

Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea

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The beam-trawl fishery for flatfish produces large amounts of dying discards as well as damaged and disturbed benthos. The importance of these food sources to scavenging benthic species was investigated. To identify epibenthic species showing scavenging behaviour and to detect their food preferences, traps (370 overall) baited with different kinds of carrion (fish, crustaceans, molluscs, echinoderms, polychaetes) were deployed at 14 locations in the southern North Sea. *Liocarcinus holsatus*, *Pagurus bernhardus*, *Asterias rubens*, ophiurids, and small gadoids were the main active scavengers feeding on different kinds of food, while lysianid amphipods (*Orchomene nanus*, *Scopelocheirus hopei*) fed mainly on crustacean carrion. Estimated attraction areas were largest for gadoids, hermit crabs, and swimming crabs. Immigration of fish and swimming crabs into experimentally trawled areas was observed by sampling repeatedly in a trawled strip. Differences in the response to trawling (feeding activity, food niche breadth, and resource partitioning) between selected fish species are described. *Limanda limanda*, *Pleuronectes platessa*, *Merlangius merlangus*, *Callionymus lyra*, and *Eutrigla gurnardus* all showed strong responses, using different feeding strategies. *In situ* clearance rates of dead discarded fish exposed on the sea floor were estimated. Discards as well as moribund benthos were consumed within a few days. The balance between the amount of food materials produced by beam-trawl fishery and the amount of food consumed by potential scavengers was translated in a model of the food flows as mobilized by beam trawling. In general, the direct importance of the additional food resource for populations of scavengers is considered to be relatively small. However, the importance may be relatively larger for scavenging fish than for invertebrates. It is estimated that after a single beam trawling about 1.27 g m^{-2} ash-free dry biomass, or 6% to 13% of the annual secondary production of macrobenthos per unit area, would suddenly become available to scavengers and to the detritus food chain. It is suggested that beam trawling leads to shortcuts in trophic relationships and therefore may enhance secondary production.

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Key words: beam-trawl fishery, benthic scavengers, discards, food consumption, moribund benthos, southern North Sea.

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Introduction

The beam-trawl fishery on sole (*Solea solea*) and plaice (*Pleuronectes platessa*) is the single most important fishery in the southern North Sea. Almost 70% of the total nominal sole catches is landed by the Netherlands (FAO, 1998). Beam-trawl effort has more than doubled between 1971 and 1993 (Heessen and Daan, 1996). The annual trawling frequency varies from 1 to 2 over large areas (30%). Locally, trawling intensity may be much higher, while other areas may be trawled less than once every five years (Rijnsdorp *et al.*, 1998).

The legal mesh size of 8 cm (stretched) in the codend results in large amounts of unwanted by-catch, which are thrown overboard during the sorting of catches. The annual amount of discards produced by beam trawlers in the southern North Sea was estimated at about 150–190 000 t dead fish (mainly dab) and up to 85 000 t dead invertebrates (Lindeboom and de Groot, 1998). The chances for survival of discarded fish are low, but higher for most crustaceans and molluscs (40–50%) and for starfish (90%; Fonds, 1994).

Beam trawls are rigged with 10 to 20 iron tickler chains in front of the ground rope, which drag over the

ground and penetrate into the sediment up to a depth of 2 to 6 cm, depending on sediment type and trawling speed (Bergman and Hup, 1992). The track is marked by flattened surface ripples, marks of the trawl shoes, and by dead, damaged, and disturbed benthic animals that were not caught by the net. Evidently, beam trawling results in two potential food sources for scavengers: (i) discarded by-catch and (ii) disturbed, damaged, and dead benthic fauna in the trawl track.

In the offshore area, several seabird species benefit from discards as a food resource, and discards support a considerable part of their populations (Camphuysen *et al.*, 1995). However, most of the discards from beam trawlers sink to the sea floor: 80% of the flatfish, 20% of the roundfish, and 90% of the invertebrates were not taken up by birds. Several studies (e.g. Kaiser and Spencer, 1994) have pointed out that predatory crabs and fish accumulate and feed in recently trawled areas on moribund benthic fauna.

Our study focuses on three objectives: (i) identification of the most important benthic scavengers that make use of these additional food resources; (ii) estimation of clearance periods of discards and damaged benthos by benthic scavengers and of the food partitioning among species; (iii) assessment of the importance of the food produced by beam trawling for scavenger populations and the benthic ecosystem.

Material and methods

Sampling locations and gears

The beam-trawl fishery for flatfish occurs mainly in the relative shallow southern part of the North Sea, beyond the 12 mile limit up to the 50 m depth line. Field investigations were carried out at 14 different sites (Fig. 1). Experimental trawling was done with a standard 12 m beam trawl as used in the fishery. Densities of epi- and endobenthic organisms were estimated from catches with a 3 m beam trawl (equipped with six tickler chains, a net with a stretched mesh size of 14 mm, electromagnetic-device counting wheel rotation to estimate the distance covered), and with a deep-digging benthos dredge (Triple-D; Bergman and van Santbrink, 1994). *Echinocardium cordatum* and small infauna were estimated with a van Veen grab. Wet weights were converted into ash-free dry weight, according to Fonds (1994), Lindeboom and de Groot (1998), and Groenewold (1999).

Trap experiments

After initial trials with 10 different types of traps, transparent tube traps, Danish prawn traps, and small (transparent plastic) amphipod traps appeared to be most suitable (details in Groenewold, 1999; Lindeboom

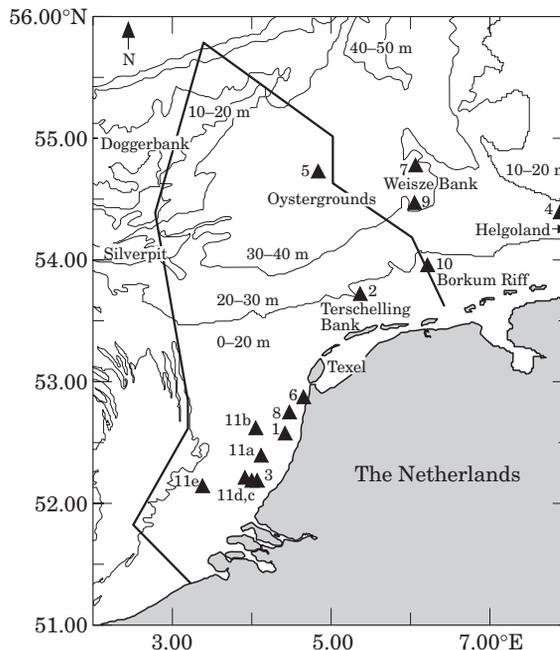


Figure 1. Map of locations in the southern North Sea investigated. Traps were deployed at 1–11d; sampling of intensively trawled strips in combination with stomach content analysis was carried out at 4, 5 and 9; the balance between amount of food produced by beam trawling and potential food consumption by scavengers was estimated for 4, 5, 9, and 11b.

and de Groot, 1998). Sets of three to 15 traps were attached to iron chains of 50 m in length, which were stretched between two heavy weights on the sea floor. Traps were usually exposed for two days and for at least two tides, including one night, to compensate for effects of changing tidal currents or diurnal effects. Traps were baited with five different kinds of bait. Each series included unbaited traps as a reference. For some commonly caught species, Manly's α values for food preferences were calculated (Krebs, 1989), based on normalized mean catch rates in comparable trials:

$$\alpha = \left(\frac{r_i}{n_i} \right) \sum_{j=1}^m \left(\frac{r_j}{n_j} \right), \quad (1)$$

where r_i is the proportion of a certain species caught in traps baited with type i (j), n_i is the proportion of traps baited with bait types i (j), and m is the number of possible bait types. The critical values of α depends on the number of possibilities (choices) and therefore differs for individual species in relation to the number of trials (here four to six, including blanks) included in the calculation. Values above the critical value ($= 1/m$) up to 1 (maximum) indicate preference, and values below the critical value indicate no preference.

Levin's standardized measure of food-niche breadth (B; Krebs, 1989) was estimated from catches of all traps exposed at several locations under comparable conditions:

$$B = \frac{\left(1 \sum_{j=1}^m p_j^2 - 1\right)}{m - 1}, \quad (2)$$

where p_i is the proportion of individuals caught in traps baited with the bait i , and m is the number of possible resource states (here six possibilities). The scale ranges from 0 (highly specialized) to 1 (no specialization). The concept of niche breadth is here adapted to trap catches offering different kinds of baits plus unbaited blanks, indicating the degree of specialization in certain bait types.

Areas of attraction (A) of baited traps were estimated per location by comparing the mean catch rates (Nt) in the traps with the mean background densities (Nb; ind. m^{-2}) of a scavenger species in the vicinity of the traps:

$$A = Nt/Nb. \quad (3)$$

Stomach analysis

For comparative stomach analysis of demersal species, a strip of 70 by 1000 m (location 4) was intensively trawled with a commercial 12 m beam trawl. Fish were sampled by a fine-meshed 3 m beam trawl at 12-h intervals before, shortly after, and up to 25 days after trawling in the strip and in an untrawled reference area nearby. The stomach filling index (SFI: weight of stomach content as percentage of fish weight) was calculated to obtain comparable values for fish of different sizes. The diet composition was recorded by both the frequency of occurrence in proportion of fish and the relative frequency in stomachs (Hyslop, 1980). The latter formed the basis for estimating Levin's index of food-niche breadth according to (2). To compare food preferences of different fish species, Manly's α was calculated for different prey items according to (1) with $1/m=0.06$. Organisms were defined as available prey if they were found in any of the stomachs of the six fish species investigated in the area. At the Oysterground (location 5), stomach fullness was recorded at 12-h intervals in dab scavenging in a recently trawled strip.

Clearance rates of carrion

To follow the fate of sinking (dead) discarded fish on the bottom, typical specimens were attached to 7 m long lines that were connected to weights and exposed on the sea floor. Distances between fish carrion were about 1.50 m if the line was properly stretched. Fish were usually exposed for two days. The fish were weighed

before exposure and after retrieval, and inspected for characteristic marks of scavenger activity. At the same time, dead fish of similar sizes were stored on board in tanks with running sea water at ambient temperature to estimate changes in weight without scavenger activity. The mean weight loss of fish carrion was expressed as *in situ* clearance rate (g weight loss per fish per day⁻¹), corrected for the weight loss measured in the controls, and converted to ash-free dry weight using a factor 0.175 for flatfish and 0.15 for roundfish.

In separate laboratory experiments, the duration of the decay process of fish in relation to temperature was measured. A linear regression model was developed that predicts the period when fish carrion remains available and edible for macrobenthic scavengers before complete decomposition by micro-organisms.

Food balance

The general idea was to estimate the maximum possible food consumption of potential scavengers in some defined areas and to compare the potential consumption with the amount of food made available, only those epibenthic fish and invertebrates were considered that were both abundant in each area and identified as scavengers. Models on maximum daily food consumption of the main scavengers were compiled from the literature: *Limanda limanda* (Pandian, 1970), *Pleuronectes platessa* (Fonds *et al.*, 1992), *Callionymus lyra* (van der Veer *et al.*, 1990), *Eutrigla gurnardus* (De Gee and Kikkert, 1993), *Merlangius merlangus*, *Asterias rubens*, *Astropecten irregularis*, *Ophiura ophiura*, *Crangon crangon* (Lindeboom and de Groot, 1998), *Buccinum undatum* (Evans *et al.*, 1994), and *Liocarcinus holtsatus*, *Pagurus bernhardus* (Groenewold, 1999). Catches by dredge and 3 m beam trawl were used for estimating densities and size distribution. The potential food consumption of a population was estimated by summing up the individual food consumption rates on a defined bottom area (100 m²). For the baseline food balance it was assumed that no immigration of local scavengers takes place.

For estimating the food produced by beam trawling in the same area, the catch composition of 12 m beam trawl hauls (1–2 h duration) in the area were analysed. The amount of discarded fish reaching the bottom was calculated, considering discard mortality (Fonds, 1994), and the fraction utilized by scavenging seabirds (Camphuysen *et al.*, 1995). Estimates of the amount of moribund benthos were based on mortality rates caused by a single haul as observed by Bergman and van Santbrink (2000). It was not possible to estimate precisely the mortality for mobile epibenthos (*Liocarcinus*, *Pagurus*, and *Asterias*), because these species show increased densities after trawling (Fig. 2) and appear to migrate actively into recently trawled areas. Therefore, a

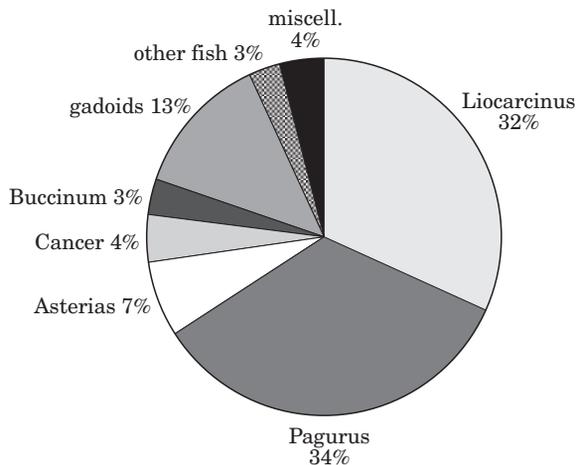


Figure 2. Catch composition (% biomass, ash-free dry) of pooled catches of all 370 traps exposed in the southern North Sea (miscell, miscellaneous taxa).

minimum mortality was calculated as the product of their catch efficiency by 12-m beam trawl and their total discard mortality (Fonds, 1994). Mortality rates of 5% were assumed for *Nephtys* sp. and 10% for *Pectinaria* (*Lagis*) sp. and *Lanice* sp.

Food balances were calculated for four different locations, using several scenarios for aggregations of scavengers and different water temperatures.

Results

Trap experiments

Excluding 48 000 amphipods (three species), 5568 individuals (43 different species) were caught. Catches in numbers and biomass (ash-free dry weight) were usually dominated by only two to four species per location.

About three-quarters of all catches consisted of *Liocarcinus holsatus*, *Pagurus bernhardus*, and *Asterias rubens* (Fig. 2). Shrimp (*Crangon crangon*) were frequently caught but contributed little to the biomass, whereas whelks (*Buccinum undatum*), edible crabs (*Cancer pagurus*), and fish were caught less frequently but represented considerable fractions in terms of biomass. Two brittle stars (*Ophiura ophiura* and *O. albida*) were recorded regularly in baited traps, sometimes in relatively high numbers. Two lysianid amphipod species were caught in remarkably high numbers. *Scopelocheirus hopei* (length 7–10 mm) were only caught at the Oyster-grounds (location no. 5; 40 m depth). *Orchomene nanus* (length 5–7 mm) was caught at most locations, with the exception of those close to the shore. In comparison with crabs and echinoderms, fish were less frequently caught and accounted for 3% of the total catch in numbers and for 16% in biomass (Fig. 2). Most of the fish caught were gadoids: bib (*Trisopterus luscus*), poor cod (*T. minutus*), and cod (*Gadus morhua*). Solenette (*Buglossidium luteum*) and gobies (*Pomatoschistus minutus*) were also caught several times, while dab (*Limanda limanda*) were seldom recorded.

The area of attraction relates mean catch rates in traps (per location) with the density of the species in the vicinity (Table 1). The pooled gadoids had estimated attraction areas up to 1200 m², while *Natanolana*, hermit crabs, and swimming crabs also showed attraction areas larger than 100 m². For starfish, whelks, dab, shrimp, and brittle stars, attraction areas ranged between 10 and 100 m², whereas attraction areas less than 10 m² were estimated for gobies, solenette, sea urchins, and sandstars.

The different scavengers showed more or less clear food preferences as indicated by Manly's α values (Table 2). Dead fish and molluscs were the preferred bait for *Liocarcinus*, while fish and (crushed) echinoderms were most attractive for *Pagurus*. For *Asterias*, molluscs were

Table 1. Estimated mean and maximum attraction area (AA) for selected benthic organisms (gadoid fish include *Trisopterus* sp., *Merlangius merlangus*, *Gadus morhua*), number of observations (n), and total catch (C, number in 370 traps, exposed at location 1-11d).

Ranked species	AA (m ⁻²)		n	C
	Mean	Maximum		
Gadoid fish	280.9	1202.0	7	77
<i>Natanolana borealis</i>	159.3	200.0	2	25
<i>Pagurus bernhardus</i>	134.9	284.0	10	1179
<i>Liocarcinus holsatus</i>	117.5	132.9	10	2163
<i>Buccinum undatum</i>	49.6	74.1	2	103
<i>Asterias rubens</i>	26.9	98.0	5	1120
<i>Limanda limanda</i>	23.0	43.9	2	7
<i>Crangon crangon</i>	9.0	29.4	4	386
<i>Ophiura texturata</i>	8.3	21.0	3	54
<i>Psammechinus miliaris</i>	8.0	—	1	8
<i>Astropecten irregularis</i>	3.5	7.0	2	8

Table 2. Catch in numbers (C), Manly's α values of preferences of scavenger species for different trap baits (N, no bait; F, fish; C: crustaceans; P, polychaetes; E, echinoderms) with indication of critical value (1/m), and Levin's index (L) for niche breadth (NA, not available).

	C	1/m	N	F	M	α				L
						C	P	E	L	
<i>Crangon</i>	95	0.25	0.11	0.22	0.31	0.36	NA	NA	0.83	
<i>Pagurus</i>	291	0.16	0.02	0.25	0.18	0.19	0.13	0.23	0.79	
<i>Ophiura</i>	86	0.16	0.13	0.35	0.25	0.07	0	0.20	0.61	
<i>Asterias</i>	920	0.16	0.01	0.27	0.30	0.27	0.06	0.09	0.61	
Gadoid fish	28	0.16	0	0.22	0.22	0.25	0.31	0	0.58	
<i>Liocarcinus</i>	555	0.16	0.02	0.47	0.23	0.07	0.12	0.09	0.46	
<i>Buccinum</i>	102	0.20	0	0.02	0.70	0.15	NA	0.13	0.22	
<i>Orchomene</i>	42 000	0.16	0	0	0	0.85	0.02	0.13	0.07	
<i>Natatolana</i>	25	0.20	0	1.00	0	0	0	NA	0.00	

the first choice, but crustaceans and fish were also positively selected. *Crangon* were mainly attracted by crustacean and mollusc bait. *Buccinum* were mostly caught in traps baited with molluscs. Although a few species (e.g. *Ophiura* and *Crangon*) occurred in unbaited traps, Manly's α values were below the critical value. The isopod *Natatolana* was caught only on fish bait, and most amphipods (*Orchomene nanus*) were found in traps baited with crustaceans. The four species of gadoids (bib, poor cod, whiting, cod) showed little differences in their response to different baits and hence have been pooled.

Levin's index (Table 2) indicates that *Orchomene* and *Natatolana* are highly specialized, whereas shrimp were most opportunistic in bait selection.

Aggregation and stomach contents

Compared with reference hauls in nearby untrawled areas, dab, dragonets, and swimming crabs showed increasing levels of abundance in the trawled strips, clearly indicating immigration into the trawled tracks (Fig. 3a, b). Dab and dragonet also showed significantly higher stomach-filling indices (SFI) in the recently trawled strip than in nearby reference areas (Fig. 4). Plaice, whiting, and tub gurnard also showed higher median stomach fullness in the trawled strip, but variation was large and differences were not significant at the 5% confidence level. No differences were found in median stomach fullness of bullrout. The proportion of empty stomachs in fish caught 12 h after trawling was lower for all six fish species than in reference hauls (Table 3). No empty stomachs were recorded for dab, dragonet, whiting, and tub gurnard from trawled areas.

In the reference areas, dragonet, dab, and plaice had eaten a wide range of different prey items, while tub gurnard, whiting, and bullrout fed on only two or three different prey species (Table 3). In the trawled strip, all species except bullrout had broadened their diet, as

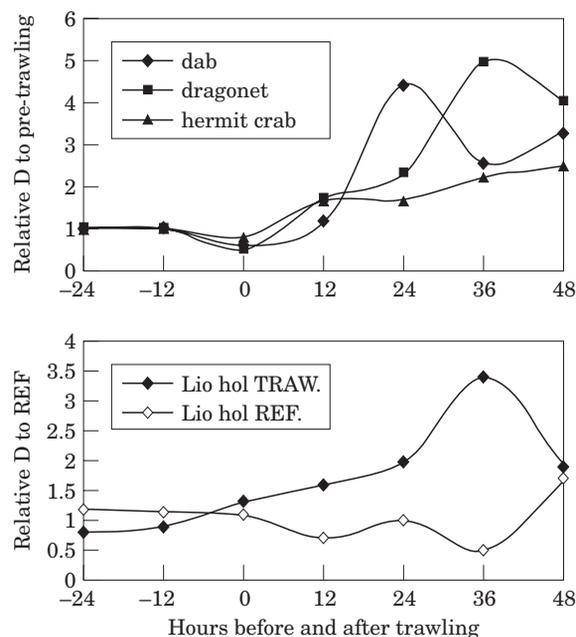


Figure 3. Relative changes in densities (D) of (a) dab (*Limanda limanda*), dragonet (*Callionymus lyra*), hermit crab (*Pagurus bernhardus*), and (b) swimming crab (*Liocarcinus holsatus*) before and after trawling a strip experimentally. In (b) data from the trawled strip are compared with an untrawled area (REF).

indicated by an increase in Levin's index for food-niche breadth. In general, flatfish utilized broader food niches in the trawled area than did roundfish.

The changes in food composition indicate that trawling had made more benthic species available, but different fish species used this source in different ways. Manly's α relates densities of prey species to the food selection of scavenging fish (Table 3). In dab, for instance, strong selection for shrimp and for the sedentary polychaete *Lanice conchilega* was recorded in

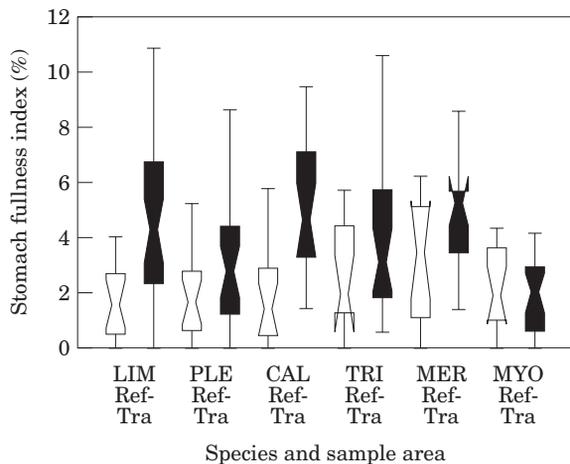


Figure 4. Box-whisker plots of stomach fullness of six different fish species (LIM, *Limanda limanda*; PLE, *Pleuronectes platessa*; CAL, *Callionymus lyra*; TRI, *Trigla gurnardus*; MER, *Merlangius merlangus*; MYO, *Myoxocephalus scorpius*) sampled in a trawled strip (Tra, filled symbols) and in a reference area (Ref, open symbols) at location 4, 12 h after trawling the strip. Significant differences ($\alpha=0.05$) are indicated by non-overlap of notches. See also Table 3.

reference areas, while in the trawled strip the soft body parts of *quahog* (*Arctica islandica*) and gobies were highly selected. Plaice and whiting also showed preferences for quahogs in the trawled strip, while tub gurnard fed more intensively on gobies. Dragonet shifted food selection from *Ophiura* towards the intestines and gonads of *Echinocardium* and the sedentary polychaete *Lanice*.

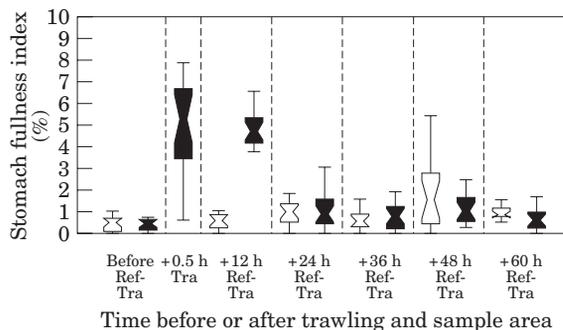


Figure 5. Box-whisker plots of stomach fullness of dab (length 14–17 cm) at location 5 sampled in an experimental strip (Tra, filled symbols) and in a reference area (REF, open symbols) at time intervals of 12 h before and after experimental trawling (0 h: immediately after). Significant differences ($\alpha=0.05$) are indicated by non-overlap of notches. See also Table 4.

Immediately after trawling, a strong increase in median SFI in dab to 5.3 indicated strong feeding activity (Fig. 5). Although variation was large (0.6–8.1), the difference with dab caught before trawling and at the same time in a reference area nearby, was highly significant. It seems possible that the large variation in SFI can be explained by immigration of fish that had not yet filled their stomachs. One night (12 h) after trawling, the median SFI on the trawled strip was a little lower (4.8) and variation was less, but 24 h after trawling, stomach fullness was almost as low as before. More different prey taxa were selected by dab in the trawled area, and niche breadth also increased shortly after trawling, but only 12 h after trawling, niche breadth had decreased again to the original value (Table 4). After trawling for 60 h,

Table 3. Comparison of stomach contents of six demersal fish species (length: 16–23 cm) collected in an experimentally trawled area (ta) and in a reference area (ref) at location 4.

Species	A	n	L	E	Bi	Lc	Ec	α		
								Ot	Cc	Pm
<i>L. limanda</i>	ref	15	0.17	20	0.02	0.11	0	0.06	0.76	0
	tt	35	0.40	0	0.56	0.01	0.01	0	0.02	0.35
<i>P. platessa</i>	ref	17	0.11	18	0.01	0.02	0	0	0.95	0
	tt	28	0.12	7	0.65	0.10	0.01	0	0.17	0
<i>C. lyra</i>	ref	16	0.05	25	0.02	0.06	0	0.88	0	0
	tt	18	0.22	0	0.06	0.18	0.36	0.24	0	0
<i>M. merlangus</i>	ref	13	0.02	15	0	0	0	0	0.36	0.64
	trt	15	0.08	0	0.31	0	0.01	0	0.26	0.40
<i>T. lucerna</i>	ref	13	0.00	8	0	0	0	0	0.99	0
	ttk	29	0.01	0	0.05	0	0	0	0.67	0.17
<i>M. scorpius</i>	ref	16	0.05	19	0	0	0	0	0.20	0.80
	tt	22	0.08	14	0	0	0	0	0.11	0.88

Number of stomachs (n), Levin’s index for niche breadth (L), percentage of empty stomachs (E) and Manly’s α values (critical value=0.6) for food selection of the most important prey species. Bi, bivalvia – *Arctica islandica* and *Chamaelea* sp. pooled; Lc, *Lanice conchilega*; Ec, *Echinocardium cordatum*; Ot, *Ophiura texturata*; Cc, *Crangon crangon*; Pm, *Pomatoschistus minutus*). See also Figure 4.

Table 4. Results of stomach content analysis of dab (*Limanda limanda*) collected at different time intervals before and after trawling a strip at location 5 (0 h: just after trawling): number of stomachs, density (n 10 000 m⁻²), % empty, number of different prey taxa, Levin's index of niche breadth, mean prey weight (g ww), and relative frequency of the most abundant prey (%). NA: not available. See also Figure 5.

	- 12 h	0 h	12 h	60 h
Number of stomachs	18	20	20	17
Density	368	NA	876	1862
Percentage empty	22	0	0	12
Number of taxa	4	12	6	7
Levin's index	0.01	0.07	0.02	0.04
Mean prey weight	0.11	0.67	0.07	0.10
Relative frequency				
Bivalves	1.8	21.7	7.3	1.6
<i>Amphiura</i> sp.	94.5	62.8	87.1	73.4
<i>Callinassa</i> sp.	—	5.1	—	9.4
<i>Orchomene</i> sp.	—	—	—	10.9
Miscellaneous taxa	3.7	10.4	5.6	4.7

Table 5. *In situ* clearance rates (CR; g d⁻¹) with coefficient of variation (cv) and number of observations (n) of dead fish exposed at different locations and seasons (T, temperature in °C; M, month) in the North Sea.

Location	No.	T	M	CR	cv	n
Weisze Bank	7	6	II	0.9	0.87	16
West of Holland	8	7	III	0.8	0.60	16
Weisze Bank	9	12	V	2.4	0.90	24
Borkum Riff	10	12	V	4.5	0.76	18
West of Holland (transect)	11b	19	IX			
4 nm offshore				3.4	0.23	11
8 nm offshore				2.9	0.67	11
12 nm offshore				2.2	0.48	10
West of Holland	11c	19	IX	2.4	0.28	15
West of Holland	11d	19	IX	2.4	0.68	16

stomachs contained only a few bivalves, but the scavenging amphipod *Orchomene nanus* was new in the diet.

Clearance rates

Field experiments on *in situ* clearance rates indicated how fast discarded dead fish were consumed (Table 5). In all trials retrieved, fish were partially consumed by scavengers and, judging from the characteristics scars on the carrion, mainly by swimming crabs, hermit crabs, and starfish. *In situ* clearance rates (ash-free dry weight per carrion) ranged from 0.9 in February to 4.5 g d⁻¹ in May, when smaller fish were eaten to the bone within three days. Carrion exposed along a transect perpendicular to the coast were consumed faster with decreasing distance from the shore, which appeared to be correlated with increasing densities of swimming crabs, hermit crabs, and starfish towards the shore.

The regression model for the decay (d; in days) of fish without interference of scavengers (from death to complete disintegration of the soft body parts; r²=0.91, p<0.001, n=110) in relation to sea water temperature (T in °C) was:

$$d = 22.9 \times e^{-0.076 \cdot T} \quad (4)$$

Water temperature was the main factor determining the rate of decay, with size and species playing minor roles. Decay of fish lasted about 7 to 8 days at 15°C and 16 to 18 days at 5°C.

Balance between food production and consumption

Assuming a maximum food consumption at an ambient summer temperature of 15°C, the potential total daily food consumption (ash-free dry weight) of the selected

Table 6. Balance of estimated daily food consumption (g AFDW 100 m⁻²) of selected scavengers and the amount of food produced by a single beam-trawl pass (g AFDW 100 m⁻²) for four different locations (summer season). Scenarios are expressed in terms of one trawl pass providing sufficient food for n days (d) or as percentage of consumption during 60 days.

Location	4	5	9	11	Mean
Water depth (m)	25	42	31	19	
Silt content of sediment (%)	5–7	9	5–10	1	
Megabenthos biomass (before trawling)	823	418	379	1020	660
A: Food generated					
Dead discarded fish	40.7	5.8	21.6	8.1	19.1
Moribund benthos in trawl track comprising (%):	204.1	58.9	84.9	84.7	108.2
<i>Echinocardium</i>	15	23	67	65	38
Bivalves	72	29	15	23	35
Crustaceans	7	33 ^a	14	9	16
Other taxa	6	15	4	3	7
Total food production	244.8	64.7	106.5	92.8	127.2
B: Daily food consumption at 15°C (g AFDW 100 m ⁻²)					
<i>Liocarcinus holsatus</i>	3.52	0.21	0.16	5.48	2.3
<i>Pagurus bernhardus</i>	0.71	0.32	1.71	8.46	2.8
<i>Asterias rubens</i>	1.92	0.74	0.02	1.03	0.9
<i>Crangon crangon</i>	0.22	0.02	0.53	0.93	0.4
<i>Astropecten irregularis</i>	0.01	6.31	1.32	—	2.5
<i>Ophiura texturata</i>	8.15	0.02	0.02	1.21	2.4
<i>Buccinum undatum</i>	—	—	0.31	—	0.3
<i>Limanda limanda</i>	2	0.77	0.42	0.12	0.8
<i>Pleuronectes platessa</i>	3.84	0.05	0.01	0.1	1.0
<i>Callionymus lyra</i>	1.04	<0.1	0.19	0.3	0.5
<i>Merlangius merlangus</i>	0.1	0.08	0.25	<0.1	0.1
<i>Trigla lucerna</i> , <i>Eutrigla gurnardus</i>	0.17	0.02	0.05	—	0.1
Total invertebrates	14.5	7.6	4.1	17.1	10.8
Total fish	7.2	0.9	0.9	0.5	2.4
Total scavengers (g)	21.7	8.5	5.0	17.6	13.2
C: Scenarios					
1. At 15°C (d)	11.3	7.6	21.3	5.3	11.4
2. Consumption during 90 days (%)	13	8	24	6	11.8
3. Invertebrates only ^b (d)	2.8	4.4	7.8	0.5	3.9
4. Scavengers aggregate by f ^c (d)	4.6	4.9	9.2	1.9	5.2
5. At 10°C (d)	16.1	8.9	27.7	6.5	14.8

^a*Corystes cassivelaunus* only accounts for ca. 30%.

^b*Astropecten irregularis* excluded.

^cAggregation factors f: fish 4, *Liocarcinus* 3, *Pagurus* 3, *Asterias* 2.

scavengers (invertebrates and fish) was estimated between 0.05 g and 0.22 g m⁻² (Table 6). Carnivore invertebrates may consume much more than demersal fish. Among the fish, dab and plaice were the most important consumers at the three offshore locations (4, 5 and 9), whereas dragonet was the main consumer at location 11 (west of Holland).

The estimated amount of food materials generated by beam trawling varied between 0.65 g m⁻² and 2.45 g m⁻². *Echinocardium* contributed 18–67% to the amount of moribund benthos, bivalves 15–69%, and other taxa 12–50%. The estimated amount of discarded fish reaching the bottom varied between 0.06 and 0.40 g m⁻², depending strongly on the local catch composition.

A single passage of a beam trawl produced enough food to keep the predators going for one to three weeks

(or 8–24% of the estimated food requirements of local scavengers during summer). Assuming consumption by invertebrate scavengers only (excluding *Astropecten* because it cannot handle fish), discarded fish may be consumed within a period of a few days.

Figure 6 summarizes the effects of beam trawling on food flows and trophic relationships. A single beam trawl at these locations yielded about 0.13 g m⁻² marketable fish, mainly sole and plaice, and produced about 0.25 g m⁻² fish discards. Scavenging seabirds take up about one third, and the rest sinks to the sea floor, where it is consumed mainly by swimming crabs, hermit crabs, starfish, and brittle stars. Beam trawling produces, on average, an estimated amount of 0.19 g m⁻² discarded fish and 1.08 g m⁻² moribund benthos on the sea floor.

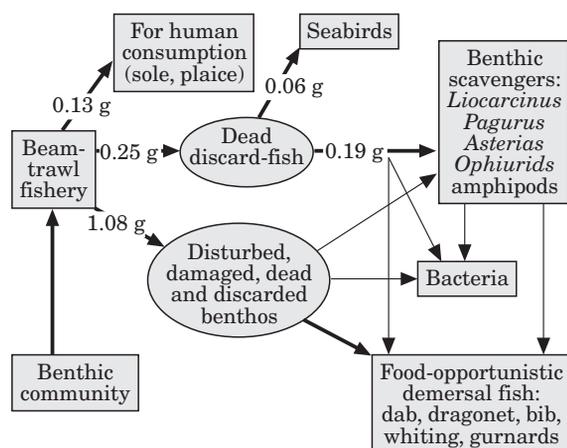


Figure 6. Model of the flow of material (g AFDW m^{-2}) mobilized by a single beam-trawl pass.

Discussion

Indications of the importance of different species as scavengers on food materials generated by beam trawling may be found in their occurrence in baited traps, the estimated size of the attraction areas, evidence for their aggregation in the trawl track, and their food uptake rate in experimentally trawled areas. Considering the evidence presented, the scavenging fauna of the southern North Sea are dominated by a few abundant and opportunistic species, such as swimming crabs, hermit crabs, starfish, ophiurids, and shrimp, and locally also whelks and edible crabs. Only three species, the isopod *Natantolana borealis* and the two amphipods *Orchomene namus* and *Scopelocheirus hopei*, were highly specialized and probably obligate scavengers (Moore and Wong, 1995). Among the demersal fish, dab, dragonet, gurnards, and small gadoids were the main users of food materials becoming available after trawling. In the Baltic Sea, North Sea, and Irish Sea, dab, plaice, gurnards, whiting, and cod have been reported to aggregate in recently trawled areas and to feed on disturbed or damaged benthos before (Arntz and Weber, 1970; Rauck, 1989; Kaiser and Spencer, 1994). Also hermit crabs (*Pagurus bernhardus*) have been observed to increase their food uptake in a recently trawled area (Ramsay *et al.*, 1996, 1997). Britton and Morton (1994) consider that a large proportion of facultative scavengers, rather than specialized, obligate scavengers, is a typical feature of benthic communities in shallow shelf seas.

The catch efficiency of traps for different benthic species is influenced by several factors (Miller, 1979). We tried to determine the differences in catch efficiencies for epibenthos and demersal fish by employing different, complementary types of traps, but they remained low for flatfish, gurnards, gobies, and solenette and also for

some invertebrates, such as sandstar and possibly for shrimp (Groenewold, 1999). This clearly affects the estimated attraction areas of those species.

Carion of fish, crabs, or bivalves will be decomposed by micro-organisms within a few weeks, if not covered by sediment or consumed by macro-scavenging (Schäfer, 1962). However, the high *in situ* clearance rates showed that dead fish are quickly eaten by scavenging epibenthos (*Liocarcinus* sp., *Pagurus bernhardus*, and *Asterias rubens*). Potentially, larger fish also play a role as scavengers, although we obtained no direct evidence. Experiments with baited traps in a subtidal habitat in the German Wadden Sea demonstrated that fish bait was consumed within hours, mainly by shore crabs (*Carcinus maenas*), swimming crabs, and shrimps (Berghahn, 1990).

Gadoid fish showed the largest attraction areas (1200 m^{-2}). Demersal fish and crustaceans are attracted by leaching amino acids (Løkkeborg and Johannessen, 1992). In Canadian waters, McQuinn *et al.* (1988) estimated an effective area of 18–278 m^2 fished by baited traps for whelks, using a release–recapture method. The ellipsoid shape of attraction areas is determined by speed and direction of bottom currents, as shown in studies on crustaceans (Sainte-Marie and Hargrave, 1987). The aggregation of dab and dragonet (Fig. 3) indicates attraction areas that may be at least 4–5 times as large as the area affected by beam trawls directly. The decreasing fraction of bivalves and increasing fraction of scavenging amphipods in the food composition of dab during 60 h after trawling may reflect the decreasing availability of this food source and suggests a high clearance rate.

Opportunistic consumers such as dab (Lozàn, 1989; Knust, 1991) and whiting (Hislop *et al.*, 1991) responded to the additional resource by widening their food niche, although different species still fed selectively on different food items. Tub gurnards feed predominantly on crustaceans (Hertling, 1924). In trawled areas, their food uptake increased without major changes in food selection. The food of dragonets consists usually of small polychaetes, bivalves, and amphipods (van der Veer *et al.*, 1990), but after trawling, especially small particles such as gonads and intestines of crushed sea potatoes or sedentary polychaetes like *Lanice* sp. were utilized. These materials may contribute a major part of the benthos left on the bottom after the passage of beam trawls. Bullrout are ambush feeders on crabs, shrimp, and gobies (Lindeboom and de Groot, 1989), and their hunting strategy may explain the poor response to beam trawling. Seasonal and diurnal feeding patterns (such as recorded for dab; Temming and Hammer, 1994) may have additional effects on food partitioning owing to temporal segregation of species.

The food of *Liocarcinus* usually consists of polychaetes, small bivalves and echinoderms, molluscs, small crustaceans, and juvenile fish (Choy, 1986). *P.*

bernhardus may feed in different ways (Gerlach *et al.*, 1976) but is obviously capable of handling dead fish. While the preference of *A. rubens* for bivalve bait (Table 3) agrees with their normal food (Allen, 1983), crustacean and fish bait appeared to be almost as attractive. Interestingly, brittle stars showed a strong preference for fish bait (Nagabhushanam and Colman, 1959), although they are usually known as micro-carnivores or detritus feeders. Taking all these features of scavenging species into account, we conclude that epibenthic invertebrates will largely consume the discarded fish that reach the bottom, dead crabs, and parts of the damaged benthic fauna, while fish will mainly consume damaged bivalves, sea potatoes, and dislodged crabs. Investigations on partitioning of food generated by fisheries are rare (Wassenberg and Hill, 1990), but our evidence suggests that the degree of food partitioning among the different scavenger species in the southern North Sea is high.

Food materials generated by fisheries may have positive effects on benthic populations (Fusaro, 1978; Flint and Rabelais, 1981; Wassenberg and Hill, 1987). The annual trawling intensity (Rijnsdorp *et al.*, 1998), as well as the length of the intervals between consecutive trawling events may have effects on the standing crop and recovery time of benthos and therefore, on food production.

The food balances for different locations and different scenarios (Table 6) point generally to a larger share of the epibenthic carnivore feeding guild than of the benthivore fish guild. This confirms estimates from a model of food web dynamics in the North Sea (Greenstreet and Hall, 1996). A few species (dab, dragonet, swimming crab, and lysianid amphipods) seem to get a relatively large share of the food materials generated and may locally cover a considerable part of their food requirements. If the timing of the extra food production matches important periods in the life cycle, or coincides with periods of food shortage, local and/or temporal positive effects on populations of these species are possible. However, the order of magnitude of the direct food supply is unlikely to be sufficient to cause large increases of scavenger populations in the entire southern North Sea.

Owing to the aggregation of predators and potential prey around the food materials produced by beam trawling, predation risk may increase (Ramsay *et al.*, 1997). Trophic feedback relationships among more than two species have been described by Ursin (1982). Our data suggest that gurnards may benefit indirectly from scavenging swimming crabs and dab may benefit from scavenging amphipods attracted to the trawl track.

Focusing on species with potential benefits, few records of long-term changes in abundance or in growth rates seem to exist. Enhanced growth rates have been recorded for dab (Lozàn, 1989) and whiting, which may have been caused by a higher food availability, caused

by trawling and/or eutrophication, an increase of the mean water temperature, or combinations of these factors (Rijnsdorp *et al.*, 1996). Lindeboom and de Groot (1998) have reported an increase in the dragonet stock in areas along the Dutch west coast and north of the Wadden islands between 1972 and 1991 and increasing trends for dab and starfish. Swimming crabs and hermit crabs are fast-growing species that reach maturity in their first year of life (Lancaster, 1989; Lindeboom and de Groot, 1998). However, these species have not shown a clear trend in changes of abundance in these areas over the same period. Some scavenging species (e.g., edible crab and whelks) are probably suffering more harm than benefit from trawling, because their abundance has decreased according to long-term data sets of by-catch species in bottom fisheries (Philippart, 1996).

In principle, beam trawling may cause a general increase in secondary production, if: (i) disturbance of the sediments releases nutrients and promotes primary production (Krost, 1989); (ii) trawling changes the size composition of species and the species composition towards more productive systems. There is evidence of a shift in species composition of the demersal fish fauna in the southern North Sea towards a less diverse and less even fish assemblage, as well as a shift towards smaller fish (Rijnsdorp *et al.*, 1996; Heessen and Daan, 1996; Walker and Heessen, 1996; Lindeboom and de Groot, 1998); (iii) trawling causes shifts in the trophic web towards lower trophic levels and shortcuts in the food chain.

Our data indicate that materials mobilized by beam trawling are rapidly recycled by scavengers. Hence, a link between enhanced production rates and trawling is possible. Damage and exposure of large and low-productive infauna releases this organic matter suddenly and transfers it back into the food web of the benthic ecosystem. This process would take many years under undisturbed circumstances. Theoretically, the shortcut in the trophic relationships may lead to a faster transfer of organic matter, higher ecological efficiency, and therefore, to higher secondary production.

The order of magnitude of this effect on a dynamic ecosystem is difficult to assess. However, the estimated amount of food material mobilized by a single trawling event (1.3 AFDW m^{-2}) may be compared with values of benthic biomass and secondary production. For large areas of the southern North Sea, *E. cordatum* is one of the most abundant species (de Wilde *et al.*, 1984; Holtmann *et al.*, 1996) and may account for about 50% of the benthic biomass at sandy sites. Cramer (1991) estimated its annual production between 0.3 (in mud sediment) and $1.4 \text{ g AFDW m}^{-2}$ (in sandy sediment), and the standing stock between 2.6 and $3.4 \text{ g AFDW m}^{-2}$, respectively. The estimated contribution of *Echinocardium* to the benthic biomass released by beam trawling varied between 18 and 67% for the four study

sites, implying that a considerable part of the annual production may become available to benthic scavengers. For the entire macrobenthic community, the total annual secondary production is estimated at about 21 g AFDW m^{-2} for the Oystergrounds (de Wilde *et al.*, 1984), 10 AFDW m^{-2} for the Broad Fourteens (West off Dutch coast), and at about 20 g AFDW m^{-2} for the entire southern North Sea (Duineveld *et al.*, 1991). This means that after a single-beam trawling, about 6.2–13% of the annual secondary production of macrobenthos would become suddenly available to scavengers and to the detritus food chain. With respect to the standing stocks of macrobenthos in the southern North Sea (4–12 g AFDW m^{-2} ; Duineveld *et al.*, 1991), the passage of a beam trawl releases about 11–32%. Hence, beam trawling probably has accelerated the flow of matter and contributed to enhanced secondary production.

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References

- Allen, P. L. 1983. Feeding behaviour of *Asterias rubens* (L.) on soft bottom bivalves: a study in selective predation. *Journal of Experimental Marine Biology*, 70: 79–90.
- Arntz, W. E., and Weber, W. 1970. *Cyprina islandica* L. (Mollusca, Bivalvia) als Nahrung von Dorsch und Kliesche in der Kieler Bucht. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung*, 21: 193–209.
- Berghahn, R. 1990. On the potential impact and shrimping on trophic relationships in the Wadden Sea. *In Trophic Relationships in the Marine Environment*, pp. 130–140. Proceedings of the 24th European Marine Biology Symposium, Oban, Scotland. Ed. by M. Barnes, and R. N. Gibson.
- Bergman, M. J. N., and Hup, M. 1992. Direct effects of beam trawling on macrofauna in a sandy sediment in the southern North Sea. *ICES Journal of Marine Science*, 49: 5–11.
- Bergman, M. J. N., and van Santbrink, J. W. 1994. A new benthos dredge (TRIPLE-D) for quantitative sampling of infauna species of low abundance. *Netherlands Journal of Sea Research*, 33: 129–133.
- Bergman, M. J. N., and van Santbrink, J. W. 2000. Fishing mortality in megafaunal benthic populations caused by trawl fishery on the Dutch continental shelf in the North Sea in 1994. *ICES Journal of Marine Science*, 57: 1321–1331.
- Britton, J. C., and Morton, B. 1994. Marine carrion and scavengers. *Oceanography and Marine Biology, Annual Review*, 32: 369–434.
- Camphuysen, C., Calvo, B., Durinck, J., Ensor, K., Follestad, A., Furness, R. W., Garthe, S., Leaper, G., Skov, H., Tasker, M. L., and Winter, C. 1995. Consumption of discards by seabirds in the North Sea. *NIOZ-Rapport 1995/5*: 1–202.
- Choy, S. C. 1986. Natural diet and feeding habits of the crabs *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae). *Marine Ecology*, 31: 87–99.
- Cramer, A. 1991. Benthic metabolic activity at frontal systems in the North Sea. PhD thesis, University of Amsterdam. 93 pp.
- Duineveld, G. C. A., Künitzer, A., Niermann, U., De Wilde, P. A. W. J., and Gray, J. S. 1991. The macrozoobenthos of the North Sea. *Netherlands Journal of Sea Research*, 28(1/2): 53–65.
- Evans, P. L., Kaiser, M. J., and Hughes, R. 1994. Behaviour and energetics of whelks, *Buccinum undatum* (L.) feeding on animals killed by beam trawling. *Journal of Experimental Marine Biology and Ecology*, 197: 51–62.
- FAO 1998. Fishery statistics, catches and landings 1995. *FAO Yearbook*, Rome.
- Flint, R. W., and Rabelais, N. N. 1981. Gulf of Mexico shrimp production: a food web hypothesis. *Fishery Bulletin*, 79(4): 737–748.
- Fonds, M. 1994. Mortality of fish and invertebrates in beam trawl catches and the survival chances of discards. *In Environmental Impact of Bottom Gears on Benthic Fauna in Relation to Natural Resources Management and Protection of the North Sea*, pp. 131–146. Ed. by S. J. de Groot, and H. J. Lindeboom. *NIOZ-Rapport 1994-11/RIVO-DLO Report CO 26/94*.
- Fonds, M., Jaworski, A., Iedema, A., and van der Puyl, P. 1989. Metabolism, food consumption, growth and food conversion of shorthorn sculpin (*Myoxocephalus scorpius*) and eelpout (*Zoarces viviparus*). *Demersal Fish Committee, ICES CM 1989/G:31*, 10 pp.
- Fonds, M., Cronie, R., Vethaak, A. D., and van der Puyl, P. 1992. Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. *Netherlands Journal of Sea Research*, 29(1–3): 127–143.
- Fusaro, G. 1978. Food availability and egg production: a field experiment with *Hippia pacifica* Dana (Decapoda; Hippidae). *Pacific Science*, 32: 17–22.
- de Gee, A., and Kikkert, A. H. 1993. Analysis of the grey gurnard (*Eutrigla gurnardus*) samples collected during the 1991 International Stomach Sampling Project. *ICES CM 1993/G: 14*, 25 pp.
- Gerlach, S. A., Ekstrøm, D. K., and Eckardt, P. B. 1976. Filter feeding in the hermit crab, *Pagurus bernhardus*. *Oecologia (Berl.)*, 24: 257–264.
- Greenstreet, S. P. R., and Hall, S. J. 1996. Fishing and the ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. *Journal of Animal Ecology*, 65: 577–598.
- Groenewold, S. 1999. Effects of beam trawl fishery on the food consumption of scavenging epibenthic invertebrates and demersal fish in the southern North Sea. PhD thesis, University of Hamburg. 146 pp.
- Heessen, H. J. L., and Daan, N. 1996. Long-term trends in ten non-target fish species. *ICES Journal of Marine Science*, 53: 1063–1078.
- Hertling, H. 1924. Über den Grauen und Roten Knurrhahn (*Trigla gurnardus* L. und *Trigla hirundo* Bloch). *Wissenschaftliche Meeresuntersuchungen Helgoland*, 15: 1–53.

- Hislop, J. R. G., Robb, A. P., Bell, M. A., and Armstrong, D. W. 1991. The diet and food consumption of whiting (*Merlangius merlangus*) in the North Sea. *ICES Journal of Marine Science*, 48: 139–156.
- Holtmann, S. E., Groenewold, A., Schrader, K. H. M., Asjes, J., Craeymeersch, J. A., Duinefeld, G. C. A., van Bostelen, A. J., and van der Meer, J. 1996. Atlas of the Zoobenthos of the Dutch Continental Shelf. Ministry of Transport, Public Works and Water Management, North Sea Directorate, Rijswijk. 244 pp.
- Hyslop, E. J. 1980. Stomach contents analysis – a review of methods and their application. *Journal of Fish Biology*, 17: 411–429.
- Kaiser, M. J., and Spencer, B. E. 1994. Fish scavenging behaviour in recently trawled areas. *Marine Ecology Progress Series*, 112: 41–49.
- Knust, R. 1990. Die Ernährung der Kliesche (*Limanda limanda* L.) in der zentralen und südlichen Nordsee und die Bedeutung des Ernährungszustandes für die Erkrankungen dieses Fisches. Veröffentlichungen des Institute für Küsten- und Binnenfischerei Hamburg, 102: 1–184.
- Krebs, C. J. 1989. *Ecological Methodology*. Harper Collins Publishers, New York. 654 pp.
- Krost, P. 1990. The impact of otter-trawl fishery on nutrient release from the sediment and macrofauna of Kieler Bucht (Western Baltic). Berichte aus dem Institut für Meereskunde an der Christian-Albrechts-Universität, Kiel. Nr., 200: 1–157.
- Lancaster, I. 1989. Optimisation in the life history of the hermit crab *Pagurus bernhardus* (L.). PhD thesis, University of Wales (UK). 231 pp.
- Lindeboom, H. J., and de Groot, S. J. 1998. The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. NIOZ-Rapport 1998-1/RIVO-DLO Report C003/98. 404 pp.
- Løkkeborg, S., and Johanessen, T. 1992. The importance of chemical stimuli in bait fishing – fishing trials with presoaked bait. *Fisheries Research*, 14: 21–29.
- Lozàn, J. L. 1989. Investigations on the growth of the dab (*Limanda limanda* L.) in eight regions of the North Sea and comparisons with earlier findings. *Archiv für Fischerei Wissenschaften*, 39: 111–146.
- McQuinn, I. H., Gendron, L., and Himmelman, J. H. 1988. Area of attraction and effective area fished by whelk (*Buccinum undatum*) trap under variable conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, 45: 2054–2060.
- Miller, R. J. 1979. Design criteria for crab traps. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 39: 140–147.
- Moore, P. G., and Wong, Y. M. 1995. Activity and trapping characteristics in the field of *Orchomene nanus* (Krøyer) (Amphipoda: Lysianassoidea) at Millport, Scotland. *Journal of Experimental Marine Biology and Ecology*, 189: 143–157.
- Nagabhushanam, A. K., and Colman, J. S. 1959. Carrion-eating by ophiuroids. *Nature*, 4682: 285.
- Pandian, T. J. 1970. Intake and conversion of food in the fish *Limanda limanda* exposed to different temperatures. *Marine Biology*, 5: 1–17.
- Philippart, C. J. M. 1998. Long-term impact of bottom fisheries on several by-catch species of demersal fish and benthic invertebrates in the south-eastern North Sea. *ICES Journal of Marine Science*, 55: 342–352.
- Ramsay, K., Kaiser, M. J., and Hughes, R. N. 1996. Changes in hermit crab feeding patterns in response to trawling disturbance. *Marine Ecology Progress Series*, 144: 63–72.
- Ramsay, K., Kaiser, M. J., Moore, P. G., and Hughes, R. N. 1997. Consumption of fisheries discards by benthic scavengers: utilisation of energy subsidies in different marine habitats. *Journal of Animal Ecology*, 66: 884–896.
- Rauck, G. 1989. Welchen Einfluß haben Grundschieppnetze auf den Meeresboden und auf Bodentiere? *Das Fischerblatt*, 37: 155–158.
- Rijnsdorp, A. D., Leeuwen, P. I., van Daan, N., and Heessen, H. J. L. 1996. Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. *ICES Journal of Marine Science*, 53: 1054–1062.
- Rijnsdorp, A. D., Buys, A. M., Storbeck, F., and Visser, E. G. 1998. Micro-scale distribution of beam trawl effort between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *ICES Journal of Marine Science*, 55: 403–419.
- Sainte-Marie, B., and Hargrave, B. T. 1987. Estimation of scavenger abundance and distance of attraction to bait. *Marine Biology*, 94: 431–443.
- van Santbrink, J., and Bergman, M. J. N. 1994. Direct effects of beam trawling on macrofauna in a soft bottom area in the southern North Sea. In *Environmental Impact of Bottom Gears on Benthic Fauna in Relation to Natural Resources Management and Protection of the North Sea*, pp. 147–178. Ed. by S. J. de Groot, and H. J. Lindeboom. NIOZ-Rapport 1994-11/RIVO-DLO Report CO 26/94.
- Schaefer 1962. *Aktuopalaöntologische Studien in der Nordsee*. Senckenberg-Buch, Frankfurt. 8, 666 pp.
- Temming, A., and Hammer, N. 1994. Sex specific food consumption of dab (*Limanda limanda* L.) based on a 24 h fishery. *Archive of Fishery and Marine Research*, 42: 123–136.
- Ursin, E. 1982. Stability and variability in marine ecosystems. *Dana*, 2: 51–67.
- van der Veer, H., Creutzberg, F., Dapper, R., Duineveld, G. C. A., Fonds, M., Kuipers, B. R., van Noort, G. J., and Witte, J. IJ. 1990. On the ecology of dragonet *Callionymus lyra* L. in the southern North Sea. *Netherlands Journal of Sea Research*, 26: 139–150.
- Walker, P. A., and Heessen, H. J. L. 1996. Long-term changes in ray populations in the North Sea. *ICES Journal of Marine Science*, 53: 1085–1093.
- Wassenberg, T. J., and Hill, B. J. 1987. Feeding by the sandcrab *Portunus pelagicus* on material discarded from prawn trawlers in Moreton Bay, Australia. *Marine Biology*, 95: 387–393.
- Wassenberg, T. J., and Hill, B. J. 1990. Partitioning of materials discarded by prawn trawlers in Moreton Bay. *Australian Journal of Marine and Freshwater Research*, 41: 27–36.
- de Wilde, P. A. W. J., Berghuis, E. M., and Kok, A. 1984. Structure and energy demand of the benthic community of the Oystergrounds, central North Sea. *Netherlands Journal of Sea Research*, 18: 143–159.