

A quantitative evaluation of the impact of beam trawling on benthic fauna in the southern North Sea

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Piet, G. J., Rijnsdorp, A. D., Bergman, M. J. N., van Santbrink, J. W., Craeymeersch, J., and Buijs, J. 2000. A quantitative evaluation of the impact of beam trawling on benthic fauna in the southern North Sea. – ICES Journal of Marine Science, 57: 1332–1339.

Data on density of benthos species and on direct mortality caused by the passing of a beam trawl, together with fishing effort data for the Dutch beam-trawl fleet, were used to evaluate the annual population mortality caused by beam trawling in the Dutch sector of the North Sea. The effects of using environmental strata, instead of ICES rectangles for density distributions, and of using higher-resolution fishing-effort data on the population mortality estimates of 21 infauna and epifauna species were investigated. Variation in species abundance was markedly smaller based on sediment-depth strata than based on ICES rectangles, and the resulting population mortality estimates differed significantly among species (ratio ranged from 0.3 to 1.6) depending on the overlap of the spatial distribution of a species and of beam-trawl effort. Changing the resolution of fishing effort from ICES rectangles or sediment-depth strata to 1' minute latitude \times 2' minute longitude square ($\pm 1 \times 1$ nm) resulted in a systematic reduction of population mortality by a factor 0.7 due to the patchy effort distribution. We argue that annual fishing mortality should preferably be based on relevant environmental strata, and accuracy of the estimates increases markedly when the resolution of spatial fishing effort data sufficiently reflects the patchiness of the fleet's activities.

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Key words: beam trawl, benthos, ecotopes, environmental characteristics, fishing mortality, micro-distribution.

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Introduction

There is growing concern about the effects of bottom-trawling activities on the marine ecosystem (ICES, 1988). All mobile bottom gears scrape the surface of, or dig into, the seabed to varying degrees. The penetration depth largely depends on seabed and gear characteristics (Margetts and Bridger, 1971; Bridger, 1972; de Groot, 1972). Benthic invertebrate species, or different life stages within species, often differ in their vertical position in the substratum and/or in their fragility. Therefore, differences in vulnerability to trawling can be expected within the benthic fauna (Houghton *et al.*, 1971; Bergman and Hup, 1992; Lindeboom and de Groot, 1998), and vulnerability may depend to some extent on the type of sediment. Lindeboom and de

Groot (1998) estimated the direct mortality of various species by experimental trawling in the southern North Sea, taking account of the integrated effects of their vulnerability and vertical distribution. Because of the increase with regard to number of vessels, engine power, weight of gear, and fishing speed since the 1960s, the beam-trawl fleet in particular has been blamed for having a considerable direct impact, not only on the substratum, but also on non-target fish and benthic invertebrates.

At the population level, the annual mortality generated by a fishing depends on the direct mortality generated by each fishing event and on the overlap in spatial distribution between species and fishing effort. Duineveld *et al.*, (1991) showed that the distribution of benthic invertebrates in the southern North Sea was

related to sediment characteristics and water depth. The distribution of beam trawling will be affected by the distribution of the target species, the suitability of the seabed for fishing (stones or muddy areas may be avoided), the occurrence of physical obstacles such as wrecks and oil rigs, and the location of shipping lanes. In a study of the micro-distribution of beam-trawl vessels, *Rijnsdorp et al. (1998)* showed that beam trawling was highly patchy. For instance, in eight of the most heavily fished ICES rectangles (30' latitude \times 1° longitude), 10% of the seabed was trawled less than once every five years, 33% less than once per year, and 3% more than 10 times per year.

We evaluate four approaches to estimating the annual fishing mortality caused by the Dutch beam-trawl fleet for a selection of invertebrate megafaunal species for which data on direct mortality and spatial distribution were available. The approaches compare the effect of using: (1) environmental strata based on depth and sediment grain size instead of ICES rectangles for both faunal and effort distribution; and of using (2) a high (approximately 1 \times 1 nm) or low (mean per stratum or rectangle) resolution of fishing effort distribution.

Material and methods

Beam-trawl effort

Effort data for the total Dutch fleet are routinely collected on a spatial scale of ICES rectangle (30' min latitude \times 1° longitude; \pm 30 \times 30 nm; *Rijnsdorp et al., 1998*). Two vessel classes were distinguished based on engine power: \leq 300 Hp (class 1) and $>$ 300 Hp (class 2). Class 1 vessels are rigged with two 4 m beam trawls, and fishing speed is on average 4.2 knots (1 knot=1852 m h⁻¹). Class 2 vessels are rigged with two 12 m beam trawls, and fishing speed is on average 5.9 knots. The average effort by ICES rectangle and class was determined for the period 1993 until 1998.

The micro-distribution of beam trawling has been studied since 1993 in a sample of about 24 vessels of class 2 (\pm 10% of the Dutch fleet) and one vessel of class 1. In 1996 the sampling was extended and now comprises six class 1 vessels. Fishing positions are recorded every six minutes at an accuracy of 180 m using an Automatic Position Registration device (*Rijnsdorp et al., 1998*). The effort distribution of the sample over a 1 \times 1 nm square grid within each ICES rectangle was raised to the effort of the total Dutch fleet fishing in that rectangle.

The frequency of F (y⁻¹) with which an ICES rectangle was trawled was calculated for each Hp-class separately according to:

$$F = (D \times S \times FH \times 2W) / (30 \times 30 \times A_s \times SP), \quad (1)$$

where D =days away from port during sampling period SP (six years); S =fishing speed; FH =average duration of a fishing day (17 h for class 1, 18.7 for class 2); and W =beam-trawl width. One ICES rectangle consists of 30 \times 30 rectangle of 2' min longitude \times 1' min latitude (\pm 1 \times 1 nm). The area of one square A_s (in m²) was calculated as $1 \times 2 \times [\cos(\pi \times Lu/180) + \cos(\pi \times Ll/180)] \times 1852^2$ where Lu and Ll are the upper and lower latitudinal positions of the rectangle, respectively. The total trawling frequency is the sum of the estimates for the two Hp classes.

The procedure for the calculation of beam-trawl effort at a resolution of 1 \times 1 nm squares based on Automatic Position Registration is described by *Rijnsdorp et al. (1998)*. The same two Hp classes were distinguished. The frequency with which a 1 \times 1 nm square was trawled was calculated according to:

$$F = [(RF/10) \times (TF/TS) + S + 2W] / (A_s \times SP),$$

where $RF/10$ =total number of hours recorded fishing in a particular square (recordings are taken every six minutes); TF =total number of fishing hours of the Dutch fleet in the ICES rectangle in which the square is located; TS =total number of fishing hours of the sampled fleet in that ICES rectangle; and other symbols as in equation (1). Class 1 vessels do not employ beam-trawl gear to target flatfish throughout the year, but may switch to other gear types when fishing for shrimp or roundfish. The data distinguish between gear type used and record for each vessel the total catch per fishing trip. With this information, only registrations of those trips that employed the beam trawl were selected.

Environmental strata

Data on grain-size distribution of the sediment in the Dutch sector of the North Sea were obtained from the TNO Department of Geology. Four grain-size classes were distinguished according to the Wentworth scale: (1) very fine sand, <0.125 mm; (2) fine sand, 0.125 mm and <0.25 mm; (3) medium sand, 0.25 mm and <0.5 mm; and (4) coarse sand, ≥ 0.5 mm. Data on the depth distribution were obtained from the RWS North Sea Directorate. Some 11 5 m depth classes were distinguished (0–5, 5–10, ..., >50). The grain-size/water depth at the centre of each square was assumed to be representative of the entire square.

Megafauna

Megafauna (>1 cm; belonging to both infauna and epifauna) were sampled at 110 stations spread out over the Dutch sector in 1997 (*Bergman and van Santbrink, 1998*). Sediment grain size and water depth at each station were derived from the environmental data set at

Table 1. Estimated direct mortality (%; proportion of initial density in the trawl track) of benthic invertebrates in two types of sediment after an average trawling frequency of 1.5. Based on Lindeboom and de Groot (1998).

Code	Scientific name	English name	Direct mortality	
			Sand	Soft
abral	<i>Abra alba</i>		39	39
aphac	<i>Aphrodita aculeata</i>	Sea mouse	38	38
arcis	<i>Arctica islandica</i>	Quahog	16	16
astir	<i>Astropecten irregularis</i>	Burrowing starfish	45	22
chagl	<i>Chamelea gallina</i>	Striped venus >2 cm	7	40
chags	<i>Chamelea gallina</i>	Striped venus <2 cm	7	6
corcj	<i>Corystes cassivelaunus</i>	Masked crab juvenile	63	63
corcm	<i>Corystes cassivelaunus</i>	Masked crab male	48	27
corcf	<i>Corystes cassivelaunus</i>	Masked crab female	22	26
doslu	<i>Dosinia lupinus</i>	Smooth artemis	44	44
enssp	<i>Ensis</i> spp.	Razor shells	13	3
eusca	<i>Euspira catena</i>	Large necklace shell	61	61
garfe	<i>Gari fervensis</i>	Sunset shell	81	81
macco	<i>Macra corallina</i>	Rayed-through shell	11	28
ophte	<i>Ophiura texturata</i>	Brittle star	6	6
pelco	<i>Pelonaia corrugata</i>		18	18
phape	<i>Phaxas pellucidus</i>		15	38
spiso	<i>Spisula solida</i>	Thick-through shell	31	31
spisu	<i>Spisula subtruncata</i>	Cut-through shell	21	21
thisc	<i>Thia scutellata</i>	Thumb-nail crab	22	22
turco	<i>Turritella communis</i>	Tower shell	14	14

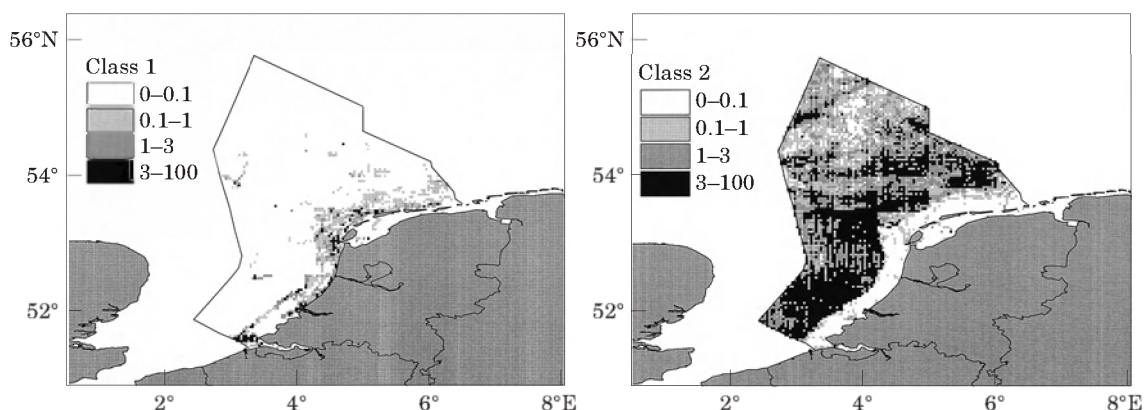


Figure 1. Spatial distribution of the Dutch beam-trawl fishery in the Dutch sector of the North Sea distinguished according to engine power: (a) Class 1 (engine power ≤ 300 Hp); (b) Class 2 (engine power > 300 Hp).

a 1×1 nm square resolution. Direct mortality estimates for 18 invertebrate species (Table 1) were based on Lindeboom and de Groot (1998). For *Chamelea gallina*, a distinction was made between larger and smaller specimens, while for *Corystes cassivelaunus*, juveniles and sexes were distinguished. For some species separate estimates of direct mortality were available for coarse (grain size > 0.175 mm) and fine sediment (grain size < 0.175 mm). If only a single estimate was available, direct mortality was assumed to be independent of sediment type. The direct mortality estimates reflect the mortality caused by a trawl frequency of 1.5 (the second

tow half overlapping the first) and are expressed as a fraction of the initial density in the seabed.

Estimates of annual fishing mortality in the populations of each species (class) in the Dutch sector of the North Sea were based on the distribution of the species, the direct mortality estimates, and the distribution of total Dutch beam-trawl effort. When estimating population fishing mortality by ICES rectangle or per sediment-depth stratum, the distribution of species within these strata was assumed to be homogeneous. For each type of stratification, the effort distribution by stratum and at a 1×1 nm resolution was applied. In the

latter case, effort was consequently heterogeneous within those strata.

The numerical abundance of each species by ICES rectangle or sediment-depth stratum was estimated by averaging the densities (N per 100 m²) from the available benthos sampling data in each stratum. For those ICES rectangles or sediment-depth strata in which more than one sampling station was located, the standard error of the numerical abundance was determined. The average standard error per species is considered as an indication of the suitability of the stratification to represent the abundance of that species.

In the calculations of the annual population fishing mortality, the fishing mortality (F_i) was first estimated at each spatial window i (either a stratum or a 1×1 nm square):

$$F_i = 1 - (1 - M)^{0.67T_i},$$

where M =direct mortality after trawling an area on average 1.5 times (Table 1) and T_i =trawling frequency (y^{-1}) in window i . The factor 0.67 is required to correct for the direct mortality estimates that were derived after a trawling frequency of 1.5. The correction makes the results directly comparable with the estimates of annual fishing mortality in 1994 (Bergman and van Santbrink, 2000). The total fishing mortality F over the Dutch sector of the North Sea was calculated as the average weighted by the density of the species in window i (N_i):

$$F = \sum_i F_i \times N_i / \sum_i N_i.$$

Results

The overall level and the micro-distribution of the beam-trawl effort clearly differed between Hp-classes (Fig. 1). The smaller vessels constituted a relatively small part of the total fishing effort and generally fished in coastal waters, whereas the larger ones fished in offshore waters and along the borders of the 12 mile zone and the plaice box. Consequently, the distribution of recordings in relation to depth and sediment (Table 2) also differed between Hp classes. Notably the distribution of fishing activities of the larger vessels in the northern part follows the contours of the sediment (Fig. 2), suggesting that the distribution of the fleet is related to environmental characteristics.

The frequency distribution of beam-trawl intensity estimated at a resolution of 1×1 nm is shown for the eight most important sediment/depth strata in terms of area covered (Fig. 3). Within each stratum, beam-trawl intensity was not distributed homogeneously; the level of heterogeneity differed markedly between strata. For example, the cumulative frequency distributions show that the deeper waters (>30 m) with sediments of

Table 2. Surface area (in nm²), number of benthos sampling stations (#), and mean trawling frequency (yr^{-1}) of two engine-power classes (Hp1: ≤ 300 Hp; Hp2: >300 Hp) per sediment-depth stratum.

Strata		Surface	#	Trawling frequency	
Sediment	Depth			Hp1	Hp2
0	5	3		3.3	0.1
0	10	4	1	0.6	0.1
0	15	15		1.3	0.2
0	20	3		0.3	0.0
0	25	65		0.2	0.0
0	30	158		0.2	1.9
0	35	598	2	0.1	1.3
0	40	1178	6	0.1	1.1
0	45	1506	16	0.0	0.8
0	50	1815	23	0.0	0.9
1	5	171	2	0.3	0.1
1	10	244	4	1.0	0.0
1	15	243	1	0.7	0.1
1	20	330	2	0.3	0.0
1	25	1214	3	0.3	1.8
1	30	2564	11	0.1	2.1
1	35	1643	9	0.1	1.3
1	40	1077	6	0.0	1.2
1	45	816	11	0.0	1.2
1	50	434	1	0.0	1.3
2	5	31		0.3	0.0
2	10	53		1.1	0.0
2	15	140		1.0	0.5
2	20	394	1	0.3	0.6
2	25	1364	6	0.5	2.9
2	30	811	3	0.2	2.0
2	35	483	2	0.0	2.2
2	40	176		0.1	1.4
2	45	80		0.0	1.0
2	50	38		0.0	0.6
3	10	6		0.9	0.0
3	15	17		1.1	0.1
3	20	8		1.3	0.0
3	25	10		0.5	0.4
3	30	1		1.6	0.0
3	35	3		0.0	1.1
3	40	4		0.0	1.5
3	45	2		0.0	0.4

medium sands are more intensively fished with about 38% of the surface trawled less than once a year. In contrast, 65% (depth <40 m) and 69% (depth 40 m) of the surface of the whole depth range of sediments with very fine sand were trawled less than once a year.

Not all sediment depth strata were covered by the benthos-sampling programme (Table 2). The sampled strata, however, made up more than 95% of the area of the Dutch sector. The estimated densities of species per sediment-depth stratum are given in Table 3. The estimated densities clearly differ between strata; some species occur mainly in a specific sediment type (e.g. *Ensis* spp. or *Spisula*), while others seem to be restricted to a specific depth range.

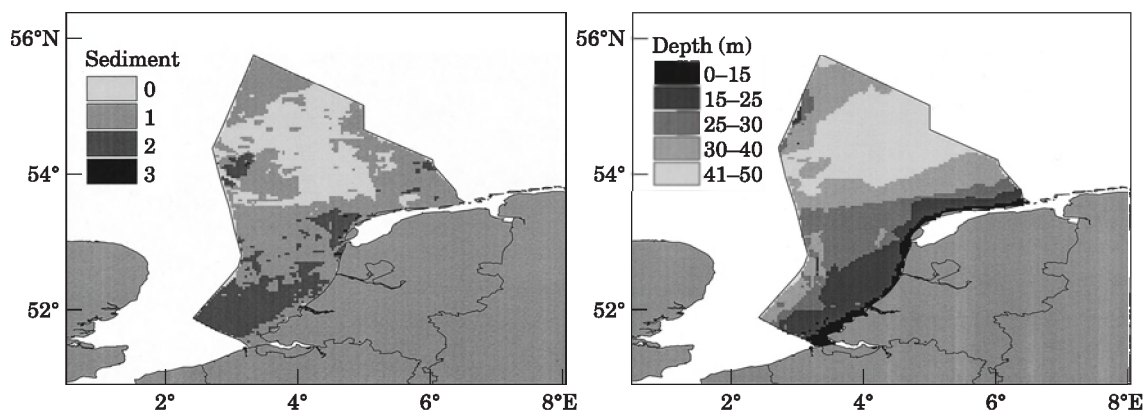


Figure 2. Strata in the Dutch sector of the North Sea used: (a) sediment grain size (0, very fine sand; 1, fine sand; 2, medium sand; 3, coarse sand); (b) depth.

Comparison of the average standard error of abundance, when stratified according to ICES rectangles versus sediment-depth strata, shows generally lower values for the stratification based on environmental characteristics (Table 4A). This indicates that for most species this stratification is more appropriate. The only two exceptions were *Euspira catena* and *Spisula solida*.

The annual fishing mortality estimated for individual species differed considerably depending on the approach used (Table 4B). For most species, the estimates based on sediment-depth strata were slightly higher (average 0.45) than those based on ICES rectangles (average 0.42). For *Gari fervensis*, mortality was even approximately 50% higher. At the other extreme, mortality of *Spisula subtruncata*, based on sediment-depth strata, was less than 50% of the mortality based on ICES rectangles. Fishing mortality was significantly ($p < 0.001$) lower when calculated using fishing effort at a 1×1 nm resolution. The annual fishing mortality based on higher effort resolution or sediment-depth strata and ICES rectangles were on average a factor 0.61 and 0.63, respectively, lower than when a homogeneous fishing intensity for the entire stratum or ICES rectangle was assumed.

Discussion

The abundance and distribution of benthic fauna is highly dependent on sediment characteristics (e.g. grain size and silt content) and other environmental variables such as water depth and temperature (Duineveld et al., 1991). This is confirmed by the observation that variation in species abundance was markedly smaller when based on environmental strata than when based on ICES rectangles. However, the environmental variables available to distinguish different strata were restricted to depth and grain size. Moreover, because not all strata present were sampled, the estimates of species density

and spatial distribution employed should be considered as a first approximation. The estimates may be improved by an increased sampling effort of the benthic fauna and by collecting additional environmental variables at a sufficiently high resolution.

The mortality estimates based on fishing effort at 1×1 nm resolution were calculated from the micro-distribution data for a subsample of the Dutch fleet, and raised to the average number of fishing days of the fleet in the period 1993–1998. However, during the first years, only one class 1 vessel (<300 Hp) was sampled, and only from 1996 onwards was this number increased to six. Therefore, the data for this category may not be representative, and the absolute values of the mortality estimates should be considered only as preliminary.

The annual fishing mortalities of benthic invertebrate megafauna estimated at the resolution of ICES rectangles are comparable to those found by Lindeboom and de Groot (1998). Those estimated for ICES rectangles based on 1×1 nm resolution for the fishing effort are, on average, similar to the estimates by Bergman and van Santbrink (2000), who allowed for a heterogeneous distribution of fishing effort by arbitrarily allocating effort to nine sub-rectangles within an ICES rectangle. However, when considering individual species, marked differences can be observed between these studies. The overall similarity is remarkable, considering that Lindeboom and de Groot (1998) and Bergman and van Santbrink (2000) analysed the impact of the combined effort of the Dutch, Belgian, German, and British fleets, whereas our study was based on the effort of the Dutch fleet only. Another difference lies in the assumption of the proportion of a day at sea spent fishing. We assumed that each fishing day comprised 17.0 (class 1) or 18.7 (class 2) fishing hours, whereas the other estimates were based on the work by Pope et al. (2000), who used an average of 13.6 h trawling per day at sea based on information from discard trips. Because the Dutch fleet

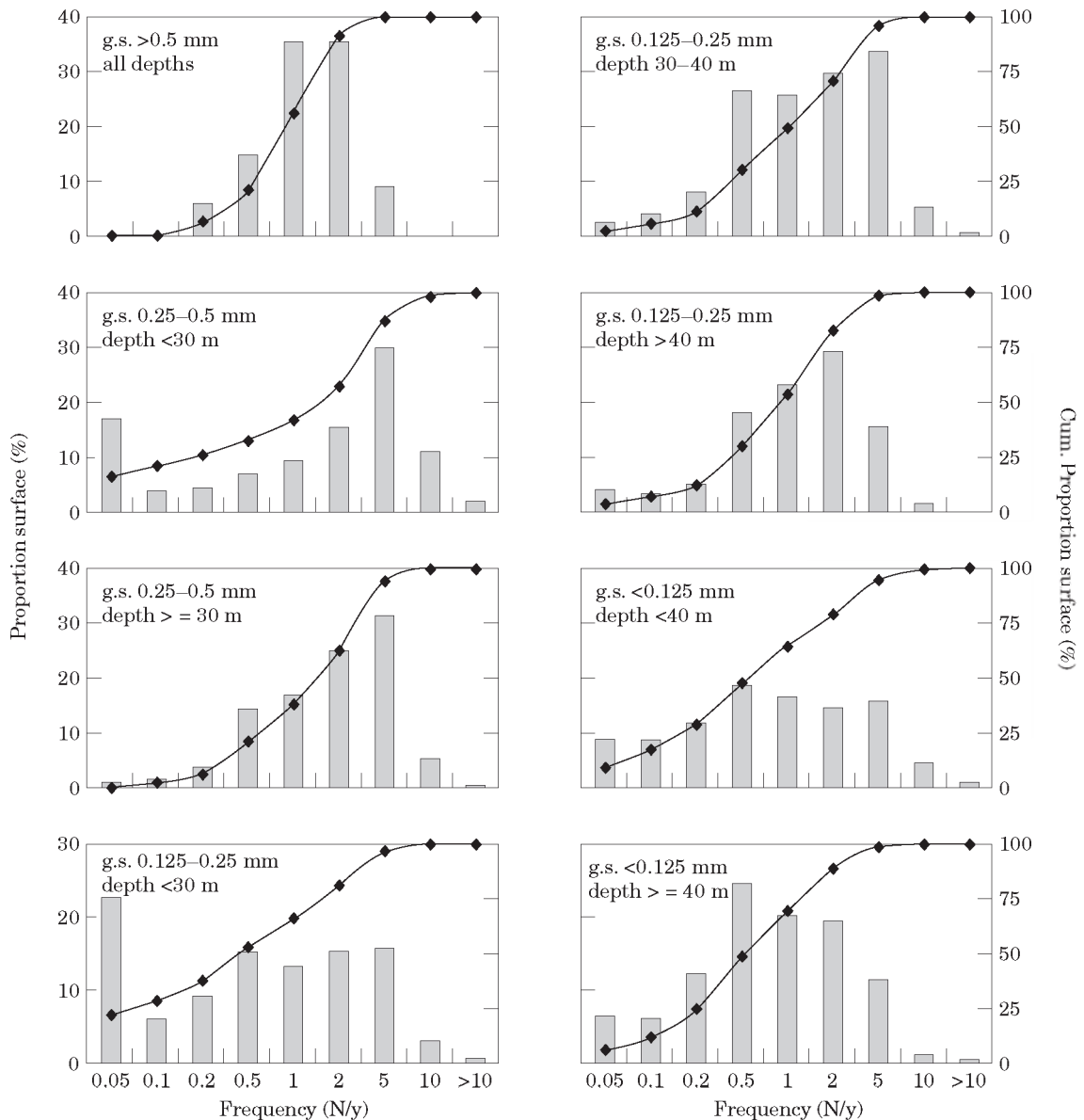


Figure 3. Beam-trawl frequency of total Dutch fleet within eight ecotopes defined by grain size (g.s.) and depth in the Dutch sector of the North Sea. Left y-axis is for the absolute proportion of the surface (bars), right y-axis for the cumulative proportion of the surface (lines).

is responsible for over 85% of the fishing effort in the Dutch sector, the higher estimate of hours trawling per day at sea apparently compensates for the lower estimate of the total number of days at sea.

The fishing mortality based on environmental strata differed considerably from the fishing mortality based on ICES rectangles, at least for some species. This can be explained to a large extent by the fact that both the benthos densities and the beam-trawl effort distribution seem to follow the environmental strata. This suggests that the spatial distribution of the fish that are targeted

by the fleet is determined by the same environmental variables that determine the spatial distribution of the benthic species selected.

The observation that these species still occur in the southern North Sea, in spite of estimated annual fishing mortalities over 50%, suggests that their populations are sustainable at the present level of additional mortality caused by beam trawling. This, of course, is no guarantee that all benthic invertebrate species originally present have been able to withstand these levels of fishing mortality. Presumably the species selected possessed

Table 3. Estimated densities of benthic invertebrate species per sediment-depth stratum (for species codes see Table 1; for sediment and depth classes see Table 2).

Strata																			
Sediment	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2
Depth	10	35	40	45	50	5	10	15	20	25	30	35	40	45	50	20	25	30	35
Code	Densities (N/100 m ²)																		
abral	0	0	10	2	2	0	0	0	0	0	0	2	12	1	7	0	0	1	0
aphac	0	0	10	8	19	0	0	0	0	0	0	0	6	7	26	0	0	0	0
arcis	0	0	4	4	12	0	0	0	0	0	0	2	5	1	0	0	0	0	0
astir	0	174	31	43	43	0	0	0	0	2	10	16	79	29	59	0	0	0	0
chagl	0	26	78	31	20	0	0	4	0	1	10	35	30	43	26	4	1	0	0
chags	0	33	20	12	12	0	0	0	0	6	12	24	20	18	40	0	0	0	0
corej	0	11	28	14	8	0	0	0	0	0	1	8	29	13	15	0	0	0	0
corem	0	39	29	17	7	0	0	0	0	1	12	21	12	22	11	4	1	0	0
coref	0	39	72	77	38	0	0	0	0	2	29	56	38	59	55	0	3	11	0
doslu	0	4	49	21	19	0	0	0	0	0	0	6	7	35	44	0	0	0	0
enssp	1188	4	1	2	1	574	589	1303	403	52	114	94	34	1	0	244	348	37	0
eusca	0	0	0	0	0	7	0	0	0	54	33	2	1	0	0	0	0	0	0
garfe	0	0	1	1	1	0	0	0	0	0	3	21	1	2	0	0	0	0	0
macco	0	0	0	0	0	0	4	0	0	0	1	1	0	0	0	0	0	0	0
ophite	2	1	16	3	8	0	6	24	173	13	55	79	8	3	0	2	6	2	23
pelco	0	0	3	5	8	0	0	0	0	0	0	0	2	1	0	0	0	0	0
phape	0	0	7	2	7	0	0	0	0	0	0	3	40	3	7	0	0	0	0
spiso	0	0	0	0	0	0	0	0	0	39	0	0	0	0	0	0	9	0	4
spisu	37	0	1	0	1	415	1428	20 148	15 1500	2	0	4	7	0	0	485	129	0	0
thisc	0	0	0	0	0	0	4	0	0	42	11	28	0	0	0	19	28	15	78
turco	0	11	378	110	97	0	0	0	0	1	0	0	164	34	26	0	0	0	0

life-history characteristics (e.g. early reproduction, high reproductive rate, and low longevity) that enabled them to maintain a population in spite of the beam-trawling activities. Densities of species that do not possess such life-history characteristics might have decreased because of commercial trawling earlier this century (Lindeboom and de Groot, 1998) to such low levels that they could not be used in this study. Another explanation for the persistence of some species follows from the observation that fishing mortality decreases when a higher resolution of the spatial distribution of fishing effort is applied. This decrease is caused by the fact that the micro-distribution of beam-trawling activities is patchy (Rijnsdorp *et al.*, 1998). Even in the most heavily trawled ecotopes about 57% of the area was fished less than once a year. This may have provided refuges that allowed species to survive, whereas in the case of an even distribution of trawling intensity they might have disappeared.

The calculated annual fishing mortalities should be considered maximum estimates for species whose direct mortality depends on the time interval between successive fishing events. For species that live buried in the sediment, such as *Arctica islandica*, the actual direct mortality after one fishing event may be lower than the estimated mortality based on an experiment in which two successive, partly overlapping tows (within two hours) were made, because only the second fishing event is expected to result in a substantial mortality of the

Table 4. A: Average standard error of the abundance per species when stratified according to ICES rectangles (rect) and sediment-depth strata (S-D). B: Annual fishing mortality estimates for the Dutch sector for the two types of stratification, when a homogeneous (low-resolution: LR) and when a heterogeneous (high-resolution: HR; 1 × 1 nm) fishing effort distribution was applied (for species codes see Table 1).

Code	A: Standard error		B: Fishing mortality			
	Rect	S-D	Rect		S-D	
			LR	HR	LR	HR
abral	3.1	2.6	35	27	35	22
aphac	5.2	3.2	29	20	34	21
arcis	2.5	2.0	15	11	14	9
astir	19.4	11.2	20	15	24	16
chagag	14.1	7.7	30	20	30	19
chagal	6.8	6.4	5	4	6	5
corcaj	7.0	7.1	53	35	59	35
corcam	5.5	3.6	28	19	33	22
corcav	12.8	9.1	22	16	24	16
doslu	9.5	6.0	41	26	40	24
enssp	100.0	81.9	13	12	16	13
eusca	6.6	13.8	68	44	70	50
garfe	4.0	2.5	45	31	79	50
macco	1.5	1.3	16	12	16	13
ophite	20.1	11.8	6	6	6	6
pelco	3.0	1.8	16	12	15	10
phape	11.9	8.0	21	18	31	20
spiso	16.2	21.9	43	29	40	32
spisu	3768.6	173.5	25	22	9	8
thisc	19.0	13.0	31	24	29	24
turco	48.4	45.1	16	11	12	8

animals that have been dug out of the sediment during the first event. However, this effect cannot be evaluated because data on the time interval between successive commercial trawling events on a particular patch are not available. Information from the fishery suggests that skippers try to fish close to previous fishing positions, but also try to avoid fishing exactly the same position. To what extent organisms are able within these time intervals to reposition themselves in the sediment remains unclear.

Our general conclusion is that as long as high-resolution data on distribution of benthic species and fishing effort are not available, aggregation based on relevant environmental characteristics is preferable to that on statistical rectangles. However, high-resolution data on the distribution of fishing activities provide systematically lower estimates of annual fishing mortality of non-target species, which are considered more realistic because the heterogeneous distribution of fishing effort is incorporated.

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