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Long-term impact of bottom fisheries on several by-catch species of demersal fish and benthic invertebrates in the south-eastern North Sea

Catharina J. M. Philippart

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Within the last few decades, the main bottom fishery in the south-eastern North Sea has changed from otter to beam trawling with beam trawling effort increasing from 1960 onwards. During this period, the Zoological Station in Den Helder (The Netherlands) has collected and registered by-catch species caught by commercial fishermen. The annual numbers of registered specimens were used to estimate the species-specific catch efficiencies of otter and beam trawlers between 1945 and 1983. This analysis was restricted to 7 fishes (sharks, rays, skates) and 10 invertebrate species (whelks, urchins, squids, crabs) all of which have a demersal life style and were regularly delivered throughout the study period.

For most species, the observed variations in annual numbers of fish and invertebrates delivered to the Zoological Station appeared to be related to the changes in type of gear and fishing effort. Results from the model suggest that otter trawlers caught relatively more fish than invertebrates, whilst beam trawlers caught proportionally more invertebrate species (i.e. velvet swimming crab, slender spindle shell) that were rarely delivered during periods of greatest otter trawling effort. On average, the catch efficiency of the beam trawl fleet appeared to be 10 times higher than that of the otter trawl fleet. Furthermore, the trends shown by the model in species delivered suggested that bottom fisheries had a considerable impact on several demersal fish and benthic invertebrates.

Key words: otter trawl catch efficiency, beam trawl catch efficiency, by-catch species, North Sea.

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C. J. M. Philippart: Netherlands Institute for Sea Research, Department of Marine Ecology, PO Box 59, 1790 AB Den Burg (Texel), The Netherlands. Tel: +21 222 369 563; fax: +21 222 319 674; e-mail: katja@nioz.nl

Introduction

The impacts of fisheries on seabed communities have increased considerably since the industrialization of the fleet at the beginning of this century. By 1930, sailing vessels and steam trawlers in the south-eastern North Sea had been largely replaced by motor trawlers (Polet, unpublished data). The first Dutch otter trawlers appeared in 1910 and their numbers had increased to a maximum of over 500 vessels by 1940. The development of beam trawling for flatfish began just after the Second World War, but effort remained insignificant until the beginning of the 1960s. The maximum number of beam trawlers occurred around 1970, but beam trawl effort peaked in 1988 as a result of an increase in effort per vessel (Rijnsdorp and van Leeuwen, 1994).

The long-term effects of bottom fisheries on benthic marine ecosystems remain a point of debate (de Groot, 1984; Jones, 1992; Hall, 1994; Dayton *et al.*, 1995). Investigations by means of experimental trawling showed that bottom fisheries increase the mortality not only of both target and by-catch species (Duineveld *et al.*, 1987; Kaiser and Spencer, 1996a), but also of benthic species that are not caught in the nets but damaged by the passing fishing gear (Bergman and Hup, 1992; Eleftheriou and Robertson, 1992; Bergman and van Santbrink, 1994; Thrush *et al.*, 1995; Currie and Parry, 1996). In general, large long-lived species with a low fecundity, such as bivalves, are more likely to be adversely affected than small short-lived species with high fecundity, such as polychaetes. On the other hand, fisheries may be beneficial for scavenging species if their

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increased mortality is counterbalanced by an increasing food supply from discarded offal, by-catch and damaged animals in trawl tracks (Fonds and Groenewold, 1996; Kaiser and Spencer, 1996b).

The effect of bottom fisheries on particular demersal fish and benthic invertebrates depends on the action of fishing gear in relation to the vertical distribution of the species. In otter trawls, the ground-rope glides over the seabed whereas beam trawls are fitted with heavy tickler chains. The chains cause the target flatfish species to leave the bottom which results in their capture. Consequently, otter trawls catch mainly demersal fish and epifaunal invertebrates whereas beam trawls also catch infauna (Creutzberg *et al.*, 1987), i.e. those animals that live within the upper-layer of the sediment (approx. 5 cm).

The evaluation of the long-term effects of bottom fisheries on benthic ecosystems are problematic as (i) most experimental work refers to short-term effects, i.e. immediate changes in abundance after one or several trawls (Bergman and Hup, 1992; Trush *et al.*, 1995; Ramsay *et al.*, 1996), and (ii) consistent long-term datasets that record the abundance of non-commercial species are scarce, as non-commercial species are often ignored in fisheries research. Scientific surveys in the Dutch coastal zone that included by-catch fish and invertebrates did not start before the early 1970s, i.e. after a long period of intensive fishing (e.g. van Leeuwen *et al.*, 1994; Heessen, 1996). Subsequently, longer-term or earlier effects of bottom fisheries on demersal by-catch species have to be extracted from available time series, even though the data may not have been collected for this purpose.

In 1930, the Zoological Station in Den Helder (now the Netherlands Institute for Sea Research on Texel) started a scheme to collect information on the distribution and abundance of North Sea species, caught as by-catch by commercial fishermen. For every specimen, the species name, date, sampling location and registration number of the vessel were noted. The archive was continued until 1993, and data were, as much as possible, obtained in the same way during these 60 years (de Vooys and van der Meer, 1997). In the present paper, the trend in numbers of animals delivered to the Zoological Station is examined to see whether or not it may reflect the trend in their abundance in the sampling area after correction for fishing effort and species-specific catch efficiency of otter and beam trawlers.

Material and methods

Selection of species, sampling area and study period

Specimens were delivered by fishermen either by request (e.g. to be sold to universities for experimental purposes) or when a rare or unknown species was caught. In all cases the individuals were bought by the institute. For commercial species an amount about equal to the market price was paid, while non-commercial species and specimens were bought for a set price.

The present analysis was restricted to those by-catch species (Table 1) that (i) have a demersal life style, and (ii) were considered to be regularly delivered to the Zoological Station during the entire sampling period, i.e. the demand of the institute for these species was consistent through time and specimens were never rejected by the employees of the station (de Vooys *et al.*, 1991, 1993; de Vooys and van der Meer, 1997). Note that due to the fact that the animals were not sampled on a scientific basis, consistency of the dataset can never be guaranteed.

All specimens originated from an area located northwest of the Netherlands, between 3° to 7° East and 52° to 55° North (Fig. 1). The study period for the present analysis had to be restricted compared to the entire sampling period. First, due to a change in collection of the by-catch data and a suspicion of change in the behaviour of fishermen in delivering animals to the Zoological Station, the data from 1983 onwards are thought to be inconsistent with those from former years. Second, the use of a catch-efficiency model made it necessary to restrict the study period to one without missing values, i.e. the period following the Second World War. For the remaining period, the time series of total annual numbers of animals were smoothed by taking 5-year running averages to diminish the noise of year-to-year variation and subsequently emphasize the long-term trends between 1947 and 1981. Note that as a consequence of smoothing the by-catch data, the model results will only be indicative of long-term trends in abundance, and thus possible short-term effects due to events such as severe winters will be obscured.

Fishing effort

Fishing effort (E) is related to the number of vessels and the effort per vessel, e.g. the number of fishing hours, the type of fishing gear and the power of the engines (usually expressed in horsepower). Data on the number of vessels were available from national statistics. Unfortunately, data on the actual effort per vessel are scarce, incomplete and sometimes not even correct (ICES, 1995). The technological developments during the last centuries have had a profound effect on the types of fishing gear deployed in the North Sea. Effort data that do not take this aspect into account have, therefore, to be interpreted with caution.

Fishing effort of otter trawling (E_1) was available as the number of otter trawl vessels at 5 year intervals from 1946 to 1990 (Polet, unpublished data). Estimates of mean annual otter trawl fishing effort were calculated by

Table 1. Scientific name, common name and vertical distribution of by-catch species of demersal fish and benthic invertebrates delivered to the Zoological Station by commercial fishermen between 1945 and 1981.

Scientific name	Common name	Vertical distribution
FISH		
Mustelus mustelus*	Smooth hound	Demersal shark
*Scyliorhinus canicula**	Lesser-spotted dogfish	Demersal shark
*Raja clavata**	Roker	Demersal ray
*Raja batis**	Common skate	Demersal skate
*Dasyatis pastinaca**	Stingray	Diel burying demersal ray
*Trachinus draco**	Greater weever	Diel burying demersal fish
*Lophius piscatorius**	Anglerfish	Burying demersal fish
INVERTEBRATES		
*Buccinum undatum**	Common whelk	Burying epifauna
neptunea antiqua	Red whelk	Burying epifauna
Colbus gracilis	Slender spindle shell	Burying epifauna
*Loligo vulgaris**	Common European squid	Demersal epifauna
Eledone cirrosa	Lesser octopus	Swimming epifauna
*Homarus gammarus**	European lobster	Diel burying epifauna
*Nephrops norvegicus**	Norway lobster	Diel burying epifauna
*Cancer pagurus**	Edible crab	Diel burying epifauna
Liocarcinus puber	Velvet swimming crab	(Swimming) epifauna
Corystes cassivelaunus	Masked crab	Diel burying epifauna
Psammechinus miliaris	Green sea urchin	Non-burying epifauna
Spatangus purpureus	Purple heart urchin	Burying epifauna
Tealia felina	Dahlia anemone	Sessile epifauna
Aphrodite aculeata	Sea mouse	Shallow burying epifauna

*Also targeted by commerical fisheries.

linear interpolation of these numbers, smoothed by the 5-year running averages. For this type of fishing gear it had to be assumed that the fishing effort per vessel had not changed during the study period, i.e. from 1945 to 1983.

Fishing effort of beam trawling (E_2) was available in horsepower days, i.e. the number of fishing days of the Dutch beam trawl fleet multiplied by the total engine power (HP) of those vessels (Rijnsdorp and van Leeuwen, 1994). Mean annual beam trawler effort was also smoothed by taking 5-year running averages.

Both the fishing effort of otter (E_1) and beam (E_2) trawling was scaled to 1 (Fig. 2) by dividing the effort in a particular year ($E_{j,t}$) by the maximum effort during the post-war period of the specific type of fishing gear:

$$e_{j,t} = E_{j,t}/E_{j,t=\max}$$

whereas the maximum efforts after the Second World War are

$E_{1,1958} = 210$ vessels in 1958 for otter trawling,
$E_{2,1988} = 692\ 10^5$ HP days in 1988 for beam trawling.

Sampling effort

The composition of the fleet involved in sampling this kind of by-catch was assumed to be similar to that of the entire Dutch fleet (e.g. an equal ratio between otter and beam trawlers and similar fishing effort per vessel) and the fraction of the sampling fleet compared to the total Dutch fleet was assumed to be constant.

When delivering by-catch to the Zoological Station, the registration numbers of the providing vessels were consistently noted from the early 1950s onwards. This record indicated that over 250 different vessels were involved. Most ships originated from the ports of Den Helder, Texel and Wieringen and only a few ships came from other ports. Some ships delivered animals haphazardly whilst others showed a more consistent delivery pattern over time. Between 1952 and 1990, 1088 of the total of 4177 by-catches of invertebrates (i.e. more than 25%) were delivered in a regular fashion by 7 vessels. Within the study period, the annual numbers of the main fishing vessels involved remained at the same level of about 40 to 60 ships (de Vooys and van der Meer, 1997). Most specimens were therefore delivered by a small group of fishermen who appeared to be consistent in bringing all caught specimens of particular species to the Zoological Station.

Catch-efficiency model

The number of animals in an area can change as a result of birth, mortality, immigration and emigration. For the present, Model I assumed that immigration and

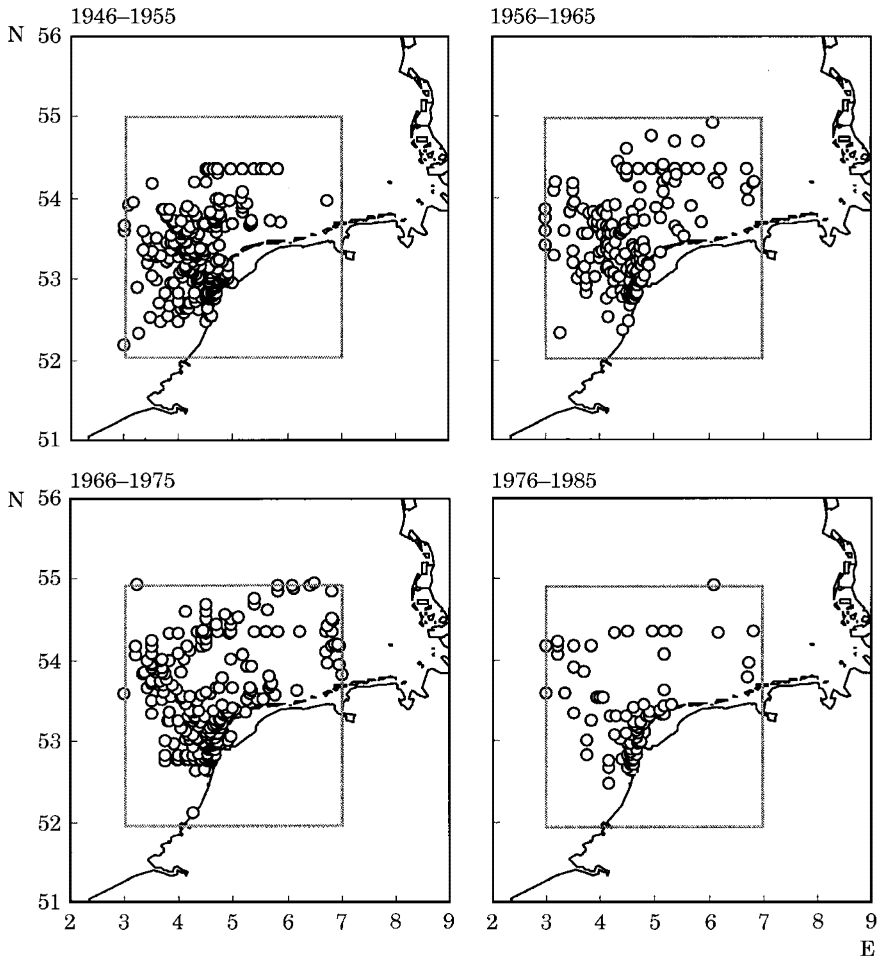


Figure 1. Location of sampling locations (○) within sampling area of by-catch species (rectangle) of benthic invertebrates delivered to the Zoological Station by commercial fishermen between 1946–1955, 1956–1965, 1966–1975 and 1976–1985.

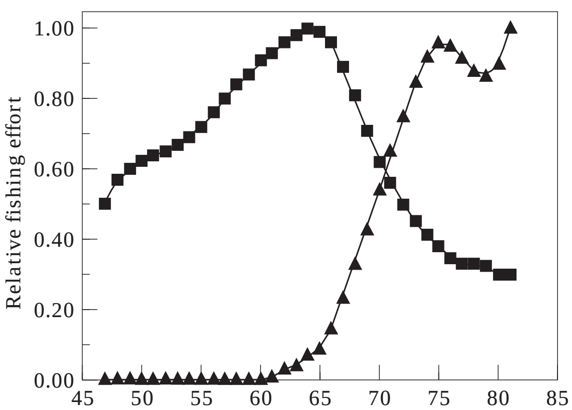


Figure 2. Running averages (5 years) of relative fishing effort of the Dutch fleet expressed as the relative number of otter trawlers (black squares) and the amount of HP days of 10^5 of beam trawlers (black triangles) as used in the catch-efficiency model.

emigration did not occur and that birth rate was equal to natural death rate. Other, less restrictive assumptions resulted in severe parameter estimation problems. Note that due to these assumptions, population sizes of the by-catch species could not increase during the study period, and were bound to decrease if animals were caught.

The expected number of animals caught in a particular year (B_t) was assumed to equal the total number of animals present at the beginning of a particular year (N_t) multiplied by the fishing mortality during that year (F_t). So, for the first year $B_1 = F_1 \cdot N_1$. As the number of animals at the start of a particular year equals the exploitable population size at the beginning of the previous year minus the number of animals caught during that previous year, i.e. $N_{t+1} = N_t - B_t$, the expected catch for the second year can be written as $B_2 = F_2 \cdot N_2 = F_2(N_1 - B_1) = F_2(1 - F_1)N_1$. Similarly, the expected catch for all other years j can be written as a function of the fishing mortalities and the initial abundance:

$$B_j = F_j \cdot \prod_{k=1}^{j-1} (1 - F_k) \cdot N_1.$$

The fishing mortality in a specific year (F_j) equals the fishing effort of otter trawlers (X_j) and beam trawlers (Y_j) multiplied by the gear-specific catch efficiency coefficients of the otter (q_1) and beam trawler (q_2), respectively: $F_j = q_1 X_j + q_2 Y_j$.

The three unknown parameters, i.e. the otter trawl catch efficiency coefficient (q_1), the beam trawl catch efficiency coefficient (q_2) and the number of animals that were present at the beginning of the study period (N_1), were estimated by minimizing the sum of the squared residuals, i.e. the differences between the observed and expected catches. The STEM software package, which uses a Nelder-Mead (Simplex) procedure for minimization, was applied (ReMeDy, 1990). The programme also provides 95% confidence intervals under the assumption that the catch data were independently and identically normally distributed.

If one of the catch efficiency parameters approached zero and at the same time the correlation between two out of three parameter estimates was high, i.e. was almost 1, then this particular parameter was set to 0, and only the remaining two parameters were estimated.

Results

Model fits

The catch-efficiency model appeared to fit for most of the demersal fish and benthic invertebrates (Figs 3 and 4) with the exception of the purple heart urchin. The model results of Norway lobster, masked crab and sea mouse were thought to be unreliable because correlations between parameter estimates were high, i.e. >0.9 (Table 2). Broad patterns in the variation in numbers of by-catch appeared therefore to be reasonably well described by a model that included the variation in gear and effort of bottom trawlers and decrease due to fisheries for 17 out of the 21 species considered.

Otter trawl catch efficiency

Otter trawl catch efficiency was set to zero for the slender spindle shell and velvet swimming crab. These invertebrates were rarely delivered to the Zoological Station by commercial fishermen before 1960 (Fig. 4) which implies that they were not caught in the otter trawls. For all other species, the otter trawl catch efficiency estimates ranged between 0.07 and 0.31 $N\ N^{-1}\ e^{-1}\ y^{-1}$ for fish, and between 0.01 and 0.06 $N\ N^{-1}\ e^{-1}\ y^{-1}$ for invertebrates (Table 2).

According to the model results, otter trawling appeared to have resulted in an about 95% decline in the exploitable populations of roker and greater weever in the sampling area between 1947 and 1960 (Fig. 5). Smooth hound, common skate and angler fish populations decreased by more than 75%, whilst lesser-spotted dogfish, stingray, European lobster and edible crab decreased by more than 50% during this 14-year period (Fig. 5).

Beam trawl catch efficiency

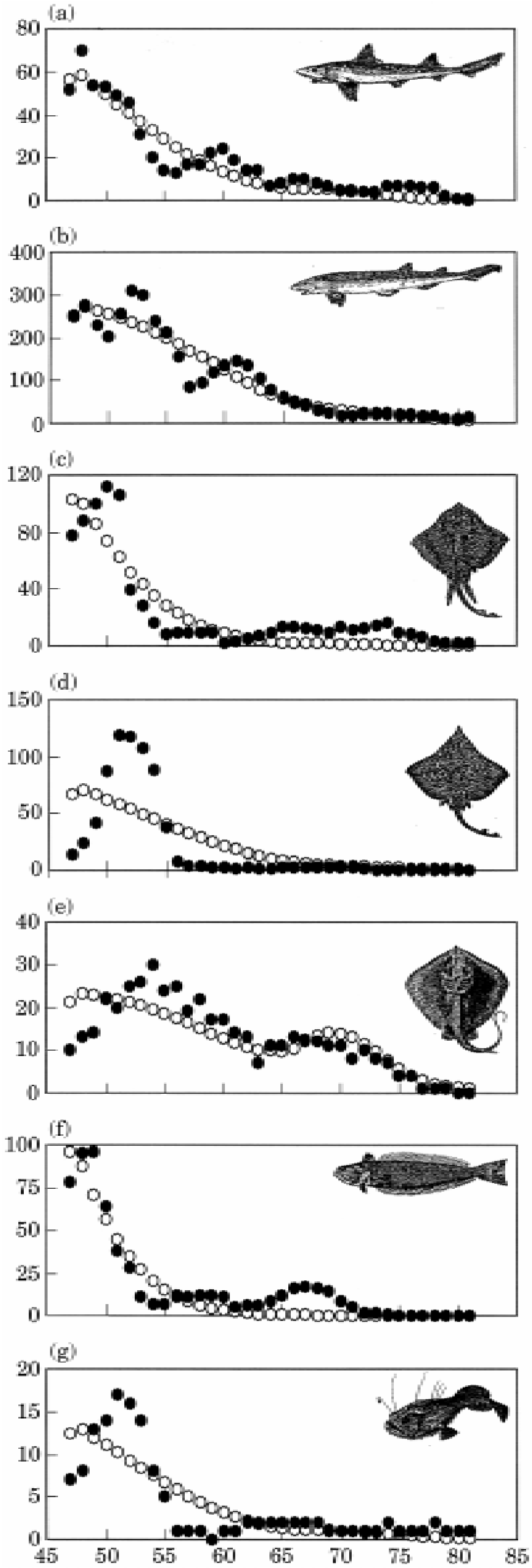
For lesser-spotted dogfish and common skate, the estimate of the beam trawl catch efficiency in the study area was almost zero (Table 2). These low values were most probably due to the fact that, according to the model fits, no specimens of these two fish species were delivered to the Zoological Station after the introduction of the beam trawls. For several other by-catch species (greater weever, common whelk, European lobster, edible crab) the estimate of the beam trawl catch efficiency exceeded $1\ N\ N^{-1}\ e^{-1}\ y^{-1}$ (Table 2). The high value of this estimated parameter implies that the populations of these particular species were reduced to very low abundances before maximum beam trawl effort occurred in the sampling area, i.e. before 1988. With the exception of the common whelk, these species were indeed rarely delivered from the mid-1970s onwards (Fig. 4). For all remaining species, beam trawl catch efficiency ranged from 0.18 $N\ N^{-1}\ e^{-1}\ y^{-1}$ for common European squid to 0.47 $N\ N^{-1}\ e^{-1}\ y^{-1}$ for roker (Table 2).

According to the model results, the slender spindle shell, velvet swimming crab and dahlia anemone were hardly affected by otter trawling but rapidly declined from 1960 onwards to less than 20% of the original population size at the end of the study period (Fig. 5). In addition, the increase in beam trawling coincided with a further reduction of smooth hound, roker, stingray, anglerfish, red whelk and lesser octopus to less than 5% of their original abundance in 1947 (Fig. 5).

Discussion

Model assumptions

In this study, the catch efficiency was set equal to fishing mortality for the species under consideration. It was therefore assumed that all specimens of interest that were caught in the nets were delivered to the Zoological Station, and none were marketed or discarded by the fishermen. The model did not include the possibility that undersized animals were discarded and subsequently survived the catch, nor that animals that were merely present in the area were killed by the passing fishing gear. The latter assumptions seem reasonable for most fish species. In general, the survival chances of flatfish and roundfish that are caught in the nets and discarded



are nil (Fonds, 1994). For non-commercial invertebrates, however, part of the discarded by-catch may survive and additional non-catch mortality may have occurred for commercial and non-commercial invertebrate specimens alike (Bergman and Hup, 1992; Bergman and van Santbrink, 1994; Kaiser and Spencer, 1996a).

Other assumptions in the catch-efficiency model were that (i) migration was absent and (ii) that birth rate equalled natural mortality. These assumptions are rather unlikely. Mobile fish and invertebrates will have migrated into and out of the area. For example, stingray is a southern species that migrates through the Channel into the Dutch coastal zone during spring, resulting in a regular new supply of animals in the study area. Recruitment of by-catch species is expected to increase when the population is reduced (e.g. Myers *et al.*, 1996), i.e. when the conditions change from relatively unexploited to heavily exploited by fisheries. Unfortunately, estimation of additional parameters, such as migration and density-dependent birth rates, was not possible because this resulted in more significant correlations between parameter estimates.

Results from the model have, therefore, to be interpreted with caution because they are only valid if all assumptions were true, i.e. (i) the sampling procedures were consistent, (ii) the size and composition of the fleet involved in delivering the by-catch to the Zoological Station reflected that of the Dutch fishing fleet, (iii) catch efficiencies equalled fishing mortalities, (iv) migration did not occur, and (v) birth rates were equal to natural mortalities. Although these conditions were probably not met, the historical dataset is so unique that a tentative assessment should be made of long-term trends in abundance of demersal fish and benthic invertebrates in the south-eastern North Sea based on the results from the model.

Long-term trends

For those species for which reliable field data were available, the results from the model of long-term trends in abundance fitted the field data, both for demersal fish and benthic invertebrates.

During the past century, elasmobranchs generally disappeared from the coastal waters along the continent (Rijnsdorp *et al.*, 1996). Between 1951 and 1960, the abundance of roker and common skate decreased considerably off the Dutch coast and both have remained

Figure 3. Five-year running averages (black dots) and model estimates (white dots) of the number of demersal fish species delivered to the Zoological Station by commercial fishermen between 1947 and 1981, (a) smooth hound, (b) lesser-spotted dogfish, (c) roker, (d) common skate, (e) stingray, (f) greater weever, and (g) anglerfish.

Table 2. Parameter estimates (and 95% confidence intervals between parentheses) and correlation coefficients r between parameter estimates for data presented in Figures 3 and 4, where q_1 is the otter trawl catch efficiency, q_2 is the beam trawl catch efficiency and N_1 is the total exploitable population size in the sampling area during the first year of the study period.

Species	q_1 $N N^{-1} e_1^{-1} y^{-1}$	q_2 $N N^{-1} e_2^{-1} y^{-1}$	N_1		r $q_1 q_2$	$q_2 N_0$	$q_1 N_0$
Smooth hound	0.15 (0.03)	0.40 (0.87)	558	(69)	0.33	− 0.29	− 0.75
Lesser-spotted dogfish	0.09 (0.02)	0.00 (0.04)	4267	(635)	0.32	− 0.33	− 0.86
Roker	0.24 (0.06)	0.47 (2.60)	639	(1.22)	0.05	− 0.01	− 0.68
Common skate	0.12 (0.00)	0.00 (0.00)	805	(225)	− 0.60	0.11	− 0.86
Stingray	0.07 (0.01)	0.44 (0.31)	435	(54)	0.37	− 0.41	− 0.41
Greater weever	0.31 (0.07)	1.53 (9.52)	445	(71)	− 0.01	0.01	− 0.74
Anglerfish	0.14 (0.04)	0.23 (0.82)	129	(30)	0.22	− 0.19	− 0.68
Common whelk	0.04 (0.02)	1.37 (1.15)	3822	(1060)	0.47	− 0.58	0.23
Red whelk	0.04 (0.01)	0.36 (0.12)	627	(75)	0.23	− 0.44	− 0.01
Slender spindle shell	0.00	0.20 (0.10)	405	(126)	—	− 0.65	—
Common European squid	0.02 (0.01)	0.18 (0.07)	21 287	(3671)	0.20	− 0.69	0.12
Lesser octopus	0.02 (0.01)	0.33 (0.12)	399	(69)	0.11	− 0.43	0.22
European lobster	0.06 (0.01)	3.26 (1.45)	143	(17)	0.07	− 0.27	0.06
Norway lobster*	0.01 (0.00)	0.05 (0.04)	34 814	(16 487)	0.93	− 0.99	− 0.91
Edible crab	0.06 (0.01)	1.12 (0.53)	1956	(264)	0.23	− 0.15	− 0.04
Velvet swimming crab	0.00	0.21 (0.07)	3274	(667)	—	− 0.62	—
Masked crab*	0.06 (0.07)	0.04 (0.29)	6183	(5828)	0.82	− 0.85	− 0.95
Green sea urchin	0.02 (0.00)	0.28 (0.08)	19 092	(2367)	0.16	− 0.60	− 0.06
Purple heart urchin†	—	—	—		—	—	—
Dahlia anemone	0.01 (0.01)	0.28 (0.08)	19 092	(2367)	0.16	− 0.60	− 0.06
Sea mouse*	0.00	0.01 (0.05)	194 070	(13 836)	—	− 1.00	—

*Correlation coefficient parameter estimates >0.9.
†No fit.

scarce until the present day (Walker and Heessen, 1996). In addition to this decline, the average length of roker also decreased (Walker and Heessen, 1996) which indicates overexploitation by fisheries (Myers *et al.*, 1996).

The greater weever has virtually disappeared from the central and southern North Sea (Rijnsdorp *et al.*, 1996). This species was exploited commercially until the late 1950s but the landings rapidly declined to zero in the early 1960s (de Vooys *et al.*, 1991; Rijnsdorp *et al.*, 1996). This sharp decline of the greater weever is considered to be either an effect of the severe winter of 1962/1963 and/or the introduction of beam trawlers in 1960 (Nijssen and de Groot, 1987; Rijnsdorp *et al.*, 1996). The results of the model suggest that the observed long-term trend for this species could also be attributed to high fishing mortality associated with otter trawling.

From the mid-1920s onwards, the common whelk started to decline and has now completely disappeared from the Dutch Wadden Sea. Whelks from coastal waters have no longer been delivered to Dutch fish auctions since 1970. The disappearance of the common whelk from the western Wadden Sea from the mid-1920s onwards is thought to be caused by fisheries followed by reproduction failures due to tributyltin-based (TBT) antifouling paints that came into use from the early 1970s onwards (ten Hallers-Tjabbes *et al.*, 1994; Cadée *et al.*, 1995).

Based on the number of specimens stranded on Dutch beaches between 1946 and 1985, there appears to have been a decline of several invertebrate species such as the common whelk, common European squid, edible crab, green sea urchin and sea mouse from 1965 onwards in the Dutch coastal waters. Numbers of the velvet swimming crab and the masked crab, on the contrary, that were found stranded appeared to have increased between 1930 and 1985 (Oosterbaan, 1989).

Catch efficiency and vulnerability

There are two main factors influencing long-term changes in distribution and abundance: (i) the species-specific and gear-specific catch efficiency; and (ii) the ultimate effect of this exploitation at the population level for the different species, i.e. vulnerability.

The species-specific catch efficiency of bottom fisheries for demersal fish and benthic invertebrates was expected to depend on the type of fishing gear in relation to the vertical distribution of the species under consideration. It was found that three benthic invertebrates (slender spindle shell, velvet swimming crab and dahlia anemone) were rarely caught by otter trawlers which implies that these species are not vulnerable to this type of fishing gear. This can be because they passed through the codend, were buried deep enough into the sediment to avoid capture in these trawls (e.g. slender spindle shell)

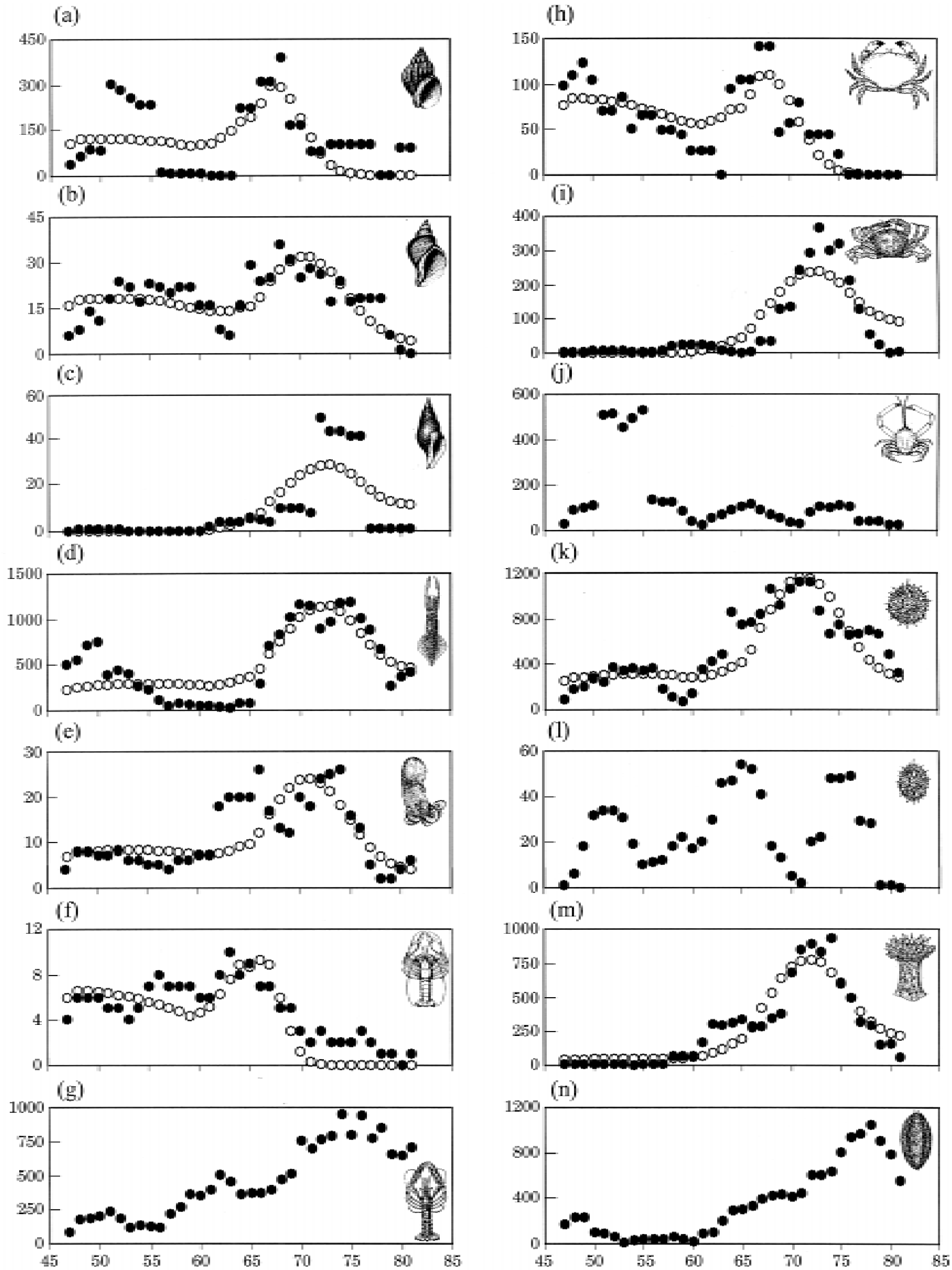


Figure 4. Five-year running averages (black dots) and model estimates (white dots) of the number of benthic invertebrate species delivered to the Zoological Station by commercial fishermen between 1947 and 1981, (a) common whelk, (b) red whelk, (c) slender spindle shell, (d) common European squid, (e) lesser octopus, (f) European lobster, (g) Norway lobster, (h) edible crab, (i) velvet swimming crab, (j) masked crab, (k) green sea urchin, (l) purple heart urchin, (m) dahlia anemone, and (n) sea mouse.

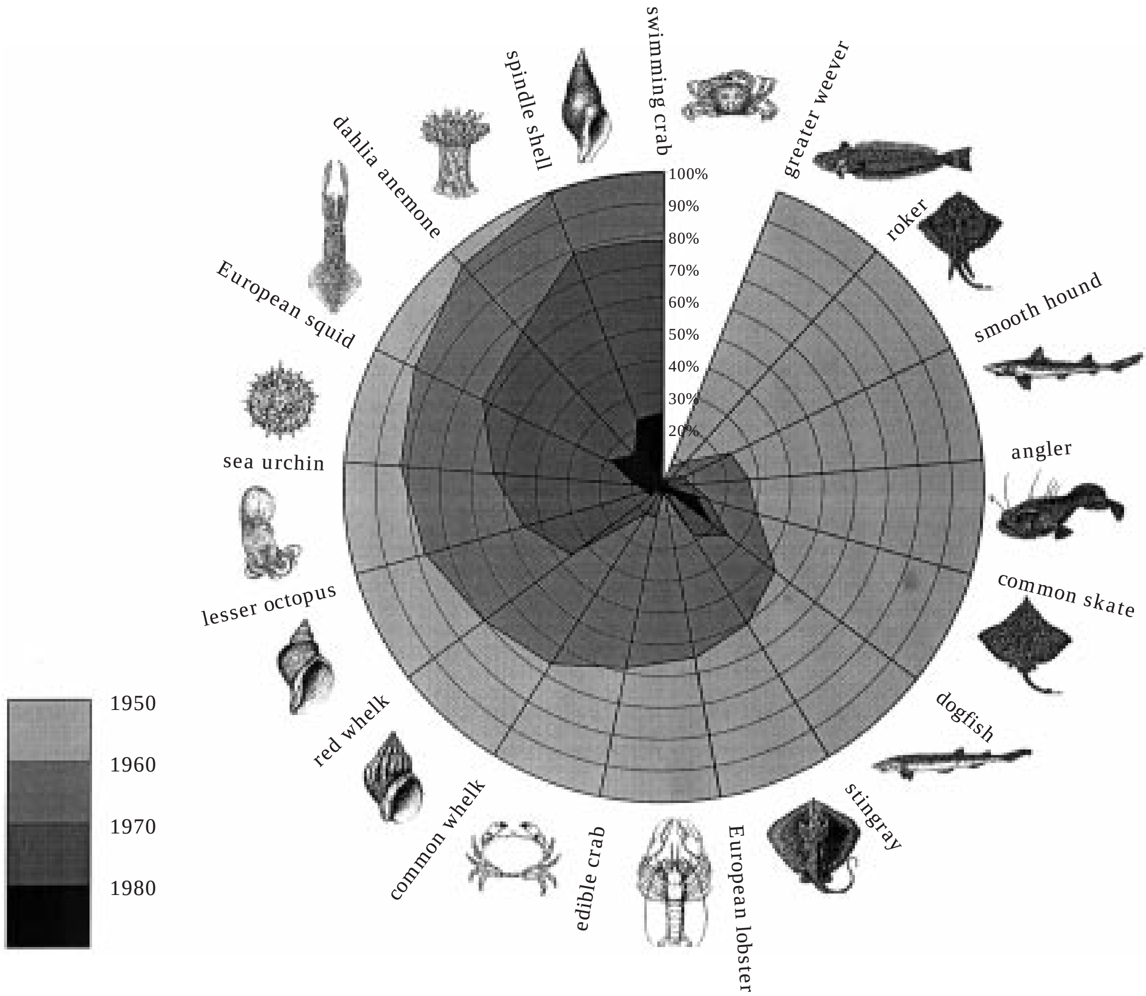


Figure 5. Results from the model of long-term trends in relative abundance of demersal fish and benthic invertebrates in the south-eastern North Sea between 1947 and 1981. Species are ranked from greater weever to swimming crab (clockwise) based on the adverse affection by otter and beam trawling.

or were found in a specific habitat that was rarely fished before the introduction of beam trawling (e.g. dahlia anemone which lives attached to rocks and stones).

The long-term effect of fishing on the population size does not only depend on fishing mortality, but also on how this value relates to the natural mortality under unexploited conditions (M). In general, long-lived species which have a relatively low natural mortality rate are less resilient than short-lived species (Holden, 1977; Brander, 1981). Most selected fish species are long-lived (Table 3) and, therefore, expected to be vulnerable to the fishery pressure in the south-eastern North Sea in particular if fishery-induced egg, hatching and immature mortality are included. For the relatively short-lived greater weever, the total mortality (sum of natural and by-catch mortality) approached $1 \, N \, N^{-1} \, y^{-1}$ which will result in extinction within one year. Note that this species is a catch rather than a by-catch species which implies that mortality due to fisheries may be higher than that derived from the by-catch data.

Furthermore, the probability of additional *in situ* fishery mortality has to be added for benthic invertebrates. If this mortality is more of less equal to the direct by-catch mortality, than the total mortality approximates $1 \, N \, N^{-1} \, y^{-1}$ for most benthic invertebrate species under consideration (Table 3).

In conclusion, the results of the catch-efficiency model suggest that the by-catch records may be used as indicators of the abundance of several demersal fish and benthic invertebrate species after correction for fishing effort by bottom trawlers and making several assumptions on the consistency of the dataset and the population dynamics of the species under consideration. The subsequent estimates of the sizes of the exploitable

Table 3. Maximum age t_{max} (P. A. Walker, J. IJ. Witte and/or M. Fonds, per. comm.), mortality rate of unexploited stock M calculated from maximum age according to Hoenig (1983), average fishing mortality F calculated from results from the catch-efficiency model (this paper), and total mortality Z (=M+F) between 1947 and 1981.

Species	t_{max}	M $N N^{-1} y^{-1}$	F $N N^{-1} y^{-1}$	Z $N N^{-1} y^{-1}$
Smooth hound	35	0.12	0.19	0.31
Lesser-spotted dogfish	25	0.17	0.08*	0.25*
Roker	30	0.14	0.26	0.40
Common skate	50	0.08	0.11*	0.19
Stingray	25	0.17	0.15	0.32
Greater weever	8	0.53	0.37†	0.90†
Anglerfish	25	0.17	0.14	0.31
Common whelk	50	0.13	0.35	0.48
Red whelk	50	0.13	0.11	0.24
Slender spindle shell	50	0.13	0.08§	0.21§
Common European squid	10	0.50	0.06	0.56
Lesser octopus	10	0.50	0.09	0.59
European lobster	20	0.28	0.15	0.43
Edible crab	20	0.28	0.30	0.58
Velvet swimming crab	10	0.50	0.08§	0.58§
Green sea urchin	10	0.50	0.08	0.58
Dahlia anemone	20	0.28	0.07	0.35

*Average fisheries mortality between 1947 and 1959 (mainly due to otter trawling).
†Average fisheries mortality between 1947 and 1972 (species was absent from 1972 onwards).
§Average fisheries mortality between 1960 and 1981 (mainly due to beam trawling).

populations suggest that bottom fisheries have had a considerable impact on the abundance of these by-catch species. Between 1945 and 1960, otter trawlers caught large numbers of by-catch fish such as sharks, rays and skates. The high catch efficiency of these long-lived species appeared to have resulted in a considerable decline of the exploitable stocks in the south-eastern North Sea during this period. The introduction of beam trawling in 1960 seems to have further increased fisheries mortality for fish and in particular for invertebrate species such as whelks, urchins, squids and crabs. This was probably caused not only by an increase of the catch efficiency of this gear for demersal fish and benthic invertebrates (and an increase in total fishing effort), but probably also due to the exploitation of new areas that formerly experienced less fishing effort.

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References

Bergman, M. J. N. and Hup, M. 1992. Direct effects of beamtrawling 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. Direct effects of beam trawling on macrofauna in sandy areas off the Dutch coast. *In* Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Ed. by S. J. de Groot and H. J. Lindeboom. NIOZ Report 1994-11, RIVO-DLO Report C026/94.

Brander, K. 1981. Disappearance of common skate *Raia batis* from Irish Sea. Nature, 290: 48–49.

Cadée, G. C., Boon, J. P., Fischer, C. V., Mensink, B. P., and Hallers-Tjabbes, C. C. 1995. Why the whelk (*Buccinum undatum*) has become extinct in the Dutch Wadden Sea. Netherlands Journal of Sea Research, 34: 337–339.

Currie, D. R. and Parry, G. D. 1996. Effects of scallop dredging on a soft sediment community: a large-scale experimental study. Marine Ecology Progress Series, 134: 131–150.

Cruetzberg, F., Duineveld, G. C. A., and van Noort, G. J. 1987. The effect of different numbers of tickler chains on beam

trawl catches. Journal du Conseil International pour l'Exploration de la Mer, 43: 159–168.
Dayton, P. K., Thrush, S. F., Agardy, M. T., and Hofman, R. J. 1995. Environmental effects of marine fishing. Aquatic Conservation, 5: 205–232.
Duineveld, G. C. A., Künitzer, A., and Heyman, R. P. 1987. *Amphiura filiformis* (Ophiuroidea: Echinodermata) in the North Sea. Distribution, present and former abundance and size composition. Netherlands Journal of Sea Research, 21: 317–329.
Eleftheriou, A. and Robertson, M. R. 1992. The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community. Netherlands Journal of Sea Research, 30: 289–299.
Fonds, M. 1994. Mortality of fish and invertebrates in beam trawl catches and the survival changes of discards. *In* Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Ed. by S. J. de Groot and H. J. Lindeboom. NIOZ Report 1994-11, RIVO-DLO Report C026/94.
Fonds, M. and Groenewold, S. 1996. The production of food for opportunistic scavenging species by beamtrawl fishery in the southern North Sea. *In* Quality Status Report North Sea (in press).
de Groot, S. J. 1984. The impact of bottom trawling on benthic fauna in the North Sea. Ocean Management, 9: 177–190.
Hall, S. J. 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. Oceanography and Marine Biology Annual Review, 32: 179–239.
ten Hallers-Tjabbes, C. G., Kemp, J. M., and Boon, J. P. 1994. Imposex in whelks (*Buccinum undatum*) from the open North Sea: relation to shipping traffic intensities. Marine Pollution Bulletin, 28: 311–313.
Heessen, H. J. L. 1996. Time-series data for a selection of forty fish species caught during the International Bottom Trawl Survey. ICES Journal of Marine Science, 53: 1079–1084.
Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 82: 898–903.
Holden, M. 1977. Elasmobranchs. *In* Fish population dynamics, pp. 187–215. Ed. by J. Gulland. John Wiley and Sons, London, UK.
ICES. 1995. Report of the Study Group on Ecosystem Effects of Fishing Activities. ICES Cooperative Research Report 200.
Jones, J. 1992. Environmental impact of trawling on the seabed: a review. New Zealand Journal of Marine and Freshwater Research, 26: 59–67.
Kaiser, M. J. and Spencer, B. E. 1996a. The effects of beam-trawl disturbance on infaunal communities in different habitats. Journal of Animal Ecology, 65: 348–358.
Kaiser, M. J. and Spencer, B. E. 1996b. The behavioural response of scavengers to beam-trawl disturbance. *In* Aquatic predators and their prey, pp. 116–123. Ed. by S. P. R. Greenstreet and M. L. Tasker. Blackwell Scientific Publications, Oxford, UK.
van Leeuwen, P. I., Rijnsdorp, A. D., and Vingerhoed, B. 1994. Variations in abundance and distribution of demersal fish species in the coastal zone of the south-eastern North Sea between 1980 and 1993. ICES Paper Demersal Fish Committee C.M. 1994/G: 10.
Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1996. Hypotheses for the decline of cod in the North Atlantic. Marine Ecology Progress Series, 138: 293–308.
Nijssen, H. and de Groot, S. J. 1987. De Vissen van Nederland. Stichting Uitgeverij KNNV, Utrecht. 244 pp.
Oosterbaan, A. F. F. 1989. Veranderingen in de Hollandse kustfauna [Changes in the Dutch coastal fauna]. Wetenschappelijke Mededeling KNNV 193. Stichting Uitgevereij KNNV, Utrecht. 60 pp.
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.
ReMeDy. 1990. Simulation Tool of Easy Modelling. Manual, V(2). Enschede.
Rijnsdorp, A. D. and van Leeuwen, P. I. 1994. Changes in growth of North Sea plaice and its relation to density, eutrophication, beam trawl effort and temperature. ICES C.M. 1994/G: 9.
Rijnsdorp, A. D., van Leeuwen, P. I., Daan, N., and Heessen, H. J. L. 1996. Changes of demersal fish species in the North Sea between 1906–1909 and 1990–1995. ICES Journal of Marine Science, 53: 1054–1062.
Thrush, S. F., Hewitt, J. E., Cummings, V. J., and Dayton, P. K. 1995. The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? Marine Ecology Progress Series, 129: 141–150.
de Vooys, C. G. N. and van der Meer, J. 1998. Changes between 1931 and 1990 in by-catches of 27 animal species from the southern North Sea. Journal of Sea Research 39 (in press).
de Vooys, C. G. N., Witte, J. IJ., Dapper, R., van der Meer, J., and van der Veer, H. W. 1991. Lange termijn veranderingen in zeldzame vissoorten op het Nederlands Continentaal Plat van de Noordzee [Long-term changes in uncommon fish species in the south-eastern North Sea]. NIOZ Report 1991-6.
de Vooys, C. G. N., Witte, J. IJ., Dapper, R., van der Meer, J., and van der Veer, H. W. 1993. Lange termijn veranderingen op het Nederlands Continentaal Plat van de Noordzee: trends in evertebraten van 1931–1990 [Long-term changes in the south-eastern North Sea: trends in invertebrates between 1931 and 1990]. NIOZ Report 1993-17.
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.