

Learning Intention: Today I will

Identify important elements of a scientific journal including:

- Purpose
- Method (including: study location, sample size, target species and experimental type)
- Results
- Interpretation of results
- Discussion
- Future implications of findings

Success Criteria: I am able to

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How to read a scientific paper quickly and efficiently

Step 1: Skim the abstract

- Provides an overview of a scientific paper intended to give researchers and other scientists a general understanding of a particular study without making them read the entire paper.

Step 2: Read the discussion

- Focus on reading the first and last paragraphs.
- First paragraph: provides a summary of study findings and how they relate to the research question/hypothesis.
- Last paragraph: reinforces how study did or did not answer their research question and provides future implications and recommendations for research.

Step 3: After the conclusion, read the results

- This section gives succinct information about results - DOES NOT include interpretation or discussion of results/findings.

Step 4: Read the methods section

- Provides detailed description of study location, variables, methods used to collect data, methods of data analysis etc.



Effects of bottom trawling on ecosystem functioning

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ABSTRACT

By combining field observations with data from controlled mesocosm experiments this study demonstrated that bottom trawling has the potential to cause long-term impacts on sediment nutrient fluxes. Field observations confirmed that trawling reduced the density of important bioturbators in the study area, but revealed only weak effects of trawling on nutrient fluxes. The importance of the decline in bioturbators was demonstrated in the mesocosm experiments where the density of four key bioturbators (*Brissopsis lyrifera*, *Nuculana minuta*, *Calocaris macandreae* and *Amphiura chiajei*) showed significant correlations with nutrient flux. All four species caused an increase in the rate at which silicate was released from the sediment, but their effect on nitrogen cycling were species specific. Bioturbators that bulldoze through the sediment (*B. lyrifera* and *N. minuta*) increased the loss of dissolved inorganic nitrogen (DIN) from the sediment, whereas those that irrigate burrows within the sediment (*C. macandreae* and *A. chiajei*) caused increased uptake of DIN. This shows that the activities of the species present can determine whether the seabed acts as a source or a sink of nitrogen nutrients. By combining these experimental results with field observations of bioturbator abundances, we demonstrate the potential impacts of trawling on benthic ecosystem function. Due to the worldwide extent of intensive bottom-trawling, such effects may be globally significant and affect the nutrient balance especially in continental shelf and coastal areas.

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1. Introduction

Soft-sediment ecosystems cover almost 70% of the earth's surface and have a fundamental role in the functioning of marine systems, both for remineralization of organic carbon and nutrients and as food producers for larger macrofauna and fish. In recent years, there has been growing awareness that physical disturbance caused by bottom trawling may be one of the most important sources of anthropogenic disturbance to soft-sediment benthic communities and habitats (Dayton et al., 1995; Jennings and Kaiser, 1998; Collie et al., 2000; Pauly et al., 2002; Kaiser et al., 2006). Recent articles and correspondence led by the late Professor John Gray have shown that this is still a very highly topical area of research (Gray, 2000; Gray et al., 2006, 2007a,b). Over the last decades trawlers in the North Sea have used heavier gears and over 90% of the sea floor is trawled at least once, and in some areas six times a year (Jennings et al., 2001). The effects of trawling on structurally complex habitats and fauna have been compared to the effects of forest clear-cutting (Watling and Norse, 1999). The world fleet of trawlers sweep up to 15 million km² of seabed annually – an area 150 times greater than that of the forests cleared each year (Malakoff, 1998). As nets, beams, trawl doors, chains

and dredges pass over the seabed, the sediment surface is disturbed and a large proportion of the resident biota (e.g. bivalves, burrowing crustaceans, tube-building polychaetes and echinoderms) is damaged or removed (Craeymeersch et al., 1997; Jennings and Kaiser, 1998; Kaiser et al., 2006). Whilst it is generally accepted that bottom trawling changes the structure of benthic communities, with trawled areas being dominated by small-bodied, opportunistic species at the expense of species that are large, long-lived and potentially fragile, few studies have considered the implications of trawling on ecosystem processes (Duplisea et al., 2001; Thrush and Dayton, 2002; Tillin et al., 2006). Large parts of most shelf seas have been intensively exploited by bottom trawlers for decades. Assessing the long-term and large-scale impact of chronic bottom trawling on ecosystem functioning should therefore have priority in studies of the impact of bottom trawling (Tillin et al., 2006). In order to fully study the effects of trawling investigations should consider impact on both structure and function (de Juan et al., 2007).

Function can be defined as specific processes within an ecosystem that change the rates and properties in the system. Important ecosystem functions in soft-sediment environments are biogeochemical processes associated with remineralization of organic material and regeneration of nutrients and nutrient fluxes. Organic material produced in the pelagic and shallow benthic zones and from terrestrial runoff is deposited at the sediment surface (eg. Aller, 1982; Hall et al., 1996). Once the particles reach the sediment, the material will be

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mineralized and transported as solutes across the sediment-water interface into the water column or buried in the sediment (Aller, 1982; Ståhl et al., 2004; Norling et al., 2007). The remineralization process, through fluxes of nutrients, ultimately fuels new algal production in the euphotic zone. In the surface sediment system the macrofauna is an important component for the benthic-pelagic coupling in terms of transport and exchange of solids and solutes in sediment and water through deposition and recirculation (Graf, 1992; Aller, 1988, 1994).

Organic matter remineralization in sediments is performed mostly by the micro-organisms, both in the oxic and anoxic part of the sediments. Benthic macrofauna inhabiting the surface sediments markedly influence these processes through bioturbation that alters the habitat by reworking the sediments (e.g. Gray, 1974; Rhoads, 1974; Rhoads and Boyer, 1982). These macrofauna activities have a large impact on organic matter remineralization, transformation of nitrogen and mobilization of phosphate and silicate (Aller, 1982, 1988; Hooper et al., 2005). Through burrowing, feeding, ventilatory and locomotory behaviour, the infauna disproportionately influence biogeochemical and diagenetic reactions within the interstitial porewater and promote the vertical and lateral redistribution of sediment particles above and/or below the sediment-water interface (Solán et al., 2004). Bioturbation also directly enhances microbial activity (Aller and Yingst, 1985).

Without macrofauna in the sediments to stimulate these processes the breakdown of organic matter would be based on diffusion within the sediment and across the sediment-water interface. These processes are slow, but are greatly enhanced (2–10 times) by macrofaunal activities in the surface sediments (e.g. Rutgers van der Loeff et al., 1984; Aller and Yingst, 1985; Helder and Andersen, 1987). Overall, bioturbation by macrofauna is one of the most important functions that regulate process rates and pathways during organic matter mineralization in marine environments (Rhoads, 1974; Aller, 1982; Norling et al., 2007). Based on the knowledge we already have on the impacts of trawling we must expect it will interfere with these functional processes in coastal and shelf areas, where benthic-pelagic coupling often is tight. Studies of indirect effects of trawling on nutrient fluxes, through impact on the macrobenthic communities, are therefore important. A key to understanding the effect of trawling disturbance on the functioning of benthic ecosystems is the relationship between the function of species and their vulnerability to trawling disturbance (Larsen et al., 2005; Tillin et al., 2006).

In the present study field investigations were performed to describe sediment nutrient fluxes in trawled and non-trawled sea beds. Sediment cores were collected for determination of field fluxes of oxygen and nutrient species. Simultaneously a mesocosm experiment was designed to investigate the effects of larger, bioturbating infauna on sediment-water fluxes and quantify relations between nutrient fluxes and densities of several large, trawl sensitive species commonly found in the study area. In the experiments we manipulated the density of 7 large, naturally occurring, species of macrofauna which were considered potentially vulnerable to trawling (S. Jennings,

pers. comm., Table 1). The selected species were added to experimental buckets with natural sediments with inherent communities of micro-organisms, meiofauna and other macrofauna, which is important to mimic the seabed environment (Widdicombe and Austen, 1998; Widdicombe et al., 2004).

The 7 species of bioturbators selected for this study were the sea urchin *Brissopsis lyrifera* (Forbes, 1841), the bivalves *Nuculana minuta* (Müller, 1776) and *Astarte sulcata* (da Costa, 1778), the thalassinid shrimp *Calocaris macandreae* (Bell, 1846), the brittle star *Amphiura chiajei* (Forbes, 1843) and the polychaetes *Nephtys caeca* (Fabricius, 1780) and *Aphrodita aculeata* (L., 1758). These species are abundant in the Oslofjord and represent a range of bioturbation, bio-irrigation and burrow-formation mechanisms, as well as a range of trait profiles including feeding strategies that are potentially vulnerable to trawling. For a more complete description of these species, see Widdicombe et al. (2004). The selected bioturbating species also occur in many other areas throughout the North Sea, Irish Sea and English Channel, where trawling disturbance is absent or low. They are functionally similar to other species common in many soft-sediment habitats. The benthic fauna of the study area has been described as typical of that found in other sites in Western Europe and probably also of large areas of the European continental shelf (Mirza and Gray 1981; Valderhaug and Gray, 1984).

2. Materials and methods

2.1. Selection of field sites

The area of investigation was the outer Oslofjord, a northern branch of the Skagerrak in the North Sea, where a very large part of the seabed deeper than 60 m is regularly visited by shrimp trawlers. Their target organism is the edible shrimp *Pandalus borealis* (Krøyer, 1838), with a by-catch of demersal fish. The sediment type is mainly muddy sand, a habitat shown to be surprisingly vulnerable to trawling and with predictable recovery times measured in years (Kaiser et al. 2006; Allen and Clarke, 2007). Four areas subjected to commercial otter trawling were identified for study. These areas are visited by trawlers between 50 and 100 times per year, and based on the size of the trawls and the boat speed, each part of these areas are trawled on average 2–3 times per year. Each of the areas were surveyed using a remotely operated vehicle (ROV) equipped with an autonomous positioning system, a digital video recorder and a ROV-mounted side-scan sonar to locate trawled and non-trawled sites within each area. Trawling leaves 10–20 cm deep furrows in the seabed, which were visible on the side-scan images (Fig. 1).

Based on furrow frequencies determined from the sonar- and video-images, one trawled site and one non-trawled control site were chosen within each area (8 sites altogether, Fig. 2). Control sites were placed in areas with wrecks or areas with rocks on the bottom, which are avoided by the fishermen to prevent destruction of gear.

Study Overview

Table 1

The seven bioturbating species used for density manipulations in mesocosm experiment

Bioturbating species	Organism type	Organism characteristics	Low density	High density
<i>Nuculana minuta</i>	Bivalve	Sub-surface "bulldozing" deposit feeder	8	32
<i>Astarte sulcata</i>	Bivalve	Medium sized, suspension feeder, sits near sediment surface with upper edge of shell protruding slightly into the water column	3	12
<i>Amphiura chiajei</i>	Brittle star	Lays buried in the sediment with its disc at 4–6 cm depth. One or two arms are stretched up above the sediment to collect food at the surface, other arms may be extended deeper into the sediment below the disc.	7	28
<i>Aphrodite aculeata</i>	"Sea mouse" Polychaete	Large, oval bodied, active, mobile predator operates close to or actually on the sediment surface.	1	4
<i>Nephtys caeca</i>	Polychaete	Highly mobile, predatory worm, 15–25 cm long, creates non-permanent burrows to a depth in excess of 15 cm.	1	4
<i>Brissopsis lyrifera</i>	Heart urchin	Non-selective, infaunal, "bulldozing" deposit feeder, burrows to 10 cm depth.	1	4
<i>Calocaris macandreae</i>	Burrowing shrimp	Constructs deep, complex burrows with multiple surface openings, rarely emerges onto sediment surface	1	4

Type of organism, short description of feeding, and treatment densities (individuals per bucket, 0.1 m²).

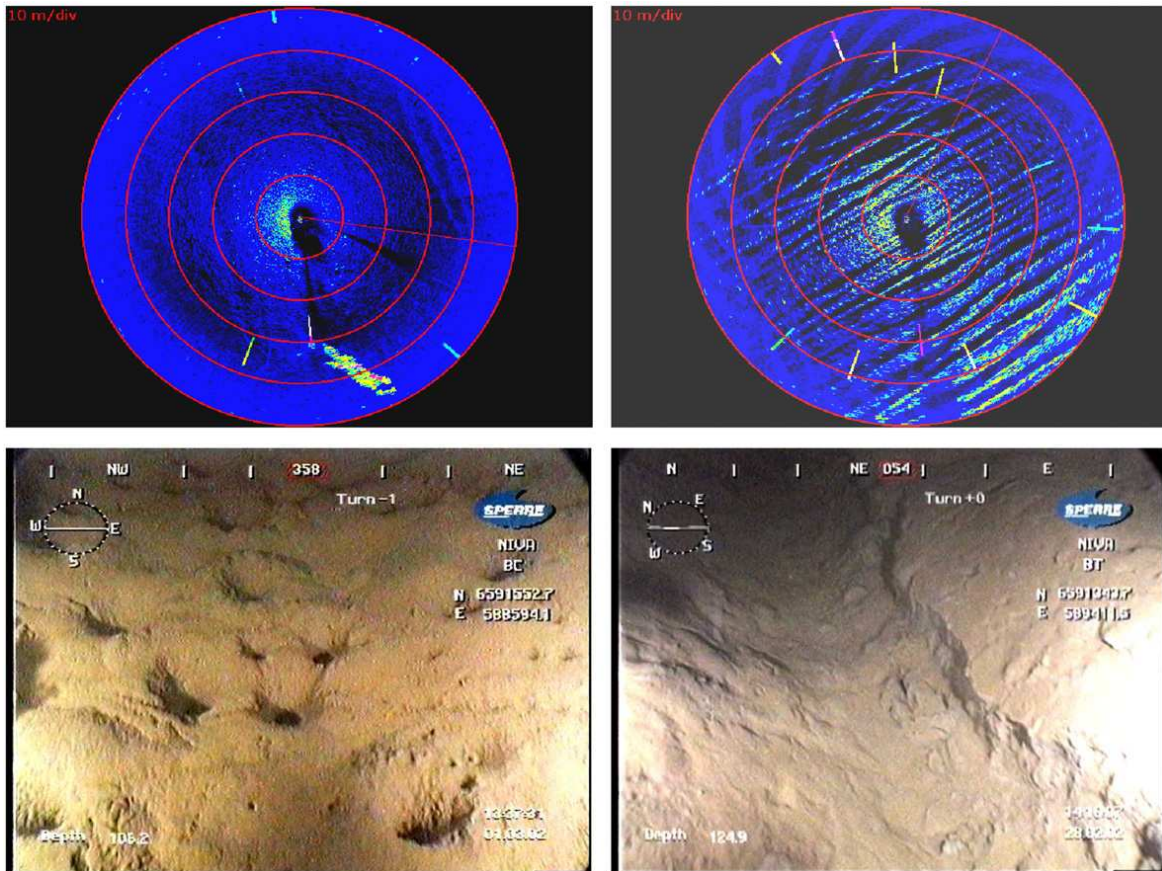


Fig. 1. Upper left: Sonar image of non-trawled area. Diameter of circle is 100 m. No visible trawl marks on the sediment. Yellow spot is the wreck of a sailing boat. Lower left: Burrow holes made by the burrowing shrimp *Calocaris macandreae*. Size of photo approximately 40×50 cm. Upper right: Sonar image of trawled area. Trawl marks from the otter-trawl doors are clearly visible on the sediment surface. Lower right: Trawl mark from the otter trawl door on the sediment surface.

2.2. Faunal samples in trawled and non-trawled areas

In June 2002, macrofaunal samples were collected with a 0.1 m² van Veen grab in the 8 experimental sub areas (5 replicates from each sub area). Samples were sieved on 5 mm and 0.5 mm sieves, sediment residue fixed in ~5% buffered formalin and Rose Bengal stain added. In the laboratory all macrofauna samples were sorted from the remaining sediment and transferred to 70% ethanol and organisms identified to the species level, or where this proved difficult, to the lowest taxon possible.

2.3. Nutrient flux measurements in field samples

Sediment cores (10 cm inner diameter, 60 cm long) were taken for determination of nutrient fluxes in winter (March 2002) and summer (June 2002) with a Bowers and Connelly multicorer. Three cores were collected at the 4 trawled and 4 control sites (Fig. 2). The sediment cores, plus three experimental blank cores (without sediment) for flux measurements were incubated in a water bath and continuously flushed with seawater extracted from 60 m depth to maintain field conditions of about 8 °C, 34 PSU and 6 mg O₂ l⁻¹. The water exchange in each core was maintained by a flow-through system using multi channel peristaltic pumps supplying the 60 m water from a common header tank through each core. After a 6 days equilibration period required to obtain steady state concentrations of O₂ and nutrient species in the overlying water, fluxes (F_x) were determined as F_x=(C_i - C_o)Q/A where F_x is the flux of nutrient×(μmol·m⁻²·h⁻¹), C_i is the mean concentration of x in the header tank (μM), C_o is the mean concentration of x in the overlying water (μM) in each core, Q is the flow of water through the core (l h⁻¹) and A is the area of the core

(m²). All fluxes were corrected by subtraction of the flux determined in the blank cores without sediment.

For the flow rates (Q) a precision better than 0.01 ml min⁻¹ was obtained by gravimetric determination of water collected from each channel for a period of at least 10 minutes. Samples for nutrient analyses were collected, conserved, stored and analysed as described in Section 2.4.

2.4. Mesocosm experiments

← Controlled experiment

The mesocosm experiments were performed between March and August 2002 at NIVA's Marine Research Station at Solbergstrand. The system has been described in detail by Berge et al. (1986). Muddy-sand sediments with natural fauna were collected at 30 m depth in Bjørnehodebukta in the Oslofjord using a van Veen grab. The sediment was used to fill contaminant-free plastic buckets (36 cm inner diameter) to a depth of 30 cm. Conspicuous bioturbating species were removed during transfer to the buckets and potential occurrence of spatial heterogeneity at the sampling location was reduced by combining sediment from a number of grabs into each bucket. The buckets were placed in a 4.9×7×3 m deep indoor concrete basin and a constant water depth of 100 cm was maintained in the basin with a continuous flow-through of seawater pumped from 60 m depth in the Oslofjord. Further details on the experimental set-up and design have been published in Widdicombe et al. (2004).

To each of the buckets 1 of the 7 species of bioturbators was added at either "high" or "low" densities (Table 1). The bioturbators were collected from a muddy-sand locality at about 30 m depth on the eastern side of Håøya Island in the Oslofjord, a locality with very high biodiversity and where it is relatively easy to get the number of

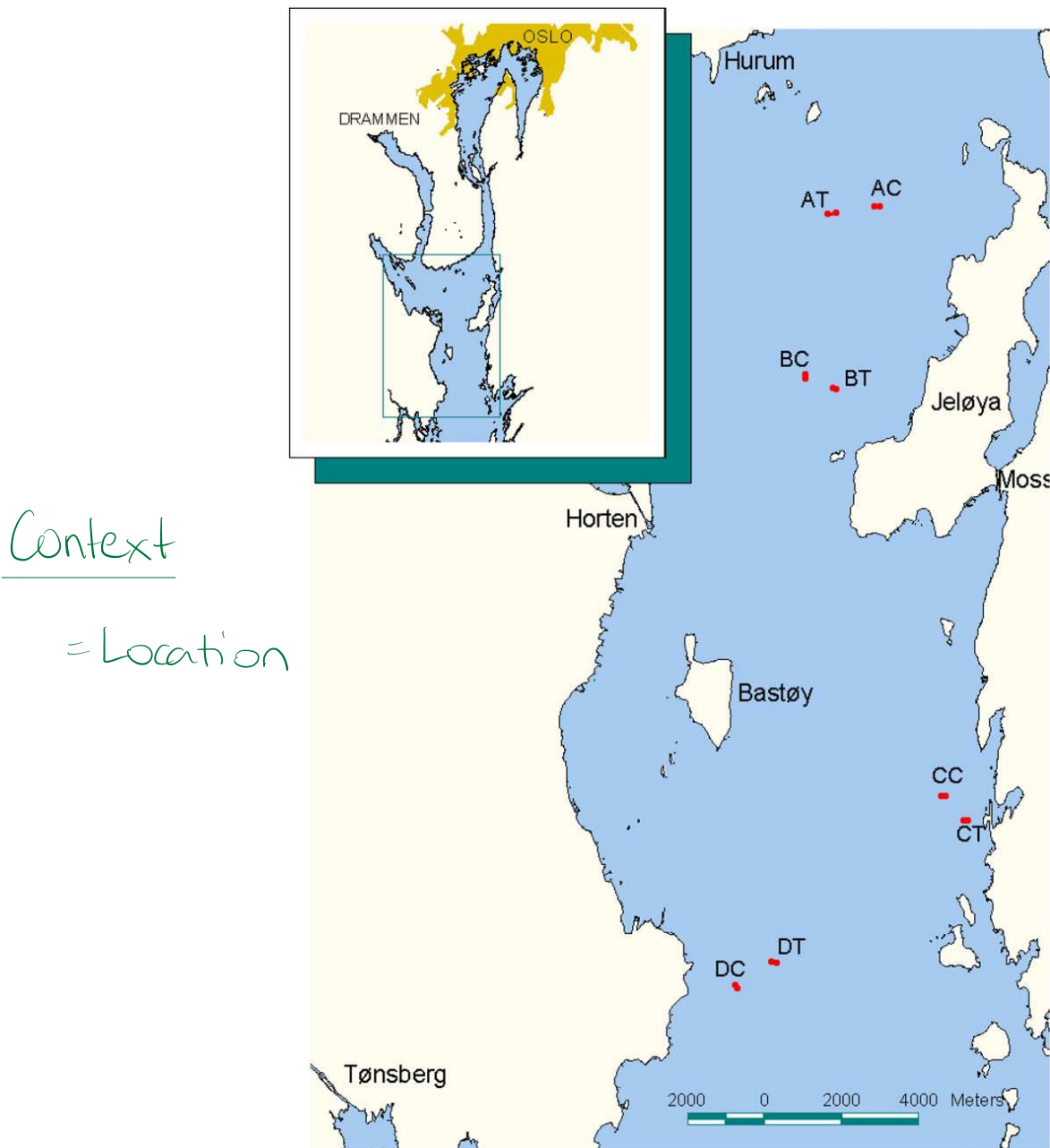


Fig. 2. Sampling locations in the outer Oslofjord, Norway. Core and grab samples were taken in the four areas A, B, C and D with samples from trawled (e.g. AT) and non-trawled control sites (e.g. AC) within each area.

organisms needed for experiments. The “high” and “low” densities used are representative of maximum recorded or most commonly reported densities respectively. These 14 treatments (7 species \times 2 densities) were each replicated 4 times. An additional 7 buckets had no bioturbators added and these acted as control buckets.

Because of the high number of simultaneous measurements of flux rates required in the mesocosm experiments compared to the field core samples, it was not possible to adopt the same flow-through technique for the mesocosm experiment. Nutrient fluxes in the mesocosm experiment were therefore measured using a “bell-jar” technique. Comparison of fluxes measured with the two different methods showed that most of the fluxes obtained in the mesocosm were within the range of fluxes determined in the field cores.

The mesocosm experiment ran for a period of 12 weeks after which nutrient fluxes were measured. Prior to sampling the water in the basin was lowered to below the rim of the buckets. Samples of the water overlying the sediment in the bucket were then taken at regular

time intervals (T0–T4). T0 was a common time-zero sampled at five different locations in the basin during lowering of the water level. T1–T4 were sampled respectively, 7, 14, 25 and 36 hours, after the water level fell below the rim of the buckets. Stirring and oxygen saturation was maintained throughout the incubation period with an airlift system carefully balanced to yield similar gas exchange and water circulation in all buckets and no resuspension of sediments.

Water samples were drawn using a 50 ml syringe rinsed once with 20 ml of the sample water before filling a 100 ml brown glass bottle for analyses of ammonium (NH_4) and NO_x (NO_3 and NO_2) and a 20 ml white plastic bottle for analyses of silicate (SiO_4). Dissolved inorganic nitrogen (DIN) was determined as the sum of NH_4 and NO_x (Officer and Ryther, 1980; Turner et al., 1998). The samples were conserved by adding 1 ml 4 M sulphuric acid to the 100 ml glass bottle and a few drops of chloroform to the 20 ml plastic bottle. The samples were stored at +4 and -20°C , respectively, until analyses. Chemical analyses of nutrients were performed in accordance with standard procedures

Table 2

The ten numerically dominant species (individuals 0.5 m⁻¹) from grab samples in non-trawled and trawled areas in outer Oslofjord

	Species	Faunal group	Non-trawled	Trawled
1	<i>Heteromastus filiformis</i>	Polychaeta	3396	4961
2	<i>Chaetozone setosa</i>	Polychaeta	1110	1092
3	<i>Polydora spp. juv.</i>	Polychaeta	324	450
4	<i>Paradoneis lyra</i>	Polychaeta	84	590
5	<i>Paramphinome jeffreysii</i>	Polychaeta	120	422
6	<i>Ophelina modesta</i>	Polychaeta	212	317
7	<i>Prionospio cirrifera</i>	Polychaeta	4	390
8	<i>Eriopisa elongata</i>	Crustacea	135	259
9	<i>Prionospio fallax</i>	Polychaeta	38	254
10	<i>Prionospio spp. juv.</i>	Polychaeta	55	221

for automated colorimetric methods based on the principles described in Grasshoff et al. (1983), modified in accordance with the acid conservation procedure.

At the end of the incubation period the water level in the mesocosm basin was returned to normal. Nutrient fluxes in the buckets (F_b) were calculated from the depth (h) of the overlying water and the slopes (b) of the linear regression of time vs. concentration at time zero and four subsequent observations in each bucket: F_b = -b·h.

2.5. Statistical analyses

Univariate data analyses (1- and 3-way ANOVA and regression analyses) were performed using JMP version 5.01 (SAS Institute Inc.) and Statistica Version 4.5. Levene's test was performed to check for homogeneity of variances. When the ANOVA indicated that there were significant differences within the dataset, Tukey's HSD test was used as a post hoc test between pairs of treatments. Multivariate data analyses (ANOSIM and MDS) were done using Primer Version 5.2.0 (Clarke and Warwick, 1994).

3. Results

3.1. Faunal samples in trawled and non-trawled areas

The faunal samples showed that the trawled areas had a higher dominance of small-bodied, opportunistic polychaetes, compared to the non-trawled areas (Table 2).

The 2-way crossed ANOSIM statistics were used to analyse for faunal differences in the sampling areas and for differences in trawled and non-trawled. Both location and trawling have an impact on faunal

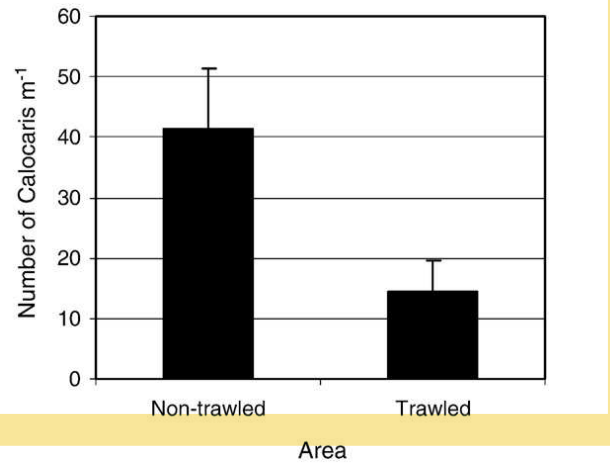


Fig. 4. Number of the burrowing shrimp *Calocaris macandreae* in non-trawled and trawled areas in the Oslofjord (mean values of the four areas, 95% confidence intervals).

composition (significant differences between locations (A–D) and between the non-trawled (C=Control) and trawled areas (T=Trawled); 2-way crossed ANOSIM, all 5 replicates used, double square-root transformation of abundance data, Area: Global R: 0.787, p=0.001; Non-trawled/trawled: Global R: 0.763, p=0.001). The MDS-ordination technique was used to visualize the differences in faunal composition between the sampling sites. MDS-ordination of the benthic communities in the grab samples showed that the trawled sites were grouped at the left-hand side of the plot (Fig. 3) and the non-trawled sites in the centre and to the right-hand side of the plot, indicating a difference in faunal composition related to trawling disturbance. The sites were also spread from the top to the bottom of the plot, (Fig. 3), indicating a difference in faunal composition between areas, especially for the trawled sites.

The grab samples showed that trawling reduced the density of the burrowing shrimp *Calocaris macandreae*. The mean abundance of *C. macandreae* was 41.5 ind. m⁻² (ci. ±9.91) in non-trawled areas and 14.5 (ci.±4.99) in trawled areas (Fig. 4). The seven bioturbating species chosen for the mesocosm experiment (Table 1) are all potentially vulnerable to trawling, but based on the grab samples in this investigation only *C. macandreae* was found to be significantly depleted in the trawled areas.

3.2. Nutrient flux measurements in field samples

In order to investigate the importance of the three factors “season” (March vs. June), “fjord area” (A, B, C and D) and “trawling” (trawled vs. non-trawled bottoms within each area), a statistical analyses (three-way ANOVA, n=48) was performed on the fluxes determined in all of the field samples. The results showed some effects of season, but no

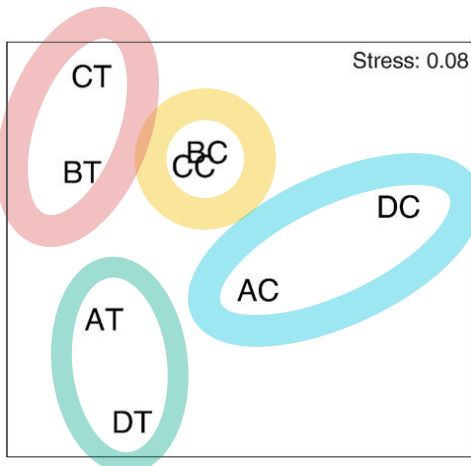


Fig. 3. MDS-ordination of the species abundance data from the different sites (A–D) in the trawled (T) and non-trawled (C=Control) areas in the Oslofjord. Data are double square root transformed prior to calculation of similarity to avoid dominance of abundant species on the ordination result.

Table 3

Effects of season, trawling, fjord area and respective interactions on nutrient fluxes shown as p-values calculated in 3-ways ANOVA analyses

	Silicate	Ammonium	NO _x
Season	0.069	0.113	0.010
Area	0.402	0.993	0.716
Trawling	0.768	0.564	0.826
Season*Area	0.874	0.513	0.969
Season*Trawling	0.801	0.510	0.333
Area*Trawling	0.190	0.252	0.821

Season=fluxes determined at same locations in March and June, respectively. Area=fjord areas A, B, C and D. Trawling=trawled and non-trawled bottoms in each area. Total number of cores n=48.

significant effects were found for fjord area, trawling or interactions between the three factors (Table 3).

The difference between the fluxes measured in March and June (i.e. effects of the factor “season”) are shown in the left-hand diagrams in Fig. 5. The mean release of silicate increased from $44 \mu\text{mol m}^{-2} \text{h}^{-1}$ in March to $65 \mu\text{mol m}^{-2} \text{h}^{-1}$ in June. Similarly, the release of ammonium increased from $1.0 \mu\text{mol m}^{-2} \text{h}^{-1}$ in March to $4.3 \mu\text{mol m}^{-2} \text{h}^{-1}$ in June, and the release of NO_x increased from $0.6 \mu\text{mol m}^{-2} \text{h}^{-1}$ in March to $9.4 \mu\text{mol m}^{-2} \text{h}^{-1}$ in June. The higher fluxes in June were most likely a result of increased biodegradation of phytoplankton deposited during spring and early summer.

Three of the cores provided anomalous fluxes of all nutrient species. These cores are shown as separate columns in Fig. 5 A, C, E

and G. One of the cores contained one individual of the tube-dwelling shrimp *Calocaris macandreae* and two of the cores one individual of the ‘bulldozing’ sea urchin *Brissopsis lyrifera*. Both species caused a major increase in the release of silicate (Fig. 5, A), but differed with respect to their impact on nitrogen fluxes (Fig. 5, C, E). The sea urchin had little impact on the flux of NO_x , but increased the loss of ammonium from the sediment. The shrimp, on the other hand, had little impact on the flux of ammonium, but generated a clearly increased uptake of NO_x .

In total, a release of $1.6 \mu\text{mol m}^{-2} \text{h}^{-1}$ DIN was observed in March in cores without the presence of large and active bioturbators. This release increased to $13.7 \mu\text{mol m}^{-2} \text{h}^{-1}$ in June. In the two cores with sea urchins present, the release of DIN showed a substantial increase

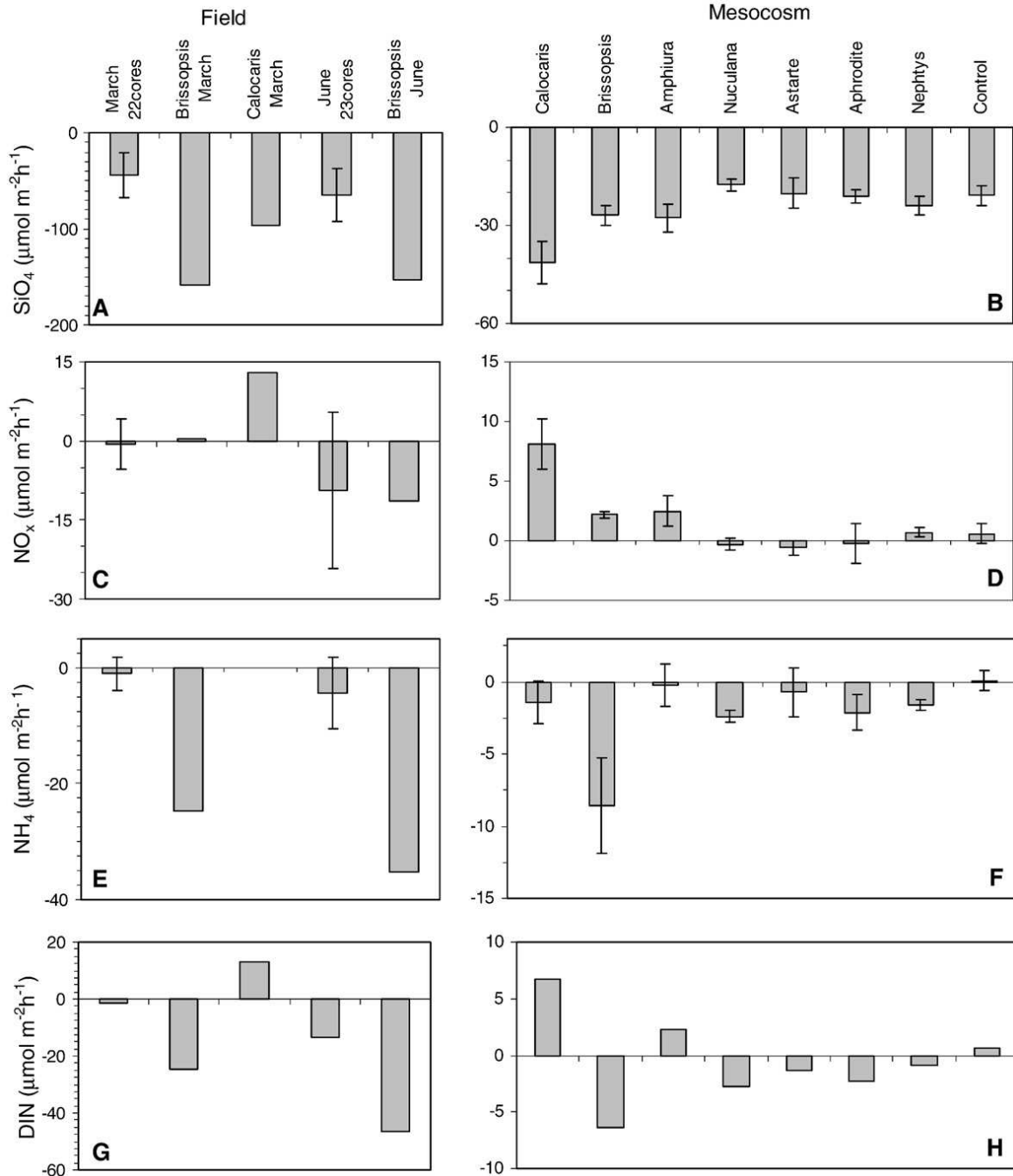


Fig. 5. A, C, E, G: Nutrient fluxes determined in field cores sampled from 24 sites in the Oslofjord at two different occasions (March and June, 2002). Three field cores with anomalous fluxes due to the activity of single individuals of the burrowing shrimp *Calocaris macandreae* or the sea urchin *Brissopsis lyrifera*, are shown with separate columns. B, D, F, H: Nutrient fluxes determined in mesocosm buckets treated with high densities (see Table 1) of seven macrobenthic species and control buckets with no species added. Negative flux means release from sediment to overlying water. Vertical bars = ± 1 S.D.

* Table highlights the relationship between different benthic species and their role in nutrient flux/cycling

Table 4

Linear regression analyses ($y=ax+b$; $10 \leq n \leq 13$) of species density (x) vs. nutrient flux (y) in the mesocosm experiment

Species	Type of organism	Nutrient	Linear regression analyses			
			a	b	r ²	p (slope)
<i>Calocaris macandreae</i>	shrimp	SiO ₄	-0.81	-22.6	0.63	0.0019
		NO _x	0.27	0.5	0.70	0.0006
		NH ₄	-0.067	-0.10	0.34	0.046
<i>Brissopsis lyrifera</i>	heart urchin	DIN	0.25	0.4	0.43	0.019
		SiO ₄	-0.16	-20.7	0.43	0.02
		NO _x	0.039	1.1	0.24	0.11, n.s
<i>Amphiura chiajei</i>	brittle star	NH ₄	-0.23	0.3	0.81	<0.0001
		DIN	-0.20	1.5	0.64	0.002
		SiO ₄	-0.023	-19.8	0.38	0.02
<i>Nuculana minuta</i>	bivalve	NO _x	0.0062	0.6	0.46	0.01
		NH ₄	-0.0013	0.4	0.018	0.66 n.s
		DIN	0.0049	1.0	0.19	0.13 n.s
<i>Astarte sulcata</i>	bivalve	SiO ₄	0.011	-21.1	0.20	0.12 n.s.
		NO _x	-0.0030	0.7	0.26	0.074 n.s.
		NH ₄	-0.0075	-0.2	0.67	0.0006
<i>Nephtys caeca</i>	polychaete	DIN	-0.010	0.6	0.60	0.0018
		SiO ₄	-0.0042	-20.2	0.004	0.9 n.s
		NO _x	-0.010	0.6	0.38	0.057 n.s
<i>Aphrodite aculeata</i>	polychaete	NH ₄	-0.0066	0.1	0.10	0.36 n.s
		DIN	-0.017	0.7	0.33	0.080 n.s
		SiO ₄	-0.095	-19.9	0.089	0.32 n.s
<i>Nephtys caeca</i>	polychaete	NO _x	0.0015	0.3	0.0002	0.96 n.s
		NH ₄	-0.060	-0.2	0.25	0.08 n.s
		DIN	-0.059	0.1	0.09	0.33 n.s
<i>Aphrodite aculeata</i>	polychaete	SiO ₄	-0.012	-20.4	0.002	0.88 n.s
		NO _x	-0.022	0.7	0.14	0.24 n.s
		NH ₄	-0.030	-0.14	0.18	0.17 n.s
		DIN	-0.052	0.59	0.20	0.15 n.s

to 24.5 $\mu\text{mol m}^{-2} \text{h}^{-1}$ in March and 46.9 $\mu\text{mol m}^{-2} \text{h}^{-1}$ in June. The burrowing shrimp, on the other hand, generated a net uptake of 12.9 $\mu\text{mol m}^{-2} \text{h}^{-1}$ nitrogen nutrients (March).

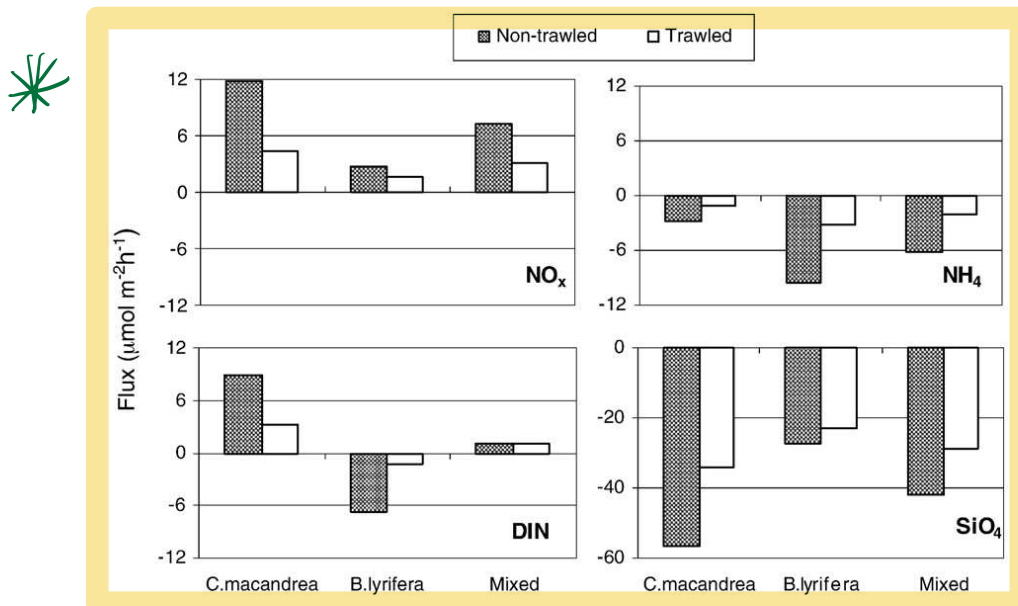
3.3. Mesocosm experiments

The nutrient fluxes in the buckets with high densities are shown in the right-hand diagrams in Fig. 5. In control buckets the nitrogen fluxes were close to zero and the release of silicate was 20.8 $\mu\text{mol m}^{-2} \text{h}^{-1}$, which was clearly less than the release observed in the field cores. Standard deviations calculated for the nitrogen fluxes indicated high

variability in both the field cores (Fig. 5 C,E) and in the control mesocosm buckets (Fig. 5 D,F), and thus the observed mean fluxes of nitrogen nutrients were not significantly different from zero. Interestingly, the release of silicate from *Calocaris macandreae* treatments was twice as high as in control and the NO_x uptake of $8.1 \pm 2.1 \mu\text{mol m}^{-2} \text{h}^{-1}$ was significantly different from zero. Zero flux of ammonium was actually determined in the field core with this organism (Fig. 5). The result was the largest net uptake of DIN ($6.7 \mu\text{mol m}^{-2} \text{h}^{-1}$) of all species tested. This was consistent with the field core observations (Fig. 5). Furthermore, *Brissopsis lyrifera* generated an increased release of silicate, a large release of ammonium and the largest total release of DIN of all species tested. Thus, experimental evidence was provided to support the trends observed in the field cores, with respect to the impact of these two species on nutrient fluxes. The other species had more subtle impacts on nutrient fluxes, but Fig. 5 shows that the nutrient fluxes provided by the brittle star *Amphiura chiajei* were similar to those provided by the shrimp.

Statistical assessment of the species impacts on nutrient fluxes were obtained by linear regression of nutrient flux vs. number of individuals retrieved from the buckets at the end of the experiment (Table 4). The analyses revealed that for the three species, *Astarte sulcata*, *Nephtys caeca* and *Aphrodite aculeata*, none of the nutrient fluxes were significantly correlated with species density ($p > 0.05$). Nevertheless, it may be of interest to note that even though not significant at the $p < 0.05$ level, the consistently negative slopes ($0.05 < p < 0.10$) showed that both bivalves contributed to increase the release of NO_x. For the two bulldozer species, *Nuculana minuta* and *Brissopsis lyrifera*, significant negative slopes for ammonium and DIN showed that both species contributed to increased release of nitrogen nutrients. The tube-irrigator *Calocaris macandreae* contributed, however, to a significant uptake of DIN. The brittle star *Amphiura chiajei* provided significant uptake of NO_x ($p = 0.01$), but not DIN ($p = 0.13$). The three species with the largest impact on nutrient fluxes; *Calocaris macandreae*, *Brissopsis lyrifera* and *Amphiura chiajei*, all contributed to increase the release of silicate.

Applying the relationships derived from the experimental data (Table 4) to the observed field densities of *C. macandreae* in non-trawled and trawled areas (Fig. 4), and assuming a similar effect on the density of *B. lyrifera*, or on the density of a hypothetical 50–50% mixed assemblage of the two species, indirect effects of trawling on nutrient fluxes were calculated. Although our field data showed no effects of trawling on *B. lyrifera*, reduced densities of this or functionally similar species have been found in other studies (e.g. Smith et al., 2000;



Graphs indicate the impact of trawling on fluxes of key nutrients in the benthic habitat. → Negative effects

Fig. 6. Calculated effects of trawling on fluxes of NO_x, ammonium, DIN (DIN = NO_x + NH₄) and silicate for the observed reduction in abundance for *C. macandreae* (from 41.5 to 14.5 ind. m⁻² in trawled areas) and similar % reduction for *B. lyrifera* and a mixed assemblage of the two species.

Graph indicates that nutrient flux (which is POSITIVE) decreases with trawling because the animals responsible for contributing are removed by trawling operations.

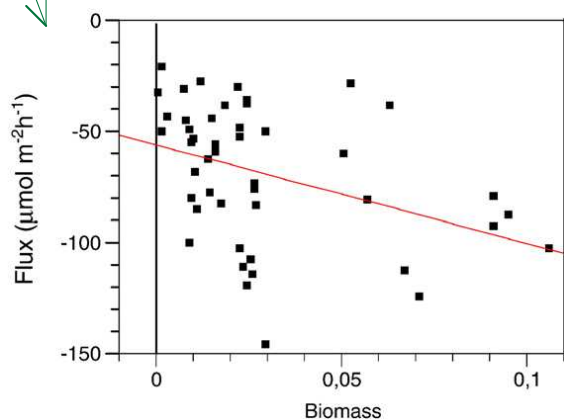


Fig. 7. Flux of silicate vs. biomass (g dry weight 0.00785 m^{-2}) in sediment cores collected in the field in March and June 2002. Linear regression analyses: $y = 441x - 55$, $r^2 = 0.149$, $p = 0.0073$, $n = 47$.

Jennings et al., 2001). The results showed that except for DIN in the mixed community, the effects of trawling would be a general reduction of the nutrient fluxes (Fig. 6).

For the nitrogen fluxes, reduced density of *C. macandreae* will reduce NO_x uptake in the sediment, whereas in contrast reduced density of *B. lyrifera* will reduce ammonium release from the sediment. As shown for the mixed assemblage (Fig. 6), for a seabed with equal abundances of the two species and equal effects of trawling on species density, trawling might have zero effect on sum nitrogen exchange. The example thus illustrates that the nutrient fluxes are highly related to identity of the larger macrofauna present. For silicate, however, trawling will reduce the release to the water masses, regardless of the actual species being diminished. This relationship gained further support from the field data, which showed a significant correlation ($p = 0.0073$) between sediment release of silicate and biomass of the macrofauna (Fig. 7).

4. Discussion

Overview of study findings (Part 1)

In this study we have found that demersal trawling reduces the density of some large-bodied bioturbators and that these bioturbators have a substantial impact on sediment-water fluxes of nutrients. The combination of laboratory experiments and field observations has shown that trawling could therefore have major effects on ecosystem function. This finding is important since until now little evidence has been reported on quantitative relationships between the impact of demersal fishing and fundamental sediment processes such as bioturbation and nutrient cycling (Malakoff, 2002). It is only through combined field and manipulative mesocosm experiments, such as the study presented here, that it is feasible to investigate these relationships. By linking field- and mesocosm studies we were able to scale up the laboratory results to make inference on the impact of trawling at the habitat scale, in a way that has not been done before.

Individual *Calocaris macandreae* were found in several cores, but intact burrows were only observed in the core shown in Fig. 5. The failure to sample both the organism and an intact tube system, showed that the small-sized cores used were not suitable for representative measurements of nutrient fluxes in areas where large organisms with complex tube systems are abundant. Thus, the absence of significant effects on nutrient fluxes from trawling activity was most probably a result of inadequate sampling method. However, flux deviations observed in the field cores with single individuals of *B. lyrifera* and *C. macandreae*, were confirmed by the mesocosm experiment.

In general most of the silicate produced by coastal sediments is a result of the dissolution of biogenic silica (DiToro, 2001) supplied via the sedimentation of diatom blooms. Silicate is not involved in redox transformations and is not consumed in common biotic or abiotic

processes in the heterotrophic sediment. Sediment uptake of silicate has been occasionally observed in shallow estuaries (Warnken et al., 2000). However, shelf transects in the Skagerrak and in the North Pacific have shown that the seabed in these areas was always a source of silicate for the overlying water (Devol and Christensen, 1993; Hall et al., 1996). Similarly, in the present investigation, the flux of silicate was always directed out of the sediment and the flux showed a general increase with number of individuals of bioturbator species. We have also shown that there was a significant relation between macrofauna biomass and fluxes of silicate (Fig. 7). Thus, the impact of bioturbation appears to be primarily a result of increased mixing across the sediment-water interface. In most trawled areas there is a reduction of macrofauna biomass compared to control areas. In a modelling study, based on a large dataset from the North Sea, Hiddink et al. (2006) found that the bottom trawl fleet reduced benthic biomass by 56%, compared with an untrawled situation. This must clearly have a negative impact on silicate sediment effluxes over large areas, particularly as the large-bodied species that show the highest reduction in density in trawled areas are at the same time the most important for the overall sediment-water nutrient fluxes.

In our study as well as others, demersal trawling appears to cause a decrease in the average body size and change the functional composition of macrobenthic communities and reducing bioturbation and bioirrigation (Frid et al., 1999; Kaiser et al., 2000; Jennings et al., 2001; Hiddink et al., 2006; Tillin et al., 2006; Querios et al., 2006; Hiddink et al., 2007). In addition, the combined results from our field- and mesocosm experiments demonstrated the dominant functional role in Oslofjord of the burrowing shrimp *Calocaris macandreae*, which had a major impact on nutrient fluxes. The abundance of this species was reduced by 65% in the trawled areas in the Oslofjord and trawling must therefore substantially change the macrobenthic mediated sediment-water nutrient fluxes in this area.

Our experiments showed that both *C. macandreae* and *B. lyrifera* contributed more to the flux rates than any other species present in the buckets, including the five other bioturbators added and the >30 other non-manipulated species (Widdicombe et al. 2004) naturally present in the buckets. This agrees with observations on *C. macandreae* made by Norling et al. (2007). This phenomenon, with a few species totally dominating the flux rates, is probably occurring in many soft-sediment systems, and can lead to a so-called idiosyncratic (*sensu* Emmerson et al., 2001) relationship between macrofauna species richness and ecosystem function. This means regulation of important ecosystem functions and properties in benthic habitats are often more strongly influenced by species-specific traits rather than by species richness as such (Loreau et al., 2001; Bolam et al., 2002; Giller et al., 2004; Hooper et al., 2005; Norling, 2007; Norling et al., 2007) particularly in bioturbated sediments (Mermillod-Blondin et al., 2005; Ieno et al., 2006; Raffaelli, 2006).

Compared to silicate, a more complex response was found for the cycling of nitrogen nutrients. It appears that the different types of bioturbation activities have different impacts on NO_x and ammonium fluxes, which may result in important differences with regard to seabed function. The mesocosm experiment showed similarities between *B. lyrifera* and the other bulldozer type of organism, *Nuculana minuta* and between the tube-irrigator *C. macandreae* and the other sediment irrigator *Amphiura chiajei*. The most likely explanation to this difference is that irrigated areas in the shrimp burrows, and maybe also around the arms of the brittle stars, provide a stable environment with favourable conditions for coupled nitrification-denitrification (Howe et al., 2004). In contrast, if the microenvironments favourable for such processes are frequently disrupted by the bulldozing movements of the sea urchin or the mobile bivalve *Nuculana minuta*, ammonium released from decaying organic matter may be more easily lost to the overlying water. Although not significant at the $p < 0.05$ level, the consistently negative slopes of the regression lines ($0.05 < p < 0.10$) showed that both of the bivalve test species

(*N. minuta* and *A. sulcata*) contributed to increase the release of NO_x . Similar results have been obtained for other infaunal bivalves and ammonium oxidation appears to be an important function associated with this group of organisms (Welsh and Castadelli, 2004).

Our study showed that the trawling-induced depletion of the shrimp *C. macandreae* and the brittle star *A. chiajei* will contribute to a larger recycling of nitrogen nutrients due to the loss of favourable sites for nitrification and denitrification and possibly food storage in ventilated burrows and cavities. The impact on nitrogen cycling was particularly large for *C. macandreae*. These shrimps are likely to be more vulnerable to trawling than the brittle stars, which are smaller and able to regenerate lost arms and recover from damage. The field investigations provided evidence that *C. macandreae* was markedly depleted in trawled areas of the Oslofjord (Fig. 4). A significant reduction in abundance (31%) of *A. chiajei* was found in trawled areas in a controlled field study on effects of otter trawling (similar type of gear used by fishermen in Oslofjord) from the Gullmarsfjord, Sweden; another branch of the Skagerrak (Hansson et al., 2000).

Our study also showed that trawling-induced depletion of the two sediment bulldozers *B. lyrifera* and *N. minuta* will contribute to less recycling of readily available nitrogen sources for primary producers from the seabed and thus have an opposite effect to the tube- and cavity dwellers *C. macandreae* and *A. chiajei*. An important difference between the two sediment bulldozers was the larger release of NO_x from the bivalve *N. minuta*. However, because ammonium and NO_x are both available to marine primary producers, the ecological significance of the different fluxes of nutrient species is probably less important. In comparison with silicate, which generally shows a reduction in efflux from sediment to the water with reduced macrofauna density, independent of species identity, the nitrogen fluxes are more dependent on species identity. For some species the NO_x efflux will increase with presence of that species while others will reduce efflux of NO_x and even reverse the flux direction and thereby causing sediment uptake of NO_x . The response (in flux rates and direction) will vary with species identity and faunal density.

The results of our mesocosm experiment, which was performed under environmental conditions similar to those prevailing at the seabed and used naturally occurring species densities, left little doubt that the identity of the larger species in the macrobenthic communities is crucial for nutrient recycling from coastal and shelf sediments. There is also evidence that it is the specific functional traits of the species rather than biomass *per se* that are important for the ecosystem functions and overall ecosystem services. There is now accumulating evidence of the importance of the macrofauna as facilitators of nutrient flux in soft-sediments (e.g. Norling et al., 2007). However, the identity of the key species in relation to importance for the flux rates will vary in space and time, as the density and size-range of species is subject to temporal and spatial variations. Major factors for such variation will probably be the type of bottom sediment, organic input, oxygen conditions in the bottom water and of course geographical area. Soft-sediment macrofauna communities are also dynamic systems with relatively high species turnover, which means that facilitating key species for sediment-water nutrient fluxes will vary over time even within the same habitat. However, larger macrofauna with traits profiles that makes them fundamentally important for these vital ecosystem processes will almost always be present in soft-sediment habitats with low natural or anthropogenic disturbance.

When considering an annual nutrient flux budget the contribution of larger macrofauna through continuous bioturbation is likely to be much more important than the short-term exchange of pulsed pore-water nutrients that can be measured in trawl furrows shortly after the passage of trawling gear (Falcao et al., 2003). It follows that the impacts of physical disturbance induced by trawling on the benthic fauna is likely to have long-term and potentially large effects on the nutrient balance of benthic and near-bottom habitats. Both field experiments and manipulative mesocosm experiments are still required

to elucidate and understand the relationships between the ploughing effect of trawl doors and release of nutrients.

If the observed reduction in the density of *C. macandreae* in trawled areas of the Oslofjord is generally applicable such that species with similar functional role in other trawled areas as the Skagerrak and the North Sea show similar declines, the estimated reduction in the release of silicate would be 39%, compared to the fluxes from non-trawled sea beds (Fig. 6). Correspondingly, a 63% reduction in the uptake of nitrogen nutrients from the sediments was estimated as a result of trawling (Fig. 6). It follows that trawling may have contributed to a shift towards a lower Si:N ratio in the highly productive shelf waters of the Skagerrak and the North Sea.

Marine phytoplankton production is dependent on the nutrient regime, the availability of nutrients and the Si:N:P ratios (Tilman et al., 1986; Sommer et al., 2002). A general ecological impact of reduced bioturbation from trawling disturbance will be a reduced Si:N nutrient ratio in the affected seawater. Silicate may in many situations be an important growth-limiting factor and lower Si:N ratios may shorten the duration of diatom blooms (Kristiansen and Hoell, 2002) and stimulate dinoflagellate growth including those that produce harmful algal blooms (Officer and Ryther, 1980), particularly in spring when diatoms would normally dominate the new production (Egge and Aksnes, 2002).

Low silicate concentrations may therefore exert a selective influence on the species composition of phytoplankton populations in the sea (Paasche, 1973a). Marine diatoms require dissolved silicate to form an external shell, and their growth becomes Si-limited when the atomic ratio of silicate to dissolved inorganic nitrogen approaches 1:1 (Paasche, 1973b; Officer and Ryther, 1980; Turner et al., 1998). Fundamental changes in the phytoplankton dynamics and in the diatom-to-zooplankton-to-higher trophic food web may occur when this ratio falls below 1:1 and the proportion of diatoms in the phytoplankton community is reduced (Turner et al., 1998). For example, in the Mississippi River continental shelf it is reported that the Si:DIN ratio has declined from around 3:1 to 1:1 during the past 40 years because of land-use practices in the watershed. Studies in this area in the 1990s showed that with Si:DIN ratios of 0.5 and 1.0, the copepods made up about 30% and 70% of the mesozooplankton respectively (Turner et al., 1998). In an experimental study using mesocosm bags, silicate limitation of diatom biomass occurred at Si:N ratios of 1:2 and 1:4 (Gilpin et al., 2004). This indicates that a substantial N loading (or reduced Si loading) is required to achieve conditions suitable for the development of Si limitation of diatom biomass. However, large increase in N loading such as those observed by Aure et al. (1998) in coastal waters of the Skagerrak, indicate that such changes are indeed possible (Gilpin et al., 2004).

In the Baltic Sea, and the southern North Sea a significant decline in silicate and increase in nitrogen concentrations has been observed over the last 30 years (Humborg et al., 2000; Sommer et al., 2002). This is also the case for the Skagerrak area (including the outer Oslofjord), where the nitrogen concentration in the upper 0–30 m has doubled since the 1980s (Aure et al., 1998). In the central areas of the North Sea, the release of silicate from the sediment has been found to be much more important than river input, and recent 3-D models for the North Sea indicate that benthic efflux of silicate is the most important source of silicate for phytoplankton (Moll and Radach, 2003; Proctor et al., 2003). Through decimation of large bioturbators, trawling may affect the efflux of silicate to an extent that alters primary production and plankton dynamics. There is already evidence of possible impacts that this might be having. In the Skagerrak area and the central North Sea there was a large bloom of the toxic flagellate *Chrysochromulina polylepis* (Manton et Parke, 1962) in 1988 (Dahl et al., 1989). On the Norwegian coast the bloom resulted in massive damage to farmed fish, seashore living fish, invertebrate animals and attached algae on rocky bottoms (Gjøsæter et al., 2000) and caused effects on soft-sediment macrofauna even at 180 m depth (Olsgard, 1993).

It has been estimated that continental shelf environments typically receive about half the nutrients needed for primary production from remineralisation within sediments (Pilskaln et al., 1998) and in some shallow coastal seas this may be as high as 80% (Dale and Prego, 2002). Hence nutrient dynamics of shelf sediments are important for the functioning of coastal ecosystems, by controlling marine phytoplankton and zooplankton dynamics and hence for the productivity of fisheries. At the same time we know that trawling efficiently removes macrofauna, meiofauna and micro-organisms from the surface sediments and thereby has a significant impact on biological function and nutrient flux regimes.

In our study we found that trawling had a significant impact on both faunal composition and nutrient flux rates. The Oslofjord sediments are broadly similar to many other areas in the Skagerrak and North Sea, and our results are therefore likely to have wider implications. This chronic and widespread disturbance of the seabed may lead to shifts within the ecological systems into alternative states, through the loss of key organisms for biodiversity and ecological services. Due to the world-wide extent of intensive bottom-trawling the flux changes induced are potentially large enough to interfere significantly with global nutrient cycles.

The present field- and mesocosm study, and several other studies, have clearly shown the importance of soft-sediment macrofauna for fluxes of nutrients. A mean reduction of faunal biomass of 60%, as found in heavily trawled areas (Collie et al., 2000; Hiddink et al., 2006; Queirós et al., 2006), will obviously reduce flux rates between the sediments and the water column and the productive surface layers. More importantly, the density of the larger species with highest impact on flux rates is kept low due to chronic trawling gear impact. In bottom-up controlled, highly productive shallow shelf systems like the Skagerrak and the North Sea, it is likely that the demersal trawling activities are interfering with the natural ecosystem production processes and may result in reduced biological yield at different trophic levels, including fish.

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