$^{-1}$ d^{-1} based on an absorption efficiency of 70% (Loo & Rosenberg 1996). Thus, the energy requirement for the experimental period for high densities of *A. filiformis* would be 58 g C m^{-2} and for moderate densities 36 g C m^{-2}. The next ranked species in biomass in the Deep Trench, *A. chiajei*, with about one-tenth of the biomass of *A. filiformis* (Rosenberg 1995), has a metabolic activity significantly smaller than that of *A. filiformis* (Buchanan 1964). This species would therefore not add extra relative weight to the budget calculations. Thus, the amounts of food given to the high and moderate densities, based on these calculations, were approximately 3.3 and 2.1 times greater than the populations of *A. filiformis* needed for their basic metabolism. This population alone made up >70% of the macrofaunal biomass at the station where the sediment for the experiments was taken (Rosenberg 1995), which suggests that the quantity of food given to these groups was more than required. Thus, food was not a limiting factor in either food treatment.

Number of animals and assessment of gonads. The experiment was started on 4 October 1995 and termi-

nated after 63 d on 6 December At the end of the experiment, 4 samples (2 from each side of the boxes) were taken in all treatments with a core (diameter 0.012 m^{-2}) down to the bottom of the boxes (Fig. 1) and sieved (1 mm meshes). *Amphiura filiformis* were counted and weighed alive to obtain their individual wet weights. The presence of gonads at the dorsal side of the disks was crudely assessed by eye.

Migratory behaviour. Migratory behaviour was studied in a separate experiment, in which 80 *Amphiura filiformis* were added to one half of each of 2 aquaria (20 × 40 cm) with sieved sediment to remove macrofauna. The aquaria were connected to the flow-through sea water system as above. To cancel out any current influences, brittle stars were added downstream of the empty half in one aquarium and upstream in the other. Activity on the surface was continuously recorded by video (5 images s^{-1}) in infrared radiation (IR) light in constant darkness for 4 wk. After this period, 5 cm vertical sections of sediment were sieved to assess any sub-surface migration of the brittle stars.

Measurements of sediment. Redox potential was measured with a digital potentiometer at the end of the experiment. Sediment was obtained by pushing 2 plexiglass cores with an inner diameter of 46 mm into each side of each of the 16 boxes. Ten platinum electrodes (∅: 1 mm) were pressed through sealed pre-drilled holes in the cores from 1 cm above sediment surface down to a depth of 8 cm below the sediment surface. Calculations of redox potential (Eh) followed those outlined in Fenchel (1969).

At the beginning and end of the experiment, samples of sediment were taken down to 5 cm, using a cut-off syringe (∅: 1.4 cm). Sediment was freeze-dried and nitrogen and total carbon were analyzed with a NA 1500 NC analyzer (Fisons).

Calculations and statistics. Mean migration fluxes of *Amphiura filiformis* between sides in each box were calculated from estimates of abundance in the 4 core samples taken at the end of the experiment in each box (2 from each side of the box; Fig. 1). Numbers obtained in these cores were subtracted from the abundances in the respectively sides of the box estimated at the start of the experiment. To test the hypothesis of density-dependent migration, a 'Random Walk' model was used. In this model, in which the *A. filiformis* migration is assumed to be a diffusion process, eventual differences in migration rates (net fluxes) between high or moderate densities and low density can be assessed. This is done by calculating a diffusion coefficient based on a solution of Fick's equation for dispersal between 2 compartments (Berg 1983).

$$C_{(x,t)} = \frac{C_0}{2}\left[1 + errorfunction\left(\frac{x}{\sqrt{4Dt}}\right)\right]$$

In this equation, C_0 (ind. m^{-2} h^{-1}) is the initial density, $C_{(x,t)}$ (ind. m^{-2} h^{-1}) is the density at the end of the experiment, D (m^2 h^{-1}) is the diffusion coefficient which is scale- and density-independent, t (h^{-1}) is the time between start and end and x (m) is the distance between samples (0.24 m; Fig. 1). For each box, the diffusion coefficient D was solved numerically using a mathematics software (MATLAB 4.2). There is a risk of overestimating the diffusion coefficient when the distance between samples is small in relation to step-length between turns in 'Random Walk' models. This should not be the case in the present study, because the distance between individuals was much shorter than the distance between samples. The diffusion model used here assumes that the tendency to move should be equal in all directions, that the sides of the boxes act as reflective surfaces and that there is no interaction between individuals.

Analyses for differences in the diffusion coefficient of *Amphiura filiformis* and mean individual wet weight between treatments were done as a 2-way analysis of variance (ANOVA) with density and food as fixed factors. Analysis for differences in N-content and total C-content in the sediment at 1 and 5 cm depth and mean redox potential between the surface and 8 cm depth were done using a nested 4-way ANOVA with boxside, density and food as fixed factors and box nested in the combinations of density and food. Homogeneity of variances was examined using Cochran's C-test (p < 0.05; Snedecor & Cochran 1967) and heterogeneity was removed by ln$x$ transformation.
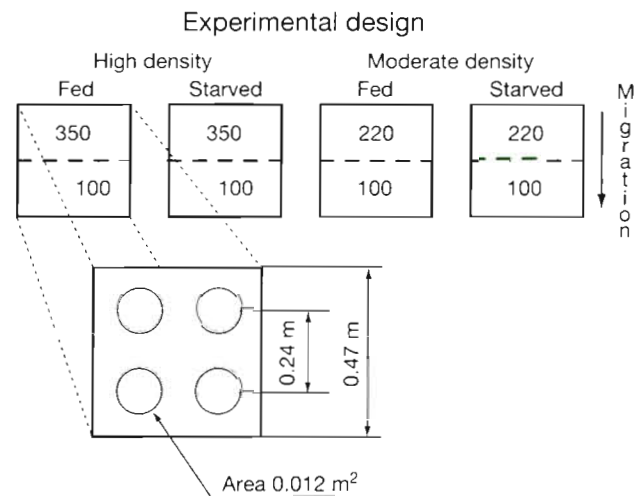
Experimental design

Fig. 1. The 2-factorial experimental design with high and moderate density of *Amphiura filiformis* and fed and starved treatments. Eventual migration route is from the high (350 ind.) or moderate (220 ind.) density side of the box to the low (100 ind.) density side. n = 4 replicates of each treatment. The enlarged box below shows how core samples were taken at the end of the experiment. The estimated distance between cores (24 cm) was used in the 'Random Walk' calculation

RESULTS

Sediment, redox potential, and carbon and nitrogen content

At the end of the experiment, the sediment surface in all boxes was generally grey-brown in colour and generally similar to its appearance at the start. Some dark spots were, however, noted in the corners of boxes with the highest densities of brittle stars. The vertical appearance of the sediment, visually inspected from the sides of the transparent boxes, seemed unchanged. A significantly smaller mean redox potential (0 to 8 cm depth) was measured in the fed treatments than in the starved treatments (Fig. 2; ANOVA, $p < 0.05$, df = 1,12). No significant difference in mean redox potential was observed between treatments with moderate and high densities (ANOVA, $p > 0.05$, df = 1,12). Data from May 1995 are also shown for comparison with measurements made in sediment cores in the field from the same area.

Mean total carbon and nitrogen in the top 0 to 1 cm sediment at the beginning of the experiment were 3.3% (SD = 0.13) and 0.25% (SD = 0.018) of sediment dry weight, respectively (C/N = 13.2). These values were not significantly different from those of the 5 to 6 cm layer At the end of the experiment, no significant differences were found between treatments (ANOVA, $p > 0.05$, df = 1,12). Thus, no accumulation of total carbon or nitrogen occurred in the sediment during the experiment.

Faunal composition

Mean abundances of the 10 dominant species recorded in the high and moderate treatments at the end of the experiment are shown in Table 1. The numerically highest ranked species were the same in both treatments. A pair-wise comparison of the abundance of each species shows that the numbers were slightly greater in the high density treatment compared to the moderate treatment, except for the gastropod *Hyala vitrea*. The numbers in the boxes were also similar to those found in the field and indicative of low experimental mortality. Only a few dead individuals were found during the experiment. Conspicuous species observed on the sediment surface at the end of the experiment were the ophiuroid *Ophiura albida* (total 9 ind. in all boxes), the polychaete *Ophiodromus flexuosus*
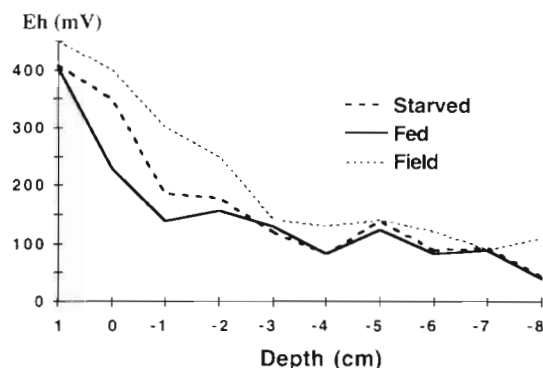

Fig. 2. Mean redox potentials (Eh; n = 32) in relation to depth of sediment at the end of the experiment (December 1995) in the fed and starved treatments, and in sediments collected in the field (May 1995, S. Agrenius pers. comm.)

(1 to 4 per box), a single anemone *Cerianthus* sp. and the amphipod *Maera loveni*. *Amphiura filiformis* made up an average of 95.5% and *A. chiajei* 4.5% of the total density of amphiurids.

Dispersal

The mean net flux of *Amphiura filiformis* from the sides of the boxes with high or moderate densities to the sides with a low density is shown in Fig. 3. No significant interaction was found between the density and food treatments (ANOVA, $p > 0.05$, df = 1,12). Significantly (ANOVA, $p < 0.05$, df = 1,12) greater diffusion coefficients, indicating faster dispersal per specimen, were observed in boxes with high densities (mean 6.136×10^{-5} m^2 h^{-1}) than in boxes with moderate densities (mean 1.801×10^{-5} m^2 h^{-1}). No significant (ANOVA, $p > 0.05$, df = 1,12) differences in diffusion coefficients were observed between fed and starved treatments.

Table 1. Mean (SD) density per m^2 of 10 dominant species found in the high and moderate density treatments at the end of the experiment, and initial numbers found in the field

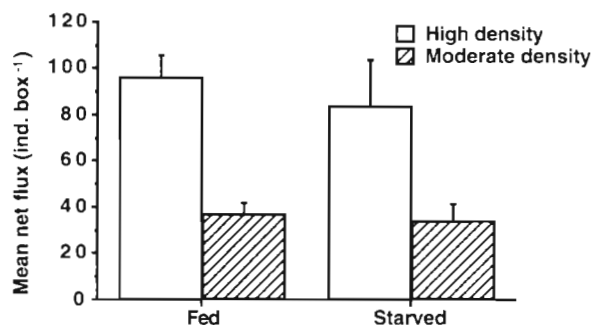|	High density	Moderate density	Field density
Amphiura filiformis	2322 (840)	1552 (560)	2250
Pholoe minuta	990 (52)	792 (52)	861
Mysella bidentata	797 (85)	667 (59)	278
Abra nitida	458 (96)	359 (11)	389
Lapidoplax buskii	260 (15)	245 (55)	194
Hyala vitrea	57 (26)	135 (7)	56
Ophiura albida	83 (22)	68 (18)	0
Pectinaria koreni	104 (0)	62 (7)	0
Pectinaria auricoma	78 (11)	42 (0)	0
Heteromastus filiformis	94 (0)	10 (7)	28

Fig. 3. *Amphiura filiformis*. Mean (SD; n = 4) rates of migration (net fluxes after 63 d) from the half of a box with high or moderate density to the half with low density in fed and starved treatments

Biomass

Individual weights of *Amphiura filiformis* are shown in Fig. 4. *A. filiformis* fed during the experiment had a significantly (ANOVA, p < 0.05, df = 1,12) greater wet weight per individual than those that were starved. No significant difference (ANOVA, p > 0.05, df = 1,12) in weight was found between individuals in moderate (mean 0.202 g ind.$^{-1}$) and high (mean 0.201 g ind.$^{-1}$) densities, or between sides of a box. Thus, *A. filiformis* assimilated the food they were given and in about equal amounts per individual in both density treatments.

Gonad development

Several *Amphiura filiformis* showed visible development of gonads on the ventral side of the disk. Gonads were observed in 42% (SD = 14, n = 26) of the fed brittle stars and in 12% (SD = 15, n = 25) of the starved individuals.
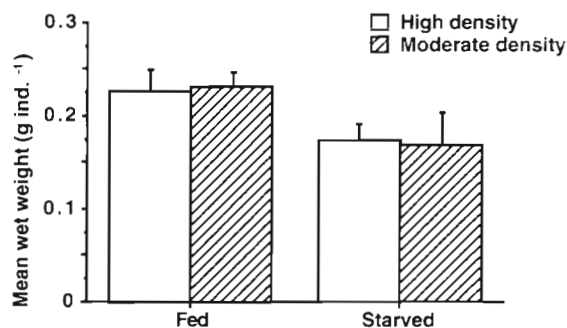

Fig. 4. *Amphiura filiformis*. Mean (SD; n = 4) individual wet weight in high and moderate densities and in fed and starved treatments

Migratory observations

No brittle stars were seen on the surface of the sediment in the boxes. When the behaviour was recorded by video, 14 *Amphiura filiformis* were observed moving on the sediment during the 4 wk of continuous observation. Some of these crossed the 'borderline' to the side of the 2 aquaria with no macrofauna, but some moved back and only 4 buried themselves into the sediment on the 'empty' side. In the analysis of sediment at the end of this experiment, 16 individuals out of 160 were found on the formerly 'empty' side; 8 of these were found more than 10 cm from the 'borderline'. There was no upstream or downstream effect on migration. Thus, *A. filiformis* are able to move on or within the sediment.

DISCUSSION

Experimental technique and food supply

The experimental technique used here, with natural sediment and fauna, was adopted from Berge et al. (1986). In the present experiment, the aquaria were supplied with water of the same salinity and a similar temperature as that at the site of collection. Except for the surface of the sediment, carbon and nitrogen concentrations and redox potential depth distribution were similar in the treatments. At the upper centimetres of the sediment, the redox potential was lower, probably as a result of food supply. Thus, sediment conditions seem to have been rather stable during the experimental period despite different treatments. No great differences were recorded in composition and abundance of dominant species, either between treatments at the end of the experiment, or between treatments and what was initially found in the field. In comparison with abundances obtained in May 1992 from the same area (Rosenberg 1995), the numbers were similar, except for *Amphiura filiformis*, which then occurred in larger numbers of about 3600 ind. m^{-2}.

'Export production', which is similar to sedimentation, has in the Skagerrak been estimated to be about 50 g C m^{-2} yr^{-1} (Stigebrandt 1991), whereas records from sediment traps during the productive part of the year have given estimates 2 to 3 times greater (Rosenberg et al. 1990, Bjørnsen et al. 1993). These quantities of sedimenting material towards the bottom are small compared to the amounts used in this experiment. Thus, the total amount seems to have been more than sufficient for all animals in the experiment. In the Deep Trench area, however, advective transport of organic matter has been recorded near the bottom. This will provide additional food to the benthic communities living there (Rosenberg 1995).

Pattern of distribution

The 'ideal free distribution' model is frequently used to describe patterns of distribution of mobile animals in relation to availability of food (Milinski 1988, Kacelinic et al. 1992). It states that each individual should choose patches so that it maximises its rate of food intake, that resources are distributed in patches and that competitors are equal in all respects. The model may be applicable to behavioural patterns in mobile animals such as fish, which can make a clear choice in this respect. It is, however, less relevant for semi-mobile benthic infauna that may not be able to notice and respond to resources some distance away.

Instead, *Amphiura filiformis* may be moving randomly. In the present experiment, some individuals may be pushed towards the sides of the boxes and may either have to stay close to the walls or to 'push back' and perhaps create pressure for movement in the opposite direction. Density-dependent dispersal in the present experiments occurs from the open half of the box where the brittle stars can move into the less densely populated side. From this borderline, the net migration will initially be more or less unidirectional. Limited by the 3 sides of the enclosure, this general behaviour pattern seems to fit the diffusion model, which states that dispersal arises from random movements and that net movement results in a more even spread of a population (e.g. MacCall 1990). If the movements of some individuals were retarded along the sides or in the 2 corners of boxes, the diffusion coefficient should have been underestimated. If that happened, however, it may not have affected the difference in rate of dispersal between the 2 densities.

In this experiment, 26% (high) to 16% (moderate) of the individuals in the crowded side of the boxes had moved into the less crowded side by the end of the experiment. As this only indicates the net flux of specimens in a 'Random Walk' model, the total movement of specimens in the sediment should be greater. A simple calculation of the capacity of *Amphiura filiformis* to rework and dislocate the sediment could be estimated from the diffusion coefficient observed in this study ($D = 6.136 \times 10^{-5}$ m^2 h^{-1}, in high density) and from field data abundance (density of ~3000 ind. m^2) obtained from the Deep Trench in the Skagerrak (Rosenberg 1995). Given in 2 dimensions, the square of the distance of dispersal during 1 h from a point of origin is r^2 = 4Dt = $4 \times 6.136 \times 10^{-5}$ m^2 h^{-1} (Berg 1983). This gives a total distance of movement of 47 m h^{-1} for all 3000 specimens of *A. filiformis* in a square metre. Such an estimate is a crude approximation because the distance is dependent on patterns, direction and speed of movement. At a density of about 3000 ind. m^{-2}, the area of sediment at about 3 to 4 cm depth covered by disks of *A. filiformis*

can be estimated as 22% (Rosenberg 1995). The capacity of such a density of brittle stars to displace sediment can be calculated at 0.18 m^2 h^{-1}. Thus, movement of *A. filiformis* should generate a more or less continuous displacement of sediment and be of great significance to the bio-geo-chemical processes in the sediment.

Food and density dependence

Several studies dealing with soft-bottom fauna have shown food to be a regulating factor for density. This is most obvious for deposit-feeding animals, which have to compete for food as a partly degraded resource (e.g. Levinton 1979). In shallow waters, suspension-feeding animals may, at least during some seasons, be able to feed on an abundant, nutritious food source. Although secondary production in suspension-feeding bivalves can be extremely high in some areas (Möller & Rosenberg 1983), other studies have demonstrated that members of this feeding category can also be food limited (Peterson & Black 1987).

In the present experiment, the weight of *Amphiura filiformis* treated with daily additions of food increased significantly more than that of starved individuals. Thus, the brittle stars assimilated the food and some of the resulting energy was allocated to germinal growth. Build-up of gonads may be a way for *A. filiformis* to store energy, which may be resorbed during periods of starvation. In a similar box experiment with a benthic community from the same Deep Trench area, Sköld & Gunnarsson (1996) demonstrated somatic and germinal growth in *A. filiformis* and *A. chiajei* in response to food supply. Comparisons between a high and a low density community in that experiment suggested that growth was density-dependent because of competition for space or food. A possible explanation for that density-dependent growth may be that the amount of food (16.8 g C m^{-2} in 2.5 mo) given to the high density treatment was not enough. It was slightly less than one-tenth of the amount (in carbon) given in the high density treatment in the present study. Contrary to the results in the Sköld & Gunnarsson (1996) experiment, Josefson (1995) found that growth was independent of density even in *A. filiformis* at densities >3000 ind. m^{-2}. These results were obtained in a field study in the Kattegat (south of Skagerrak) and growth of *A. filiformis* was estimated from measurements taken 143 d apart of oral widths. The reason for density-independent growth rates may be that abundances were related to the food resources in the sampling areas and that food availability per individual was approximately equal. Josefson's (1995) estimates of biomass increments were obtained from size correlations; growth of gonads was not included.

Based on results from a field study, it has been suggested that the benthic community examined in the present study is limited by space rather than by food (Rosenberg 1995). This assumption was made because several populations, among them *Amphiura filiformis*, had extremely large densities and biomasses. A significant contribution of food for these animals in the field was supplied by means of near-bottom horizontal currents. In our experiments, *A. filiformis* was fed daily with food in excess. Despite this, they migrated from the crowded treatments to sediments where abundance was smaller; numbers and biomasses became similar. This is the first time density-dependent dispersal has been shown experimentally in sublittoral soft-bottom populations.

Interspecific and intraspecific competition

In shallow coastal and intertidal areas, density-dependent competition and interaction have been observed in a number of studies. Ambrose (1986), for instance, provided evidence that the avoidance of large densities is a selective advantage in the amphipod *Rhenoxynius abronius*. Such migration significantly increased the emigration from the sediment to the water column, which increased the vulnerability of amphipods to predation. Based on results from an experimental study in a sandy-bottom lagoon in southern California, Peterson (1977) suggested that competition for space may be the most important biological factor determining the abundance of species in that area. Manipulations of density demonstrated emigration of a suspension-feeding bivalve, *Cryptomya californica*, which probably was a result of negative intraspecific interactions. Additional results from the same lagoon also suggested that competition, in this case interspecific interaction among suspension-feeders, for space is a primary mechanism for interaction in this system (Peterson & Andre 1980). On the other hand, in an experimental study of spatial competition in a dense infaunal intertidal community on the U.S. Pacific coast, no interspecific competitive interactions could be observed (Wilson 1984). Wilson (1983) found, however, strong density-dependent intraspecific competition in the deposit-feeding polychaetes *Pygospio elegans* and *Pseudopolydora kempi*. Although density-dependent migrations have been demonstrated in the field and in microcosm experiments, the importance of the availability of food was not evaluated.

The examples presented here suggest that intra- and interspecific competition can both affect abundance, distribution and organisation of populations. Similar results have also been obtained in studies of intertidal limpets (Creese & Underwood 1982). Several authors have suggested, based on the fact that the same species compete for the same food resources, that intraspecific (Ebert 1977, Levin 1981) and also intrafamilial (Woodin & Jackson 1981) competition are stronger and more common than interspecific competition. Competitive interactions between *Amphiura filiformis* and *A. chiajei* were not investigated here, but these 2 species are known to co-occur in many areas (e.g. Petersen 1913) and also in the Deep Trench sediments (Rosenberg 1995). Interactive behaviour between the 2 species was not observed on the surface of sediments during the experiments. Their disks are at a similar depth in the sediment and interspecific competition for space is likely when densities are high.

Intraspecific aggressive behaviour, e.g. fights for food, has been recorded in the spionid *Pseudopolydora paucibranchiata*, and recruitment patterns for this species seem to result in a uniform spacing during settlement (Levin 1981). Such territorial behaviour may be a population regulatory factor. Intraspecific aggressive behaviour in *Amphiura filiformis* was not observed at the sediment surface in the present experiments, but a few times 2 arms belonging to different specimens were noted to struggle with one another when they tried to capture the same food particle. Mutual interference may, however, occur within the sediment. The space occupied by disks of 3000 ind. m^{-2} of *A. filiformis* at about 3 cm depth in the sediment in the Deep Trench was estimated to be ~0.22 m^2 (Rosenberg 1995). In addition to this, about 3 arms of each individual are also kept in the sediment (Ockelmann & Muus 1978, Loo et al. 1996), which indicates that the space in the sediment may be densely packed with *A. filiformis*. For feeding, *A. filiformis* needs access to the surface; the area swept and occupied by the arms (sometimes 2 per individual) is larger than the disc area.

Peterson (1977) argued that the carrying capacity of infauna is only loosely associated with total volume of infauna, but more closely related to demand for contact with the water-column. It is impossible to determine whether or not the trigger for dispersal of *Amphiura filiformis* in the present experiment is interaction on the surface or within the sediment. Numerous encounters between arms on the surface may trigger movement of the animals. The activity pattern and frequency of encounter rates of arms in the sediment are not known. When food was presented to the brittle stars, the activity of arms increased immediately. This increased activity increases the encounter rates between neighboring specimens and possibly induces migratory behaviour. Thus, if this is the case, increased arm activity may have a positive impact on the rate of migration and may lead to an overestimation of the diffusion coefficient.

Migration of brittle stars is shown to occur on the surface and within the sediment. Movement within the sediment takes longer, but the risk of predation from surface-dwelling predators is less compared to migration on the surface. That brittle stars are well suited to move in the sediment was demonstrated in the initial phase of the experiment; they were able to burrow into the sediment within a few seconds. The arms (usually 3) kept in the sediment may act as an anchoring system (Woodley 1975) and for *Amphiura chiajei* have been suggested to assist in sliding movements of the animals within the burrows (Ockelmann & Muus 1978). According to Woodley (1975), it is possible that brittle stars can drag themselves through the substratum in the same way that they burrow. The present experiment provides new evidence that brittle stars are mobile and may use their arms in the sediment to adjust their position and to direct their movement, perhaps sometimes away from interfering animals. The substantial migration by *A. filiformis* in this laboratory experiment might imply that they commonly move in the sediment and change their position. Such movement will destabilize the sediment and, as a consequence, affect other infauna behaviour including settlement and recruitment. Displacement will have impacts on chemistry and compaction of sediments. Because *A. filiformis* is a conspicuous species in many areas of the east Atlantic (e.g. Petersen 1915, Duineveld et al. 1987), these suggested effects may be of significant importance to the ecosystem and need to be investigated in detail in future studies.

Colonization

The observed mobility of *Amphiura filiformis* implies that this species is capable of colonizing new patches, at least over short distances. Physical disturbances, such as demersal trawling, dredging, strong winds and seasonal deficiency of oxygen in bottom waters, may open new patches for possible immigration by adult *A. filiformis*. Zajak & Whitlatch (1991) demonstrated that demographic aspects including survivorship, fecundity, and population growth rate are important factors in soft-sediment patch dynamics. Seasonal hypoxia has been shown to force *A. filiformis* and *A. chiajei* out of the sediment (Rosenberg et al. 1991). The latter species was capable of directional migration on the surface to reach elevated patches (Stachowitsch 1984), where oxygen concentrations were presumably greater than in nearby depressions. Thus, these brittle stars, if they survive a physical disturbance or a hypoxic event, may—when oxygen conditions improve—later be able to emigrate to new patches where exploitable resources may be available.

From 1968 onwards, benthic faunal succession following abatement of sediment enrichment was studied in a Swedish fjord in October for successive years (Rosenberg 1976). In the inner part of the fjord, the benthic communities were in an early successional stage in 1969. No *Amphiura filiformis* were found in that inner area. In 1970, about 50 juvenile *A. filiformis* ind. m^{-2} were recorded at 3 stations at 30 m depth, but the following year several hundred adult *A. filiformis* with developed gonads were found at the same 2 stations (Rosenberg 1976 and unpubl. results). It takes several years for *A. filiformis* to grow to maturity in the Skagerrak (Sköld et al. 1994), so immigrants must have arrived from the adult population further out in the fjord. Emigration from outer stations, where adults were found the previous year in sufficient numbers (Rosenberg 1976), suggests a migration over distances of up to 2 km, which is too long to be the result of a diffusion process only. The diffusion equation used here suggests that migration by means of diffusion may take about 3 million years. Perhaps populations of *A. filiformis* were present on the slopes surrounding those two 30 m stations. In any event, immigration of adult *A. filiformis* to this previously low diversity area was evident.

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