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Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994

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We estimated the direct mortality of benthic fauna caused by one single passage of commercial beam and otter trawls in field experiments. The benthos dredge Triple-D was used to sample megafauna (>1 cm), while macrofauna (>1 mm) were sampled by means of a Reineck boxcorer and, in some cases, a van Veen grab. Direct mortalities ranging from about 5 up to 40% of the initial densities were observed for a number of gastropods, starfishes, small and medium-sized crustaceans, and annelid worms. For bivalve species, direct mortalities were found from about 20 up to 65%. Mortality per m^2 trawled area due to fishing with a 12-m beam trawl was not higher than that due to a 4-m beam trawl. For all species considered, the direct mortality was largely attributed to animals that died in the trawl track, either as a direct result of physical damage inflicted by the passage of the trawl or indirectly owing to disturbance, exposure, and subsequent predation. In 1994, the 12 m beam trawl with tickler chains was the dominant gear type in the Dutch sector, resulting in a mean annual trawling frequency of 1.23. The mean annual trawling frequencies with the 4 m beam trawl using tickler chains, the 4 m beam trawl with a chain mat, and the otter trawl were 0.13, 0.01, and 0.06, respectively. The annual fishing mortality in invertebrate megafaunal populations in the Dutch sector ranged from 5 up to 39%, with half of the species showing values of more than 20%. For all species studied, the 12 m beam-trawl fisheries caused higher annual fishing mortalities than the concerted action of the other fisheries. Only with respect to species restricted to sandy coastal areas did the 4 m beam-trawl fleet contribute substantially to the annual mortality. Implications of the impact of trawling on the composition of benthic communities are discussed.

Key words: direct mortality of trawling, fishing mortality, impact of beam trawling, impact of otter trawling, megafauna.

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Introduction

Trawling is a widespread method for catching demersal fish. In the North Sea, bottom trawls had been used for centuries before the beam trawl was reintroduced in the early 1960s and became the most common demersal gear in the south-eastern parts (Anon., 1921; Lindeboom and de Groot, 1998). Besides fish, invertebrate species are caught in the nets, and some will not survive after they have been returned to the sea as discards (Houghton *et al*., 1971). Evidence is available showing serious damage and mortalities in coelenterates, annelid worms, molluscs, echinoderms and crustaceans in trawl nets (Graham, 1955; Bridger, 1970; Margetts and Bridger, 1971). Fonds (1994) and Lindeboom and de Groot (1998) estimated the percentage by species that were brought aboard dead, or would die within a few hours or days, in field studies. Direct mortality, however, may also occur in animals that are hit by the gear but not retained by the nets. This is a well-known consequence of dredging for shellfish on populations of other bivalves, sabellid worms, and burrowing ceriathid anemones (Brown, 1989; Hall *et al*., 1990; Langton and Robinson, 1990). There are also indications of impacts of trawling for flatfish on the composition of small infaunal species (Holme, 1983; Rees and Eleftheriou, 1989; Bergman and Hup, 1992; Brylinski *et al*., 1994; Kaiser and Spencer, 1996). Quantitative estimates of the direct mortality of larger-sized (>1 cm) species in the trawl track are scarce. Only recently, impacts were

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Table 1. Characteristics of the commercial trawls used in the field experiments.

	12 m BT ticklers	4 m BT ticklers	4 m BT chain mat	OT
Width (m)				
Beam	12	4	4	
Net (+bridles)*				32
Between wings*				15–20
Between doors				35–55
Weight (kg 10^{-3})	5.9–7.8	1.4–1.5	2.7	1
Tickler chains				
Number	9–10	5	—	—
Weight (kg 10^{-3})	1.1–2.2	0.1–0.3	0.95	—
Net ticklers (n)	8–10	5–6	—	—
Roller diam. (cm)	25	15	25	20
Stretches mesh size (mm)				
Front	260	170	120	120
Codend	80	80	80	80–100
Towing speed (nm h^{-1})	5–7	3.5–5.5	3.5	3.5–4

BT, beam trawl; OT, otter trawl; *, contact with seabed.

described, showing a significantly altered composition of the community immediately after trawling (Kaiser *et al.*, 1998).

We present results of field studies in the south-eastern North Sea on the direct mortality of invertebrate infaunal and epifaunal species caused by commercial 12 m and 4 m beam trawls and otter trawls. The annual fishing mortality of megafaunal populations in the Dutch sector is estimated using these estimates of direct mortality and the spatial distributions of the populations and of the trawling fleets in 1994.

Material and methods

Experimental setup

The direct mortality caused by trawling was determined in field experiments by the differences in densities before and after trawling a well-defined strip. Megafauna (>1 cm) were sampled by means of the benthos dredge Triple-D (sampling depth 10 cm, stretched mesh size 1.4 cm, sampling area ca. 25 m^2; Bergman and van Santbrink, 1994). In addition, macrofauna (>1 mm) have been sampled with the Reineck boxcorer or van Veen grab. Three representative types of commercial beam trawls (12 m and 4 m wide with tickler chains, and 4 m wide with chain mat) and a flatfish otter trawl was tested (Table 1). The studies were carried out in different locations, ranging from shallow coastal sandy areas to deeper offshore silty areas, in the Dutch and German sector in spring and late summer, 1992–1995 (Fig. 1).

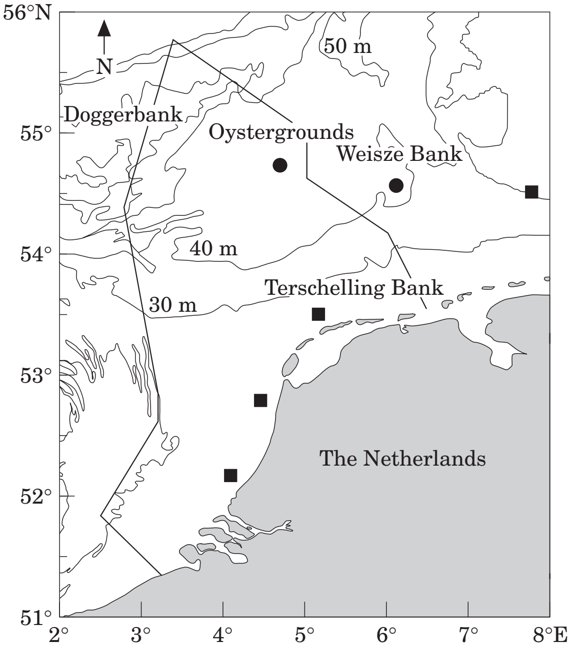

Figure 1. Locations of the field experiments on direct mortality caused by different types of trawls in the south-eastern North Sea: (■) sandy coastal areas (median grain size 200–370 µm; silt content 1–5% (●) silty offshore areas (median grain size 150–170 µm; silt content 3–10%).

Initial studies were carried out as a single-strip experiment for testing one type of trawl, while in later studies parallel strips were used for the comparison of different types of trawls. In 1995, replicate strips were trawled with each type of trawl. The length of a strip was about 2000 m, the width about 60 m, and the distance between parallel strips about 300 m. A standard sampling and trawling procedure was applied. Prior to trawling, each strip was sampled with Triple-D, boxcorer, and grab to estimate the initial densities of species (t_0-sampling). After 24 to 48 h each strip was trawled with a particular type of gear in a series of hauls. Since it was impossible to trawl a strip homogeneously without leaving untrawled patches, we aimed at an average trawl frequency of 1.5 for the entire strip. Repeated trawling of the same tracks within a few hours or days is not unusual in commercial trawling practice. At least 24 h (in 1995, 48 h) after trawling, the remaining fauna in each strip were sampled again (t_1) following the same procedures as before. Sidescan sonar was used immediately after each sampling and trawling event to check the positions.

Direct mortality

The direct mortality (M_{dir}) was calculated using the difference between the initial densities and the final densities. We assume that all mortally damaged and exposed animals in the strip had been consumed by predators in the 24–48 h interval between trawling and t_1-sampling. The proportion of a species that survived being caught in the net and discarded was subtracted from the difference between initial and final densities in the strip, because these survivors may only have been dislocated. Direct mortality was expressed as % of the initial density in the trawl track:

$$M_{dir}\,(\%) = 100\left(\frac{D_{t0} - [D_{t1} + C \times (1 - 0.01 \times M_{dis})]}{D_{t0}}\right),$$

where D refers to density (n m^{-2}), C to numbers caught (n m^{-2} swept area), and M_{dis} is the percentage mortality of animals caught (Fonds, 1994; Lindeboom and de Groot, 1998).

The differences between the geometric mean of initial and final densities were statistically tested (paired t-test on log-transformed data; one-sided for sedentary species and two-sided for mobile species), and the 95% confidence intervals of the differences were calculated. For each species, direct mortality was calculated per trawl type for coastal sandy sediments and offshore silty sediments. Replicate results, i.e., strips trawled by the same trawl type in the same type of sediment, were averaged with a weighting factor based on 95% confidence intervals. The direct mortality calculated was converted to that which would have been caused by a single passage of a trawl. Mortality only was calculated when the initial density of a species was more than 5 per 100 m^2 (Triple-D) or more than 10 per m^2 (boxcore). The comparison among types of trawls was exclusively based on studies in which parallel strips were sampled with different trawls. Only species with initial densities of more than 10 per 100 m^2 were included. To determine relative vulnerability, species in each study and for each trawl type have been ranked according to their direct mortality. Species were included only when mortality was determined in at least five different strips. The mean ranking of the species is presented for sandy and silty areas separately.

Direct mortality was calculated for sedentary and slowly moving species only, since mobile epibenthic species might migrate into and from the trawled strip in the interval before t_1-sampling. For the heart urchin (*Echinocardium cordatum*), the measured mortality was corrected for the proportion of the population actually within reach of the Triple-D from the mean-depth frequency distribution (Bergman and Hup, 1992): about 25% of the population in sandy areas and about 60% in silty areas. These figures are underestimates in the reproductive season, when heart urchins live close to the surface.

Annual fishing mortality

The fishing mortality in a number of megafaunal populations on the Dutch continental shelf was calculated using three variables: the spatial distribution of the species in 1996 (Bergman and van Santbrink, 1998), the trawling frequency of the different fleets in 1994, and the direct mortality caused by a single passage of each trawl type. The inherent assumption is that the distribution patterns of the species in 1996 and the effort distribution in 1994 are representative. Also, it is assumed that the distribution of species within an ICES statistical rectangle was homogeneous. The only species selected were those for which a reliable direct mortality estimate for at least two different types of trawls was available, and for which the mortality was >7% for at least one type. Since the results with respect to direct mortality did not show substantial differences between the mortality estimates caused by 12 m and 4 m beam trawls with ticklers, their mean estimate was used in the calculations to reduce erroneous variation in the calculations.

The trawling frequencies per ICES rectangle by the Dutch, Belgian, German, and British fleets were calculated from the surface area of each rectangle and the number of fishing hours of the fleets using 4 m and 12 m beam-trawls tickler chains, 4 m beam trawls with chain mats, and otter trawls (Lindeboom and de Groot, 1998). The relatively low effort of trawlers fishing with beams of intermediate length, and with 12 m beams with chain mats, was not included, since no direct mortality estimates for these gears were available. Rijnsdorp *et al.* (1998) analysed the distribution of a representative selection (13%) of the Dutch 12 m beam-trawl fleet and showed that effort was clustered within rectangles. To simulate a similarly clustered distribution, each ICES rectangle was divided into nine subrectangles, and the total effort of each fleet in that rectangle was distributed over the subrectangles (0.1, 0.2, 0.6, 1.1, 2.2, 5.6, 11.1, 22.2, and 56.9%, respectively). The inherent assumption is that all types of trawling show the same degree of heterogeneity in spatial distribution within ICES rectangles.

Table 2. Direct mortality (% of the initial density in the trawl track) of macrofaunal species sampled with a Reineck boxcorer (n=20) caused by a single pass of 12 m beam trawl (silty Oystergrounds) or of a 4 m beam trawl (sandy coastal zone south of Terschelling Bank).

	Size (mm)	Gear type (m)	Mortality
Bivalves	Length		
Arctica islandica	2–3	12	20
Corbula gibba	1–11	12	9
Donax vittatus	20–35	4	10
Mysella bidentata	2–3	12	4
Nucula nitidosa	2–10	12	4
Spisula spec. juv.	1–6	4	20
Tellimya ferruginosa	2–7	4	19*
Gastropods	Height		
Cylichna cylindracea	3–8	12	14
Turritella communis	5–15	12	20*
Echinoderms	Diameter		
Amphiura sp.	2–6	12	9
Crustaceans	Length	12	
Callinassa subterranea	5–40	12	4
Cumacea	3–7	12	22*
Gammaridea	2–11	12	28
Annelids	Length		
Pectinaria koreni	4–20	12	31*
Magelona papillicornis		12	30*
Scoloplos armiger		12	18
24 spp. (excl. *Pectinaria*)		12	<0.5

*Significant at p=0.05 (paired t-test on log transformed data).

In the calculations of fishing mortality, recruitment and growth were not included. The survival rate (S) of species (x) in subrectangle (r) after trawling that subrectangle with a particular gear (g) is described by the following power function:

$$S_{x,r,g} = \left(\frac{1 - Md_{g,x}}{100}\right)^{f(r,g)},$$

where Md is the direct mortality estimate expressed as a percentage of the initial density in sandy or silty sediment and f is the trawling frequency.

The fishing mortality (F) in an ICES rectangle (R) is the average of the fishing mortalities $1 - S_{x,r,g}$ in the nine subrectangles, multiplied by 100 to express it as a percentage of the initial density:

$$F_{x,R,g}\,(\%) = 100 \times \frac{\Sigma_r(1 - S_{x,r,g})}{9}$$

Finally, the fishing mortality for a species in the entire Dutch sector ($F_{x,g}$) was calculated for the different types of fisheries by dividing the sum of the specimens killed in each ICES rectangle by the sum of the actual number of individuals (n) present in those rectangles:

$$F_{x,g}(\%) = \Sigma_R(n_{x,R} \times F_{x,R,g})/\Sigma_R n_{x,R}$$

In the mortality calculations for each type of fishery, the other types of fisheries, also leading to mortalities in the same area, were not accounted for. Because the actual decline in numbers caused by the combined action of the different fleets is faster than for each fleet separately, the fishing mortality generated is overestimated. Therefore, the overall fishing mortality $F_{overall}$ for a species was calculated using the overall survival rate, instead of using the sum of the fishing mortality by gear type. This overall survival rate was calculated as the product of the survival rates (Π_g) within each type of fishery. The overall fishing mortality as a percentage of the initial density is then given by:

$$F_{overall,x}(\%) = 100 \times (1 - \Pi_g(1 - F_{x,g}/100))$$

Results

Direct mortality

Small-sized bivalves and crustaceans showed direct mortalities caused by a single passage of a 4 m and 12 m beam trawl on sandy and silty sediments up to 22% of the initial densities and annelid worms (e.g., the tube-dwelling polychaete *Pectinaria koreni*) up to 31% (Table 2). The mortality of many other small annelids observed

Table 3. Mean direct mortality (M in % of the initial density in the trawl track) of megafaunal species sampled with the Triple-D (n=10) casued by a single pass of different trawls in silty and sandy areas of the southern North Sea, with information on number of strips evaluated (n) and number of strips showing significant mortalities at p=0.05 (paired t-test on log-transformed data) given by (x).

		Silty sediments				OT		Sandy sediments						OT	
	Size	12 m BT ticklers		4 m BT ticklers				12 m BT ticklers		4 m BT ticklers		4 m BT mat			
	(cm)	n	M.	n	M.	n	M.	n	M.	n	M.	n	M.	n	M.
Bivalves	Length														
Abra alba	1–1.5	4 (1)	18	3 (2)	38	3	+	—	—	—	—	—	—	—	—
Angulus fabula	1–1.5	—	—	—	—	—	—	1 (1)	64	1 (1)	52	—	—	—	—
Angulus tenuis	2–3	—	—	—	—	—	—	—	—	2	15	—	—	—	—
Arctica islandica	8–11	3 (1)	5	2 (1)	22	2	8	—	—	—	—	—	—	—	—
Chamelea gallina	1–3	4 (1)	12	3 (2)	18	3	3	4	5	7 (1)	4	3 (1)	2	1	13
Corbula gibba	1	2	+	2 (1)	14	2	6	—	—	—	—	—	—	—	—
Dosinia lupinus	1–4	4 (2)	31	3 (2)	33	3 (1)	16	—	—	—	—	—	—	—	—
Ensis spp.	10–20	3 (2)	+	3 (2)	7	3 (2)	+	4 (1)	10	7 (2)	9	3 (1)	6	1	12
Gari fervensis	4–6	1 (1)	68	1 (1)	66	1 (1)	52	—	—	—	—	—	—	—	—
Mactra corallina	3–5	2	16	2	25	2 (1)	22	1	5	2	8	—	—	1	+
Mysia undata	1.5–3	1 (1)	35	—	—	—	—	—	—	—	—	—	—	—	—
Phaxas pellucidus	1.5–3	4 (2)	27	3 (1)	29	3 (1)	32	1	+	1 (1)	33	—	—	1	4
Spisula solida	2–5	—	—	—	—	—	—	2 (1)	26	3 (3)	20	3 (1)	6	—	—
Spisula subtruncata (l)	1.5–3	—	—	—	—	—	—	3	+	3 (1)	23	2 (1)	29	1	21
Spisula subtruncata (h)	1.5–3	—	—	—	—	—	—	—	—	1 (1)	47	—	—	—	—
Gastropods	Height														
Lunatia catena	1–3	—	—	—	—	—	—	1	10	1	10	—	—	—	—
Turritella communis	3–6	3 (1)	5	2	17	2	7	—	—	—	—	—	—	—	—
Echinoderms	Diameter														
Astropecten irregularis	3–6	4 (1)	12	3 (2)	18	3	0	1 (1)	52	1	6	—	—	—	—
Echinocardium cordatum	3.5–5	4 (4)	40	3 (3)	35	3 (2)	26	4 (4)	14	7 (6)	12	3 (3)	10	1 (1)	16
Ophiura texturata		—	—	—	—	—	—	1	8	3	2	1	7	1	12
Crustaceans	Width														
Corystes cassivelanus m.	2–3	4 (1)	22	3	15	3 (1)	20	2 (2)	39	2 (1)	31	—	—	1	30
Corystes cassivelanus f.	2	4 (2)	28	3	2	3	3	4 (1)	25	5	7	3	7	1	19
Corystes cassivelanus j.	<1.5	1 (1)	48	1 (1)	49	1	23	—	—	—	—	—	—	—	—
Thia scutellata	1–1.5	—	—	—	—	—	—	2	8	3 (1)	19	3 (1)	7	—	—
Other groups	Length														
Aphrodita aculeata	3–14	4 (1)	8	3	16	3	7	—	—	—	—	—	—	—	—
Golfingia spec.	3–7	2	20	2	5	2 (1)	33	—	—	—	—	—	—	—	—
Pelonia corrugata	3–7	3 (1)	14	3	11	3	2	—	—	—	—	—	—	—	—

Replicate studies were averaged after weighting based on the 95% confidence intervals. *Angulus fabula* was sampled with the van Veen grab (n=12–18). *S. subtruncata* (l) and (h) indicate low (0.1 m^{-2}) and high (24 m^{-2}) density, respectively; +, m<0.5.

was negligible. In megafaunal species, direct mortalities up to 68% were found for bivalves, and up to 49% for crustaceans (Table 3). Other groups exhibited similar ranges. Bivalves such as *Lutraria lutraria*, *Mya truncata*, *Nucula nitidosa*, and anemones frequently showed greater densities in the Triple-D sampling after trawling than prior to trawling. In *Corystes cassivelaunus*, direct mortality appeared to be sex dependent: females generally showed a lower mortality than males (2–28% vs. 15–39%). In *Spisula subtruncata* a density-dependent difference in mortality caused by 4 m beam trawls was observed. Specimens in low densities (about 0.1 m^{-2}) showed a mortality of about 23%, whereas in extremely high densities (>24 m^{-2}) mortality increased up to 47%.

Within some species direct mortality due to 12 m and 4 m beam trawling showed a size-dependent trend. In the gastropod *Lunatia catena*, mortality was negligible for specimens >1 cm, whereas smaller specimens suffered a mortality of 44 and 49%, respectively. The opposite was the case for the bivalve *Chamelea gallina* in silty areas: specimens >2 cm were more vulnerable (22 and 26% mortality, respectively) than smaller specimens (4 and 7% mortality, respectively). A similar trend was found for the polychaete *Aphrodita aculeata* with mortalities for specimens >7 cm of 23 and 31%, respectively, whereas no mortality was observed for smaller ones.

In silty areas, 4 m and 12 m beam trawls caused higher mortalities in *C. gallina*, *Mactra corallina*, and *E. cordatum* than in sandy areas, while the reverse occurred in male *C. cassivelaunus*.

The direct mortality caused by different gears tested in the same area simultaneously are compared in Figure 2.

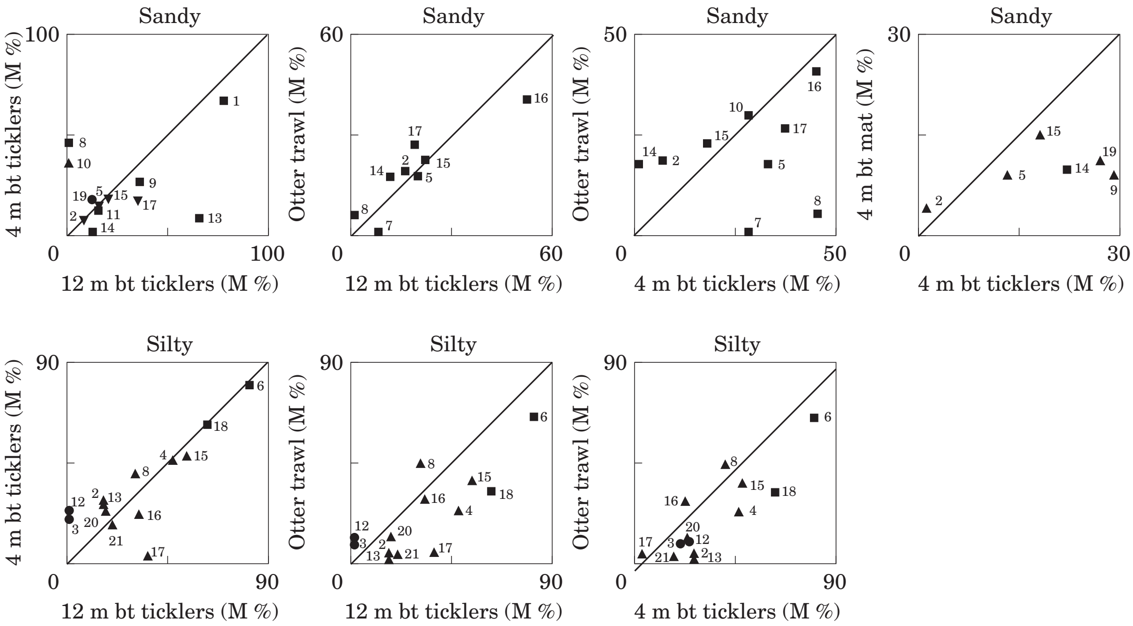

Figure 2. Comparison of the direct mortality (M_{dir}), expressed as percentage of the initial density, caused by different commercial trawls in sandy and silty areas of the south-eastern North Sea (bt=beam trawl). Symbols denote the number of studies from which the results are obtained: (■), 1 study; (●), 2 studies; (▲), 3 studies; (▼), 4 studies. (Species codes: 1. *Angulus fabulus*; 2. *Chamelea gallina*; 3. *Corbula gibba*; 4. *Dosinia lupinus*; 5. *Ensis* spp; 6. *Gari fervensis*; 7. *Mactra corallina*; 8. *Phaxas pellucidus*; 9. *Spisula solida*; 10. *Spisula subtruncata*; 11. *Lunatia catena*; 12. *Turritella communis*; 13. *Astropecten irregularis*; 14. *Ophiura texturata*; 15. *Echinocardium cordatum*; 16. male *Corystes cassivelaunus*; 17. female *C. cassivelaunus*; 18. juv. *C. cassivelaunus*; 19. *Thia scutellata*; 20. *Aphrodita aculeata*; 21. *Pelonaia corrugata*).

For the majority of benthos species involved, differences caused by 4 m or 12 m beam trawls were not obvious, neither in sandy coastal nor in offshore silty areas. In the hard-sandy coastal zone, 4 m beam trawls with tickler chains did not cause consistently higher or lower mortalities than 4 m beams with chain mats, although higher mortalities were found in at least three infaunal species (*Spisula solida*, *Ophiura texturata*, *Thia scutellata*). Otter trawls and beam trawls were compared in one sandy location only, where mortalities of the same order of magnitude were obtained for most species. However, otter trawling clearly caused less mortality than beam trawling with several species (e.g., *C. gallina*, *Dosinia lupinus*, juvenile *C. cassivelaunus*) in silty areas (three test locations).

The relative vulnerability of megafaunal species for trawling by sediment (Table 4) indicates that *E. cordatum*, male *C. cassivelaunus*, and several bivalves ranked high, whereas other bivalves and starfish were relatively resistant.

Annual fishing mortality

The distribution of fishing effort by gear type over the ICES rectangles of the Dutch sector in 1994, expressed as trawled area divided by total area, is presented in Figure 3. The 12 m beam trawl was the dominant gear type, with an average frequency for the Dutch sector of 1.23. The average frequencies for the 4 m beam trawl with ticklers, the 4 m beam trawl with a chain mat, and for the otter trawl were 0.13, 0.01, and 0.06, respectively. The different gear types were not distributed homogeneously over the sector. The 12 m beam-trawl fishery is carried out predominantly offshore, whereas the 4 m beam-trawl fishery is mainly restricted to the coastal zone. Chain mats were used exclusively in the two southernmost rectangles, characterized by mobile sand of medium grain size. Otter trawls were used throughout the sector. It should be noted that roundfish are mainly targeted by this fishery, with a by-catch of plaice. Since the development of the beam-trawl fishery, the use of typical flatfish trawls has largely been abandoned (Lindeboom and de Groot, 1998).

The estimated fishing mortality exerted by trawl fisheries on megafaunal populations in the Dutch sector in 1994 varied from 5 to 39% (Table 5). For all species considered, the 12 m beam-trawl fishery caused the highest annual fishing mortality. For species that are restricted to sandy coastal areas, where the 4 m beam-trawl fishery was concentrated, the differences in mortality caused by these two fleets were less pronounced (e.g., *S. solida*, *S. subtruncata*). This also applies to *Ensis* spp., dominated by the strictly coastal species *E. americanus*. The otter trawl and 4 m beam-trawl fisheries

Table 4. Ranking of megafaunal species according to their mean relative vulnerability to trawling in silty and sandy areas, with information on the number of study strips evaluated (n).

Silty areas	n	Rank	Sandy areas	n	Rank
Echinocardium cordatum	10	8.0	*Corystes cassivelaunus* (m)	5	9.1
Phaxas pellucidus	10	7.3	*Spisula subtruncata*	10	6.9
Dosinia lupinus	10	6.5	*Spisula solida*	8	6.6
Mactra corallina	6	6.4	*Echinocardium cordatum*	15	5.6
Golfingia sp.	6	5.9	*Corystes cassivelaunus* (f)	13	5.5
Corystes cassivelaunus (m)	10	4.9	*Thia scutellata*	8	4.3
Abra alba	10	4.9	*Ophiura texturata*	6	3.6
Turritella communis	7	4.4	*Ensis* spp.	15	3.1
Arctica islandica	7	4.4	*Chamelea gallina*	15	3.0
Corystes cassivelaunus (f)	10	3.9			
Aphrodita aculeata	10	3.9			
Pelonia corrugata	9	3.7			
Chamelea gallina	10	3.7			
Corbula gibba	6	3.3			
Astropecten irregularis	10	3.1			
Ensis spp.	9	0.8			

caused broadly similar annual mortalities. The mortality caused by the 4 m beam-trawl fleet rigged with chain mats was less than 0.5% for all populations studied.

Discussion

The single passage of a 4 m or a 12 m beam trawl, or an otter trawl, caused direct mortality in many invertebrate species ranging from 5 to 50%, for some bivalve species up to 68%, of the initial densities in the trawl track, both in sandy or silty areas (Tables 2 and 3). For the fragile heart urchin *E. cordatum*, the mortality was estimated at 10–40%, after correction for the fraction burrowing too deeply to be sampled quantitatively. Assuming that most heart urchins within reach of the trawl will be killed, the mortality might increase up to about 90% during the relatively short reproduction season in summer when animals migrate to the surface layers of the sediment (Buchanan, 1966).

Direct mortality in species with low mobility (e.g., *T. scutellata*, *O. texturata*) might be underestimated, because some of the apparent survivors in the trawl track during the t_1-sampling may in fact be immigrants. Size-dependent immigration rates might explain the absence of direct mortality observed for the larger specimens of the mobile *L. catena*. In studies in the Irish Sea, several annelids increased in abundance after trawling, which was presumably caused by immigration, or an upward migration, of specimens attracted to damaged animals in the trawl track (Lindeboom and de Groot, 1998). Increased densities were also found in some sedentary bivalves (*L. lutraria*, *M. truncata*, *N. nitidosa*) and anemone species in the Tripe-D sampling after trawling, which suggests that a larger fraction of the population had come within reach during the t_1-sampling, possibly because the top layer of the sediment was resuspended. It may be assumed that these species are hardly affected by trawling, as they usually live deeper in the sediment than the estimated 6 cm penetration depth of the trawls (Bergman and Hup, 1992).

The estimated direct mortality incorporates the mortality of animals caught in the net and of animals damaged in the trawl track. Commercial trawls generally show a low catch efficiency for invertebrates: for most species studied less than 10%, for approximately half of the species and much less than 5% (Lindeboom and de Groot, 1998). Therefore, despite the high mortality in invertebrate discards (ranging from 26 up to 88% for bivalve species, from 25 up to 67% for crustaceans, and from 11 to 21% for starfish; Fonds, 1994; Lindeboom and de Groot, 1998), discard mortality is only a few per cent of the initial density in the trawl track. Hence, discard mortality plays only a minor role in the estimated direct mortalities, and damage or exposure in the trawl track is more important by far.

The design of the field studies may have influenced the direct mortality observed. Because of lack of accuracy in the positioning of tracks to create a homogeneously trawled area, we aimed at an average trawling frequency of 1.5 for each strip. Therefore, the direct mortalities observed had to be corrected. The conversion may have introduced erroneous variation. For example, direct mortality of fragile infauna less affected by a second trawling event because the first pass has already killed almost 100% of the animals within reach of the trawl, may have been underestimated. In contrast, increased vulnerability caused by an increased attainability due to resuspension of sediment layers caused by the first trawling event might have led to an overestimation.

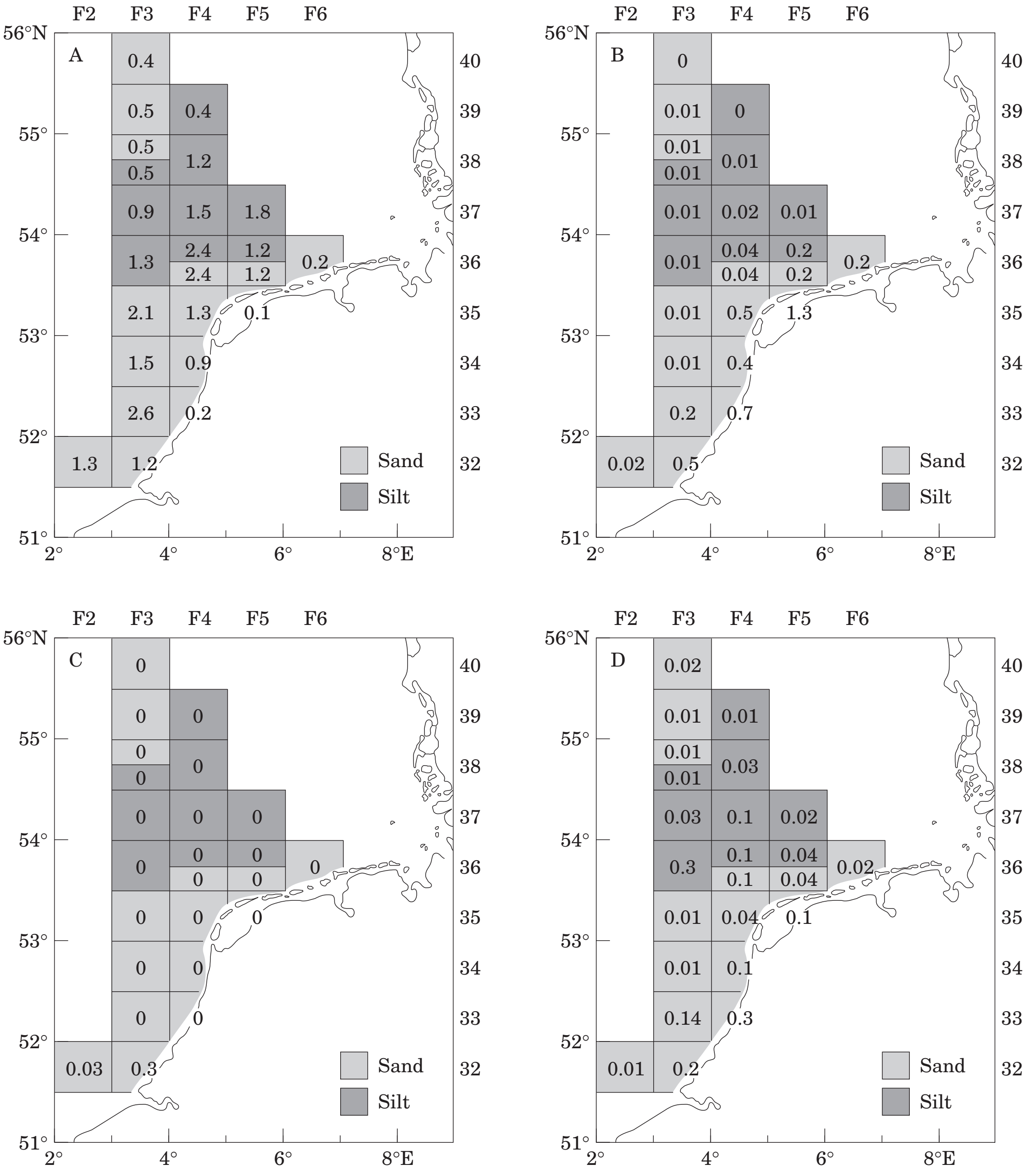

Figure 3. Distribution of trawling effort (mean trawling frequency per ICES rectangle, i.e., trawled area/total area) for different gear types in the Dutch sector in 1994 (Lindeboom and de Groot, 1998). (a) 12 m beam trawl rigged with tickler chains; (b) 4 m beam trawl rigged with tickler chains; (c) 4 m beam trawl rigged with chain mat; (d) otter trawl.

In silty areas, the direct mortality due to otter trawling was lower than that due to beam trawling for a number of burrowing species (e.g., bivalves, crustaceans; Fig. 2), probably reflecting that the groundrope and bridles of otter trawls disturbed these sediments less deeply than did beam trawls. The single study in a sandy area resulted in less consistent differences in mortality between otter and beam trawling.

Among the three different types of beam trawls tested, none resulted in consistently higher or lower direct mortality for the majority of species involved, neither in coastal sandy nor in offshore silty areas. The (sometimes

Table 5. Fishing mortality (%) in invertebrate megafaunal populations in the Dutch sector by fleet. BT, beam trawl; OT, otter trawl.

	Length (cm)	12-m BT ticklers	4-m BT ticklers	4-m BT mat	OT	All types
All sediments						
Chamelea gallina	<2	5	<0.5	<0.5	<0.5	5
Chamelea gallina	>2	22	1	<0.5	1	24
Corystes cassivelaunus f.	>1.5*	17	1	<0.5	<0.5	18
Corystes cassivelaunus m.	>1.5*	26	1		2	28
Echinocardium cordatum	>3	20	2	<0.5	3	24
Ensis spp.	>10	7	3	<0.5	1	11
Mactra corallina	>1	13	1	—	1	15
Phaxas pellucidus	>1.5	16	<0.5		1	17
Sandy sediment						
Lunatia catena	<1.5	27	17	—	—	39
Ophiura texturata	>0.5**	5	1	<0.5	1	7
Spisula solida	>1	17	8	<0.5	—	24
Spisula subtruncata	>1	12	6	<0.5	2	19
Thia scutellata	>0.5*	17	3	<0.5	—	19
Silty sediment						
Abra alba	>0.5	24	1		<0.5	25
Aphrodita aculeata	>7	20	<0.5		1	21
Arctica islandica	>8	11	<0.5		<0.5	11
Astropecten irregularis	>2.5	14	<0.5		0	14
Corystes cassivelaunus j.	<1.5*	29	1		1	30
Dosinia lupinus	>0.5	24	1		1	26
Gari fervensis	>2.5	33	<0.5		3	35
Pelonaia corrugata	>1	14	<0.5		<0.5	14
Turritella communis	>1.5	12	1		<0.5	13

—, No direct mortality estimated; blank, no overlap in effort and species distribution; *carapax width; **disc diameter.

extreme) differences observed for individual species are presumably largely generated by random variation in the data. There was a tendency for somewhat reduced mortalities caused by the 4 m beam trawl with a chain mat compared with the similar gear with ticklers, which suggests a less deep disturbance of the seabed by the former.

Direct mortality in some infaunal species (*E. cordatum*, some bivalves) was higher in silty areas than in sandy areas (Table 3), which may reflect a deeper penetration of beam trawls into a softer seabed.

Most of the larger-sized species that appeared to be more resistant to trawling (Table 4) were relatively robust (e.g., *Astropecten irregularis*, *O. texturata*, *C. gallina*, *Corbula gibba*), or burrow deeply into the sediment (*Ensis* spp.). In studies in the Western Baltic, robust bivalve species such as *Corbula* and *Astarte* were mentioned as having a high mechanical resistance in contracts with trawl doors (Rumohr and Krost, 1991). Most species in the group with the highest vulnerability were fragile (*E. cordatum*, *Phaxas pellucidus*, *M. corallina*), or live in the uppermost layer of the sediment, within reach of the trawl (*Spisula* spp.). In studies in Strangford Lough (Northern Ireland), the epibenthic bivalve *Modiolus modiolus* also showed high mortality due to scallop dredging (Brown, 1989). Apart from the species mentioned in Tables 2 and 3, we observed many other species, but their abundances were too low to estimate their vulnerability. We expect that those species that live within reach of the tickler chains, and that are not robust, will suffer significant fishing mortalities. Moreover, Mensink *et al.* (2000) conclude that even a robust species like the common whelk (*Buccinum undatum*) suffers considerable fisheries-induced mortality, because about 55% of the animals caught in a 12 m beam trawl died within six weeks.

In general, small species tend to show relatively low direct mortalities compared with larger species (Tables 2 and 3). Even within species such as *C. gallina* and *A. aculeata*, smaller individuals tend to show lower mortality than larger ones. In the Irish Sea, individuals of *D. lupinus* and *Mysia undata* collected after trawling tended to be smaller than those found before trawling, suggesting that smaller individuals showed lower direct mortality (Lindeboom and de Groot, 1998). Small individuals of *E. cordatum* (5–10 mm) occurring at a depth of 2–4 cm showed a direct mortality of 55% after three passes with 12 beam trawls (Bergman and Hup, 1992). Apparently a considerable fraction of the juvenile population was swept up undamaged. The generally lower direct mortality for smaller individuals is probably related to the type of impact of the gear. A trawl affects small-sized benthos mainly by perturbation of the sediment (which is comparable to natural disturbances, like storms), whereas it affects larger-sized benthos mainly through direct physical contact. Thus, the relatively low impact of trawling on benthos inhabiting mobile sediments suggested by Kaiser and Spencer (1996) might apply to small animals, for which the passage of a trawl is more or less similar to the natural disturbances to which these animals are adapted. For larger animals, however, the impact caused by contact with the gear is not comparable to any natural disturbance, and mortalities in mobile sediments should not necessarily be lower than in stable sediments. This view is supported by the considerable mortality (21 to 47%) found for *S. subtruncata* (1.5–3 cm) in the shallow coastal zone. The higher mortality of infaunal species like *C. gallina* in stable silty areas compared with those in mobile sandy areas is more likely related to a deeper penetration of beam trawls into a softer seabed.

Direct mortality within a species may vary not only in relation to size, but also in relation to sex and density. Short-legged female *C. cassivelaunus* living deeper than 3 cm in the seabed apparently are better protected against the impact of trawling than long-legged males walking about on the seabed. The density-dependent mortality observed in *S. subtruncata* cannot be easily explained because there may be other confounding factors.

The estimated fishing mortality on megafaunal populations in the Dutch sector ranged from 5 to 39%, with half the number of species showing mortalities higher than 20% (Table 5). For species living predominantly in silty offshore areas and for those occurring in all types of sediments, the impact of trawl fisheries other than the 12 m beam-trawl fisheries was very small, which reflects both size and distribution of the various fleets. For species restricted to sandy coastal areas, where the 4 m beam-trawl fishery was concentrated, mortality was distributed more equally among the beam-trawl fleets (e.g., *Spisula* spp.). In the 12 mile zone, where large beam trawls are not allowed, mortality could even become higher for the 4 m beamers. The low fishing mortality caused by the fleet using 4 m beams rigged with chains (for all species less than 0.5%) is due to the spatial distribution of this effort, which was restricted to the two southernmost rectangles where none of the selected species occurred in high densities. The fishing mortality caused by otter-trawl fisheries tended to be slightly lower than those caused by the small beam-trawl fleet.

Despite annual fishing mortalities of 5 up to 39%, the species investigated have apparently been able to maintain the present population density. Nevertheless, relative abundance of species may have changed owing to trawling activities over the last decades, and more vulnerable species may have become rare or may even have disappeared from certain parts of the southern North Sea. Analyses of historical data sets on occurrence, abundance, and catchability of invertebrate species gave indications of long-term impacts of fisheries. Demersal fisheries are thought to be responsible for the decreasing abundances of a number of bivalve species (*Ostrea edulis*, *M. modiolus*, *Arctica islandica*), edible crab (*Cancer pagurus*), lobster (*Homarus gammarus*), gastropods (*B. undatum*), anthozoa (*Alcyonium* spp.), sponges (*Halichondria* spp.), and tube-building polychaetes (*Pectinaria* spp.) (Cadée *et al.*, 1995; Lindeboom and de Groot, 1998). Generally, these are infaunal and epifaunal species that live within reach of the groundrope and tickler chains, and are likely to suffer significant direct mortality due to trawling. Modelling results suggest that the observed decline in stocks of crabs, lobsters, urchins, and gastropods are related to the changes in type of bottom trawl (otter trawl vs. beam trawl) and fishing effort (Philippart, 1998). In other fishing areas evidence is provided of broad-scale changes in benthic communities that can be directly related to commercial fishing. Results from a study in Loch Gareloch (western Scotland) indicated that sessile anthozoan species were adversely affected by trawling, while in general, opportunists increased in abundance (Lindeboom and de Groot, 1998). In Hauraki Gulf (New Zealand), with decreasing fishing pressure an increase was demonstrated in densities of echinoderms, long-lived surface dwellers, large epifauna, total number of species and individuals, and the Shannon–Wiener diversity index. In addition, there were decreases in the densities of deposit-feeders and small opportunists (Trush *et al.*, 1998). Since such fishery-related long-term changes in benthic communities are observed around the world, the reduction of this impact needs to play a role in discussions on the development of sustainable fisheries (Bergman and Lindeboom, 1999; Bergman and van Santbrink, 2000). Analyses of life-history characteristics are required to determine the long-term impact of fishing mortality on population structure and spatial distribution of faunal species.

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