

Changes in the brown shrimp (*Crangon crangon* L.) population off the Dutch coast in relation to fisheries and phosphate discharge

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Significant changes have occurred in the distribution pattern and recruitment success of brown shrimp (*Crangon crangon* L.) off the Dutch coast and in the fishery for this species between the period 1980–1984 and 1991–1994. The fundamental cause of these changes appears to be the reduction in phosphate discharge to this area, mainly by the river Rhine, which reached a peak in the early 1980s and decreased considerably after 1984. More pronounced changes in the brown shrimp stock have occurred along the Dutch west coast than along the north coast, which is probably related to higher nutrient concentrations on the west coast and the stronger effect of changes in phosphate discharge in this area.

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Key words: brown shrimp (*Crangon crangon*), eutrophication, fisheries, phosphate discharge.

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Introduction

Brown shrimp (*Crangon crangon* L.) is the dominant shrimp species on soft sediment along the European west coast. Historically, commercially important stocks of brown shrimp have only been found in and around estuaries. The significance of estuaries for this species depends on a complex of factors: (1) the larvae make selective use of tidal currents for transport to the shallow and silty estuarine areas suitable for settlement (Boddeke *et al.*, 1986); (2) estuarine production is relatively high compared to open marine beaches due to the natural discharge of nutrients by rivers (Lange and Hummel, 1978; Heip *et al.*, 1995), resulting in ample supply of a variety of prey for a-selective feeders like brown shrimp; (3) brown shrimp is euryhaline, occurring commonly in relatively low salinity waters of 1–5‰ (Havinga, 1930; Boddeke, 1976), while the major predators with the exception of the sand goby (*Pomatoschistus minutus*) are marine fish species (Redeke, 1941). An important invertebrate predator of juvenile shrimps, the swimming crab (*Liocarcinus holsatus*) avoids waters with salinities below 20–25‰ (Venema and Creutzberg, 1973; Bruné, 1988).

Before 1955, the Dutch shrimp fishing was largely restricted to estuaries (Fig. 1) and catches consisted

mainly of small (35–53 mm) shrimps (Boddeke, 1965). Since then several estuaries have been closed by artificial dams (Boddeke, 1978; Nienhuis and Smaal, 1994). However, landings have remained at a comparable level, even through only commercial shrimps >53 mm have been landed since 1971 (Boddeke, 1978). This is partly due to the development of a large stock of brown shrimp along the Dutch west coast since 1965. This stock inhabited an unusually wide zone of up to 40 km, in contrast to the narrow zone where shrimp could be caught along the north coast (Boddeke, 1978). Juveniles are not protected against marine predators in these waters, because salinities along the coast are $\geq 25\text{‰}$ (Anon., 1992). Fishing off the west coast yielded extremely high catches in September–November 1982, when predation pressure was relatively low (Boddeke, 1983).

Eutrophication due to river run-off from the Rhine and Meuse has been considered as a possible causal factor of the enhanced shrimp stock, because the mixed coastal water of marine and fresh water origin moves in a broad band northward along the coast (Visser *et al.*, 1991). Positive effects of eutrophication on brown shrimp stocks have been demonstrated in other areas as well (Boddeke, 1978). Densities of calanoid copepods, the major food resource for juvenile shrimps along the west coast, appear to be greatly enhanced by fertilization (Boddeke *et al.*, 1986; Ohno and Okamura, 1988).

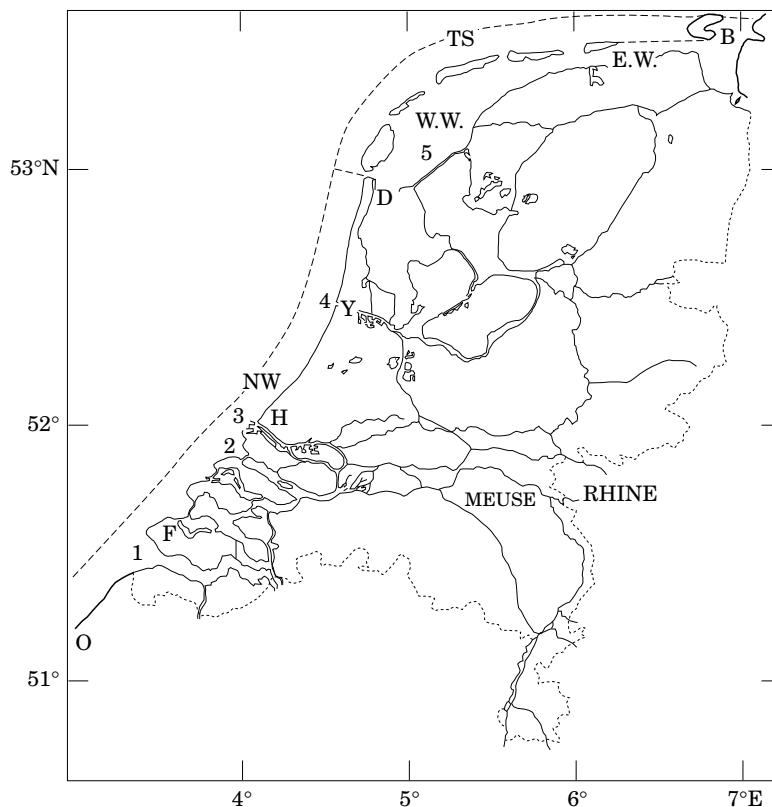


Figure 1. Study area and names and locations referred to in the text (1=Westerscheldt; 2=Haringvliet; 3=Nieuwe Waterweg; 4=Noordzeekanaal; 5=Afluitdijksluizen; NW=Noordwijk; TS=Terschelling; W.W.=Western Wadden Sea; E.W.=Eastern Wadden Sea; B=Borkum; D=Den Helder; F=Flushing; H=Hook of Holland; O=Ostende; Y=IJmuiden).

The discharge of phosphate into the Dutch coastal area reached a peak in 1981 and decreased considerably thereafter (Boddeke and Hagel, 1995), while nitrate discharges have fluctuated with river run-off without any yearly trend. The main purpose of the present study is to elucidate the possible influence of the imbalance in nutrient loads due to phosphate reduction on brown shrimp stocks and fisheries along the Dutch coast.

Materials and methods

Characteristics of the brown shrimp stocks along the Dutch west and north coasts in the early 1980s and 1990s are compared on the basis of various data sets. Distribution patterns in 1980–1982 and 1991–1993 were derived from the Demersal Young Fish Survey (DYFS) in autumn. Methods used in collecting these data have been described by Boddeke *et al.* (1970). Special recruitment surveys carried out in 1984 (Boddeke *et al.*, 1986) were repeated in 1992–1994. Weekly catch statistics of commercial shrimps per fishing day per rectangle are only available since 1983. These data provide detailed information on seasonal changes in the density of

shrimps >53 mm by area, and allow comparison of the situation in 1983–1984 and 1993–1994. Data on recruitment success in 1978–1984 have been given by Boddeke *et al.* (1986) and this information has been updated for recent years.

Data on the discharge of nutrients have been provided by the National Institute for Coastal and Marine Management (RIKZ, The Hague) and the Institute for Inland Water Management and Wastewater Treatment (RIZA, Lelystad).

Results

Distribution patterns and fisheries

Average densities of shrimp >40 mm in autumn 1980–1982 and 1991–1993 in relation to distance from the coast show an exponential relationship, although there is considerable variation caused by patchy distribution (Fig. 2a–d). Particularly along the west coast, the distribution zone was much narrower in 1991–1993 than during the earlier period. Densities in a zone 10 km wide fluctuated greatly in individual years, but average densities were distinctly lower in 1991–1993. This was also the case for commercial shrimps (Fig. 3a, b).

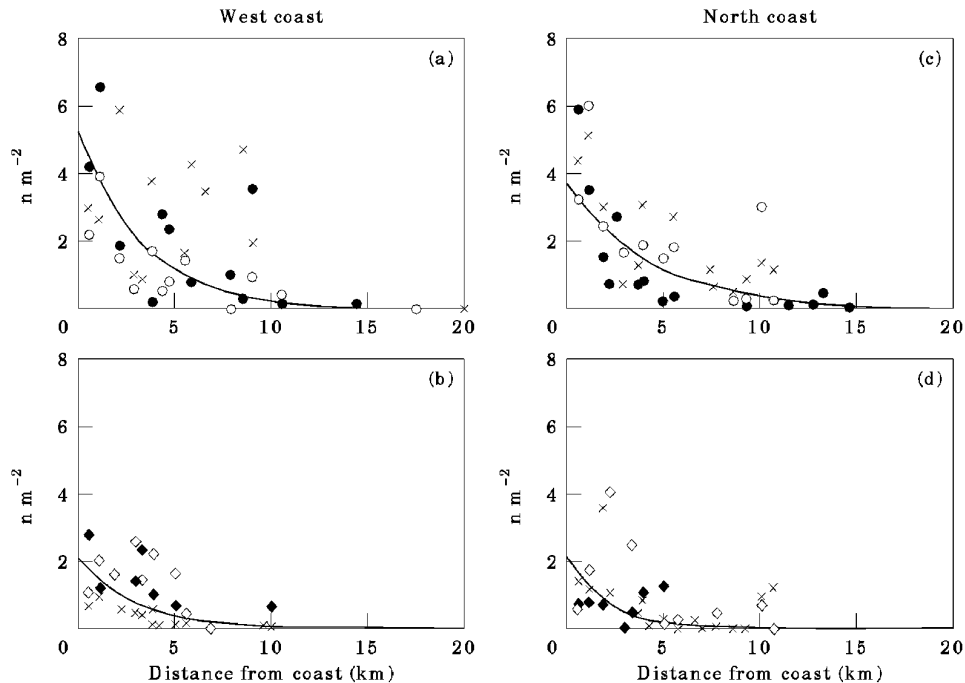


Figure 2. Relation between densities (Y) of shrimp >40 mm and distance from the shore (D). Lines represent fitted exponential relationship. (a) Hook of Holland–IJmuiden 1980–1982: $Y=5.35 \exp(-0.303 D)$; $r^2=0.80$. (b) Hook of Holland–IJmuiden 1991–1993: $Y=2.11 \exp(-0.353 D)$; $r^2=0.41$. (c) Den Helder–Borkum 1980–1982: $Y=3.68 \exp(-0.232 D)$; $r^2=0.55$. (d) Den Helder–Borkum 1991–1993: $Y=2.13 \exp(-0.502 D)$; $r^2=0.27$. (a) and (c): $\bullet=80$; $\circ=81$; $\times=82$. (b) and (d) $\blacklozenge=91$; $\diamond=92$; $\times=93$.

High correlations between densities of commercial shrimps in the surveys and commercial catches per fishing day in corresponding rectangles have been reported in the past (Boddeke, 1982), but the correlation is no longer significant (Table 1). Catches per fishing day along the Dutch west coast remained at the same level during 1991–1994, while average survey densities in the 10 km coastal zone decreased considerably (Table 2).

The differences in average catch rates in autumn 1983–1984 between west and north coasts virtually disappeared in 1993–1994 (Fig. 4). Concentration of fishing effort in a narrow zone may also have resulted in sharper decreases in the concentrations of consumption shrimps in shallow water after their spawning migration in May–June and after recruitment in September–October: the periods of relatively high catches were much shorter in 1993–1994 than in 1983–1984.

Recruitment and growth

Recruitment success has been defined as the ratio between the catch of commercial shrimps per fishing day in month $x+t$ (R) and the number of ripe eggs per fishing day in month x (P), where t is the time it takes for a shrimp to grow from ripe egg to commercial size. In May–July, t is approximately 4 months in Dutch coastal

waters (Boddeke *et al.*, 1986; Beukema, 1992). Along the west coast, the arithmetic mean for P/R was 319 in 1978–1984 and 785 in 1991–1993. Whereas levels of P were comparable, recruitment success was only half (Fig. 5).

Larvae produced in May–July have completely settled to the bottom by August at depths of 5–15 m. Since length distributions at depth hardly varied between August 1992, 1993, and 1994, the average densities by size class during the recent period were compared with those observed during the first week of September 1984 for 5, 10, and 15 m depth, respectively (Fig. 6). Highest densities during the recent period were observed in 1993 and these values are indicated to stress the point that overall densities at all depths were much higher in 1984 than in all recent years. In 1992–1994, average size at 5 m was slightly larger than at 10 and 15 m. This is in contrast with 1984, when average size of brown shrimps increased with depth, as is usually the case in estuaries (Boddeke, 1975).

The 1992–1994 data suggest stunted growth at depths greater than 5 m, where shrimps were still far below the minimum size required for consumption. However, there has been no delay in the increase in catch per fishing day in autumn 1993–1994 compared with 1983–1984 (Fig. 4), suggesting that recruitment in recent years may

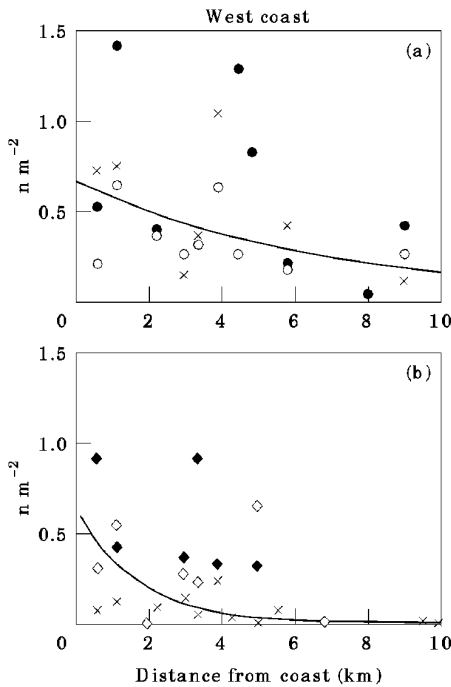


Figure 3. Relation between densities (Y) of commercial shrimps (>54 mm) and distance from the shore (D) between Hook of Holland and Den Helder. Lines represent fitted exponential relationship. (a) 1980–1982: $Y=0.67 \exp(-0.139 D)$; $r^2=0.23$. ●=80; ○=81; ×=82. (b) 1991–1993: $Y=0.64 \exp(-0.608 D)$; $r^2=0.33$. ◆=91; ◇=92; ×=93.

Table 1. Relation between commercial catch rates (C) in kg fishing day⁻¹ and average densities of commercial shrimps (D) in N 1000 m⁻² (DYFS data) per rectangle within 10 km of the west coast in September/October 1980–1982 and 1991–1994.

1980–1982	$C=298+0.50.D$	$R^2=0.72$	n=6
1991–1994	$C=397+0.28.D$	$R^2=0.18$	n=8

stem mainly from depths of less than 10 m. The relatively low abundance of juveniles in August 1993 seems to have had a negative effect on catch and density of commercial shrimps in autumn of that year (Table 2).

Eutrophication

The annual load of total nitrogen of the river Rhine at the German border rose from 3.03 kg s⁻¹ in 1952 to 9.53 kg s⁻¹ in 1961, and has fluctuated since then mainly in connection with river run-off. The load of dissolved PO₄-P (directly usable for phytoplankton) rose from 0.08 kg s⁻¹ in 1952 to a maximum of 1.03 kg s⁻¹ in 1981. After 1984, phosphorous load dropped sharply to an average of 0.16 kg s⁻¹ in 1991–1993, mainly as a consequence of phosphate removal in purification plants in Germany (Heymen, 1992). In The Netherlands, the

Table 2. Densities of shrimps >53 mm (D) in N 1000 m⁻² (DYFS data) and average catch per fishing day (C) of the commercial fleet in kg, within the 10 km zone from the coast during the same weeks in September/October.

	Hook of Holland – IJmuiden		IJmuiden – Den Helder	
	D	C	D	C
1991	560	582	295	386
1992	370	485	250	454
1993	110	322	70	341
1994	129	566	151	590

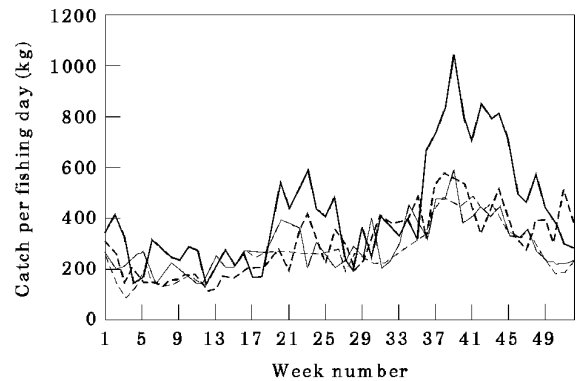


Figure 4. Average weekly catch per fishing day in 1983–1984 and 1993–1994 in the areas Hook of Holland–IJmuiden (a) and Den Helder–Borkum (b). (—)=(a) 83–84; (---)=(a) 93–94; (---)=(b) 83–84; (---)=(b) 93–94.

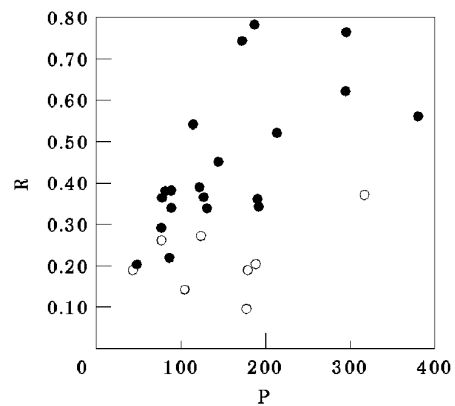


Figure 5. Relation between ripe eggs in May–July (P), and adults >54 mm 4 months later (R), both expressed in numbers caught/fishing day, for the area Hook of Holland–IJmuiden during the periods 1978–1984 and 1991–1993. ●=78–84; ○=91–93.

use of phosphate-free detergents increased rapidly in the late 1980s, becoming 100% by 1989. Discharges of total P by super-phosphate factories along the Nieuwe

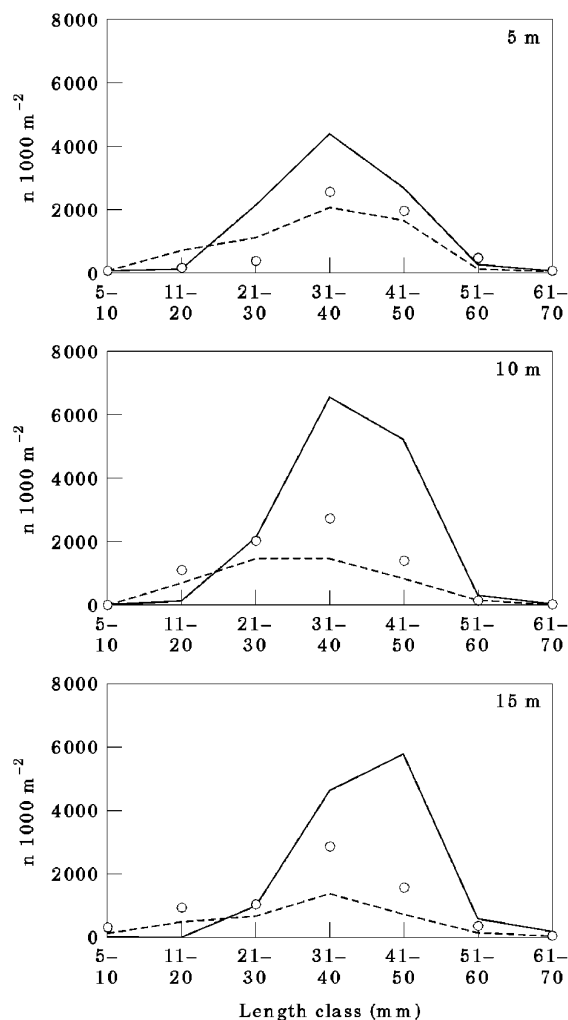


Figure 6. Average densities of juvenile shrimp by three depth zones (5, 10 and 15 m) in August–September between Hook of Holland and Den Helder in 1984 (—) and 1992–1994 (---). Densities in 1993 are indicated by points.

Waterweg decreased from 0.37 kg s^{-1} in 1989 to 0.15 kg s^{-1} in 1992 and to 0.10 kg s^{-1} in 1993 and 1994 (pers. comm. H. v. d. Meulen). Overall, loads of P (uncorrected for retention by the substratum water plants, etc.) discharged into the coastal zone decreased by a factor of 3 between 1981 and 1993 (Table 3). These figures are somewhat higher than those given by the

North Sea Task Force (Anon., 1993), which were corrected for retention (I. de Vries, pers. comm.).

The main mass of nutrients is discharged through Nieuwe Waterweg and Haringvliet (Fig. 1, Table 4) and then transported northwards. The relatively high discharge of phosphate by the Scheldt compared to run-off and the very low discharge of $\text{PO}_4\text{-P}$ through the Afsluitdijk sluices are noteworthy.

Over the period 1960–1990, a linear correlation existed between the load of $\text{PO}_4\text{-P}$ of the river Rhine (x) at the German border and winter concentrations of $\text{PO}_4\text{-P}$ at Noordwijk (y) in the zone 1–30 km offshore ($y=0.0345+2.635x$; $R^2=0.818$; Boddeke and Hagel, 1995). Although the river load has been fairly stable since 1990, $\text{PO}_4\text{-P}$ concentrations in the coastal zone at Noordwijk and Terschelling decreased further, probably as a result of decreased Dutch discharges (Fig. 7). The steep exponential distribution of phosphate over the coastal zone at Noordwijk in the past has become less pronounced in recent years (Fig. 8). The situation of the west coast is similar now to that off Terschelling, although concentrations of phosphate are still lower on the north coast (Meyden, 1991). Because concentrations and patterns of dissolved nitrogen compounds remained unchanged, the annual ratio between dissolved inorganic nitrogen and dissolved inorganic phosphate reached values in 1993 well over 20 at Noordwijk up to 20 km offshore, which is about three times the natural value of 7.2 and indicates a general surplus of nitrogen.

Discussion

The narrowing of the zone in which brown shrimps are abundant along the west coast corresponds very well with the observed changes in phosphate concentration in this area, suggesting that low recruitment success and slower growth at lower densities in recent years may be direct effects of reduced levels of eutrophication. The situation in 1993, when a relatively high abundance of juveniles in August resulted in low catch rates of commercial shrimps in autumn, suggests regulation of the stock by food supply. Narrowing of the commercially fished zone to a few kilometres offshore, as appeared from observations, seems the main reason for the disappearance of the correlation between commercial catches and survey data from a zone of 10 km (Table 1, Fig. 3a, b).

Table 3. Discharge of nutrients to the coastal zone of The Netherlands in kg sec^{-1} (data RIKZ).

	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
$\text{PO}_4\text{-P}$	1.14	1.19	0.99	1.02	0.99	0.80	0.81	0.78	0.85	0.59	0.39	0.32	0.35	0.33
Total P	1.74	1.79	1.48	1.49	1.51	1.20	1.33	1.35	1.56	0.97	0.68	0.64	0.66	0.67
Total N	17.1	19.5	15.9	16.4	18.0	13.6	16.5	20.4	18.8	12.8	10.6	11.1	13.5	11.8

Table 4. Average discharge of nutrients (kg sec^{-1}) and water ($\text{m}^3 \text{sec}^{-1}$) at different outlets in The Netherlands in 1993 (unpublished data RIKZ). Numbers in parentheses correspond with Figure 1. (Rhine run-off in 1993: $2014 \text{ m}^3 \text{sec}^{-1}$; average in 1901–1993: $2238 \text{ m}^3 \text{sec}^{-1}$).

River	Outlet	Total P	%	$\text{PO}_4\text{-P}$	%	Total N	%	Water	%
Scheldt	Westerscheldt (1)	0.07	10.4	0.025	7.6	0.86	7.3	150.4	5.4
Rhine/Meuse	Haringvliet (2)	0.08	11.9	0.05	15.2	2.37	20.0	536.1	19.5
Rhine/Meuse	N. Waterweg (3)	0.42	62.7	0.22	66.6	6.18	52.6	1492.5	54.2
Rhine	Noordzeekanaal (4)	0.04	6.0	0.025	7.6	0.34	2.9	95.4	3.5
Rhine	Afsluitdijk (5)	0.06	9.0	0.01	3.0	2.03	17.2	479.5	17.4
	Total	0.67	100	0.33	100	11.8	100	2753.9	100

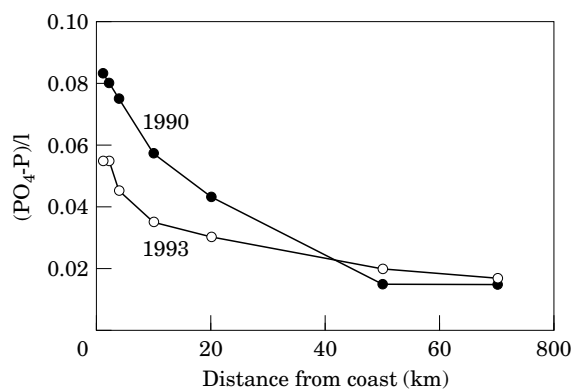


Figure 7. Distribution of $\text{PO}_4\text{-P}$ in mg l^{-1} over the coastal zone in 1990 and 1993 off Noordwijk (west coast). Data from R. N. M. Duin, RIKZ.

Phosphate reduction is a well-established measure in the freshwater environment by which to reduce excessive productivity from phytoplankton via copepods to fish. There are indications that in the marine environment phosphate reduction, resulting in an excess of nitrogen compounds favours the development of micro-algae like *Phaeocystis pouchetii* and *Noctiluca scintillans* (Zevenboom *et al.*, 1994), which are unsuitable as food for calanoid copepods (Klein Breteler and Gonzalez, 1986). Since copepods represent the main prey of juvenile brown shrimp (Boddeke and Hagel, 1995), the disturbed P/N ratio may directly affect survival of the latter.

Developments in predator stocks in the coastal zone may also be important. *Pomatoschistus* sp. feed largely on calanoid copepods and occur mainly in much deeper water than the brown shrimp of 5–18 mm on which they predate (Boddeke *et al.*, 1986), but large specimens (>25 mm) probably represent the most important predator of juvenile shrimp during the period May–August. No clear trend has been detected in this species in the coastal zone over the period 1980–1993 (Van Leeuwen *et al.*, 1994). Other major predators in the coastal zone include whiting (*Merlangius merlangus*), cod (*Gadus morhua*), bib (*Trisopterus luscus*), dab (*Limanda limanda*) and the swimming crab (*Liocarcinus*

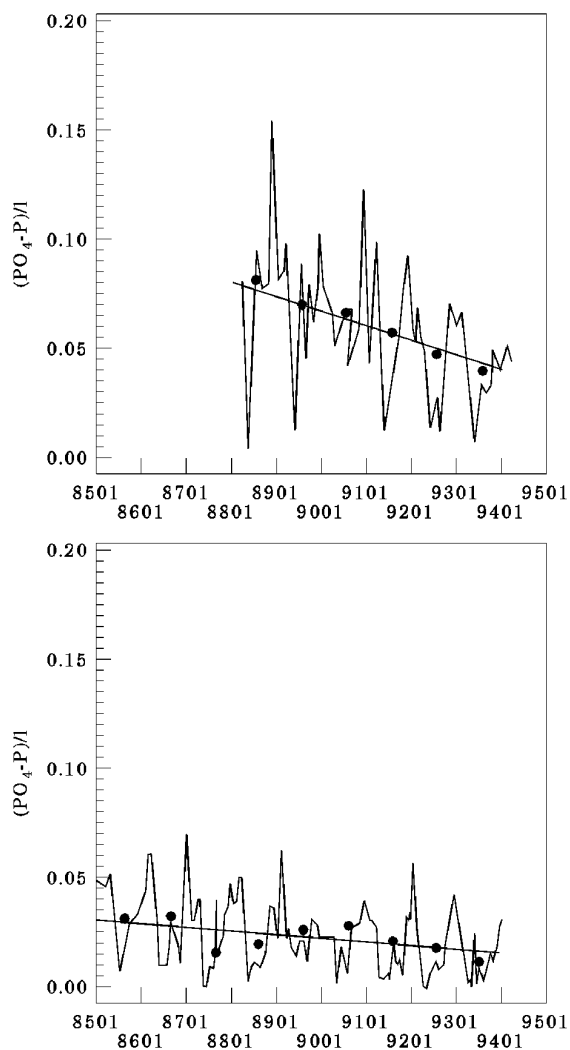


Figure 8. Concentration of $\text{PO}_4\text{-P}$ (P) in mg l^{-1} at a location 4 km offshore by year (y) (data from R. N. M. Duin, RIKZ). (Top) Noordwijk 1988–1994. Trend: $p=0.112 - 0.0069 y$. (Bottom) Terschelling 1985–1994. Trend: $p=0.031 - 0.0014 y$.

holsatus), but predation by these species does not start before August, when they enter the coastal waters as 0-group (Boddeke *et al.*, 1986; Bruné, 1988). The

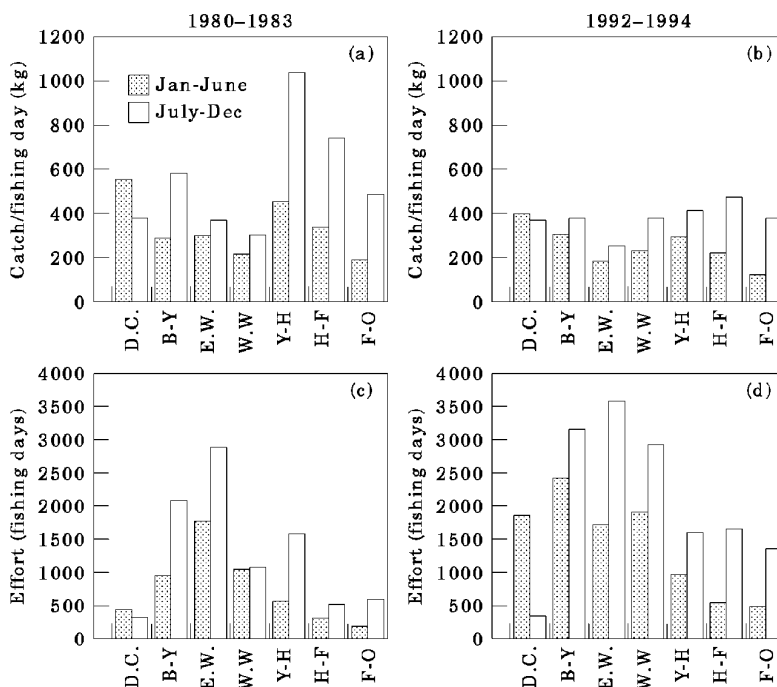


Figure 9. Average catch per fishing day in kg (c.p.u.e.) and average effort (fishing days) by 6-month periods. Areas: D.C. = Danish Coast; B-Y = Borkum-IJmuiden; E.W. = Eastern Wadden Sea; W.W. = Western Wadden Sea; Y-H = IJmuiden–Hook of Holland; H-F = Hook of Holland–Flushing; F-O = Flushing–Ostende. (a) C.p.u.e. 1981–1983; (b) c.p.u.e. 1992–1994; (c) fishing days 1981–1983; (d) fishing days 1992–1993.

relatively low densities of brown shrimp in September–October 1981 (Figs 2a, 3a) may be due to the very strong year class of cod in that year. With the exception of bib (no clear trend), densities of these species show declining trends in the Dutch coastal zone in September–October from 1980 to 1993 (Leeuwen *et al.*, 1994). For instance, the last strong year class of cod appeared in 1985 (Heessen, 1994). Along the west coast, densities of *L. holsatus* in September–October declined from 0.27 m^{-2} in 1980–1984 to 0.075 m^{-2} in 1992–1994 (unpublished DYFS data).

The decline in stocks of major predators in 1980–1993 and the associated reduction in predation mortality on shrimps in autumn–winter in recent years offers an explanation for the comparable catch rates during spring, in spite of reduced recruitment success during summer and increased fishing intensity (Fig. 9).

Duineveld *et al.* (1991) distinguish four zoobenthos regions in the North Sea based on epifauna clusters. Brown shrimp is considered an indicator species for the Southern Bight region, of which the Dutch coast is an intrinsic part. Changes in the stocks of brown shrimp along the Dutch coast in 1991–1994 compared with 1980–1984 may therefore be an indication of more general changes in this area in response to changes in phosphate concentrations. The developments in the Dutch coastal area described here underline the state-

ment by Caddy (1993) that “in coastal eutrophication the system-wide impact of the diluted nutrients and the resultant excess production on the nutrient-limited system offshore, must be considered”. Because the water of the coastal zone, enriched by the Rhine and Meuse, fans out over a much wider zone north of Den Helder, environmental changes will most likely not be restricted to the Dutch coastal area (Boddeke and Hagel, 1995).

References

- Anon. 1992. Noordzee atlas voor het Nederlands beleid en beheer. ICONA, Stadsuitgeverij, Amsterdam.
- Anon. 1993. North Sea Subregion 4 Assessment Report 1993. North Sea Task Force.
- Beukema, J. J. 1992. Dynamics of juvenile shrimp *Crangon crangon* in a tidal-flat nursery of the Wadden Sea after mild and cold winters. *Marine Ecological Progress Series*, 83: 157–165.
- Boddeke, R. 1965. Methods to improve the yield of the Dutch shrimp fisheries. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 156: 128–130.
- Boddeke, R. 1975. Autumn migration and vertical distribution of the brown shrimp *Crangon crangon* L. in relation to environmental conditions. *Proceedings 9th European Marine Biological Symposia*, 483–494. Aberdeen University Press.
- Boddeke, R. 1976. The seasonal migration of the brown shrimp *Crangon crangon*. *Netherlands Journal of Sea Research*, 16: 151–162.

- Boddeke, R. 1978. Changes in the stock of brown shrimp (*Crangon crangon* L.) in the coastal area of the Netherlands. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 172: 239–249.
- Boddeke, R. 1982. The occurrence of winter and summer eggs in the brown shrimp (*Crangon crangon*) and the pattern of recruitment. *Netherlands Journal of Sea Research*, 16: 151–162.
- Boddeke, R. 1983. The coastal zone of Holland, a new Wadden Sea, ICES CM 1983/K: 21.
- Boddeke, R., Daan, N., Postuma, K. H., de Veen, J. F., and Zijlstra, J. J. 1970. A census of juvenile demersal fish in the Dutch Waddensea, the Zeeland nursery ground, the Dutch coastal area and the open sea area of the coasts of the Netherlands, Germany and the southern part of Denmark. *Annales Biologiques, Conseil International pour l'Exploration de la Mer*, 26: 269–275.
- Boddeke, R., Driessen, G., Doesburg, W., and Ramaekers, G. 1986. Food availability and predator presence in a coastal nursery area of the brown shrimp (*Crangon crangon*). *Ophelia*, 26: 77–90.
- Boddeke, R., and Hagel, P. 1995. Eutrophication, fisheries and productivity of the North Sea continental zone. In *Condition of the world's aquatic habitats*, pp. 290–315. Ed. by N. B. Armantrout. Proceedings of the World Fisheries Congress. Oxford and IBH Publishing Co. Pvt. Ltd, New Delhi.
- Bruné, M. 1988. Voorkomen en voedsel van *Liocarcinus holsatus* (F.) in het Nederlandse kustwater en de Oosterschelde. RIVO (internal report) ZE 88–01.
- Caddy, J. F. 1993. Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. *Reviews in Fisheries Science*, 1: 57–95.
- Duineveld, G. C. A., Künitzer, A., Niermann, U., de Wilde, P. A. W. J., and Gray, J. S. 1991. The macrobenthos of the North Sea. *Netherlands Journal of Sea Research*, 28: 53–65.
- Havinga, B., 1930. Der Granat (*Crangon vulgaris* Fabr.) in den holländischen Gewässern. *Journal du Conseil Permanent International pour l'Exploration de la Mer*, 5: 57–87.
- Heessen, H. J. L., 1994. The distribution of cod (*Gadus morhua*) in the North Sea. NAFO Scientific Council Studies, 18: 59–65.
- Heip, C. H. R., Goosen, N. H., Herman, P. M. J., Kromkamp, J., Middelburg, J., and Soetaert, K. 1995. Production and consumption of biological particles in temperate tidal estuaries. *Oceanography and Marine Biology: an Annual Review*, 33: 1–149.
- Heymen, R., 1992. Resultaten van het waterkwaliteitsonderzoek in de Rijn in Nederland 1972–1991. Nota 92–047, RIZA, Lelystad.
- Klein Breteler, W. C. M., and Gonzalez, S. R. 1986. Culture and development of *Temora longicornis* (Copepoda, Calanoidea) at different conditions of temperature and food. *Sylogus*, 58: 71–84.
- Lange, G. J. de, and Hummel, H. 1978. Beschrijving van het biotisch en abiotisch milieu van het Nederlands continentaal plat. NIOZ internal report 3.
- Leeuwen, P. I. van, Rijnsdorp, A. D., and Vingerhoed, B. 1994. Variations in abundance and distribution of demersal fish species in the coastal zone of the Southeastern North Sea between 1980 and 1993. ICES CM 1994/G: 10.
- Meyden, P. A. L. van de, 1991. Total nitrogen and phosphorus in the Dutch coastal zone of the North Sea: concentrations and ratios. Min. van Verkeer en Waterstaat, Dienst Getijdenwateren, Den Haag (unpublished report).
- Nienhuis, P. H., and Smaal, A. C. 1994. The Oosterschelde estuary, a case study of a changing ecosystem: an introduction. *Hydrobiologia*, 282/283: 1–14.
- Ohno, A., and Okamura, Y. 1988. Propagation of the calanoid copepod *Acartia tsuensis* in outdoor tanks. *Aquaculture*, 70: 39–51.
- Redeke, H. C. 1941. *De visschen van Nederland*. 331 pp. Leiden, The Netherlands.
- Venema, S. C., and Creutzberg, F. 1973. Seasonal migration of the swimming crab *Macropipus holsatus* in an estuarine area controlled by tidal streams. *Netherlands Journal of Sea Research*, 7: 94–102.
- Visser, M., Ruyter, W. P. M. de, and Postma, L. 1991. The distribution of suspended matter in the Dutch coastal zone. *Netherlands Journal of Sea Research*, 27: 127–143.
- Zevenboom, W., Rademaker, M., Backus, L. C., Kamphuis, J. E., and Orth, R. G. 1994. Surface algal blooms on the Dutch continental shelf. RWS-North Sea Directorate, Report NZ-94.12, Den Haag.