

Temporal variability in southern North Sea epifauna communities after the cold winter of 1995/1996

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Epifauna communities in the southeastern North Sea were studied from 1998 to 2008 to evaluate the effect of hydroclimatic change in community structure. The spatial analysis revealed four communities along the West and North Frisian coasts, on the Oyster Ground, and on the Dogger Bank. The variability between communities was caused mainly by differing abundance of widespread species such as *Asterias rubens*, probably reflecting differences in environmental conditions, e.g. temperature variation and food supply. Community structure varied between 1998–2000 and 2003–2008 at the shallow West and North Frisian coasts. The hypothesis is that epibenthic communities in these areas were severely affected by the cold winter of 1995/1996, resulting in the outbreak of the opportunistic brittlestar *Ophiura albida* and followed by characteristic post-disturbance succession stages from 1998 to 2000. The period between 2003 and 2008 was characterized by a continuous decrease in *O. albida* and by an increase in other species and diversity in the coastal areas. In contrast, secondary production increased in all four areas after 2003, probably because of an increase in sea surface temperature (SST) and in the length of the warming season. We conclude that the cold winter affected epifauna mainly in shallow areas and that the increasing SST influenced the epifauna in the entire southeastern North Sea mainly through an increased food supply.

Keywords: cold winter, epibenthos, food supply, North Sea, primary production, sea surface temperature.

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Introduction

The analysis of an epifauna time-series on a small spatial scale (10 × 10 nautical miles; hereafter miles) in the German Bight from 1998 to 2007 revealed an epifaunal community shift in 2002 (Neumann *et al.*, 2008a). The epifauna in this shallow and well-mixed area of the German Bight was severely affected by the cold winter of 1995/1996, resulting in an outbreak of the brittlestar *Ophiura albida*. Subsequently, winter bottom temperature increased and the abundance of *O. albida* decreased simultaneously, whereas the diversity, abundance, and biomass of other species increased. These changes were linked to trophic interactions as well as mild winter temperatures, which probably resulted in lowered mortality, higher reproductive output, and enhanced food supply for benthic fauna through enhanced primary production. It appears that temperature was a key factor in the shallow German Bight, influencing the recruitment success, mortality, and migration patterns of the epifaunal species.

Nevertheless, it remains unclear whether the changes in the patterns on this small spatial scale were also valid on a large spatial scale. We therefore analysed epifaunal time-series on a large spatial scale in the southeastern North Sea ranging from the West and North Frisian coasts up to the 50-m depth contour in the north (ca. 150 × 150 miles). Sampling took place

during the ICES-coordinated International Bottom Trawl Survey (IBTS), and covered 24 ICES rectangles (30 × 30 miles). The rectangles were attributed to specific areas in the southeastern North Sea by bottom temperature and depth differences in the study area, which are important factors influencing the spatial variability of epibenthic communities (Callaway *et al.*, 2002; Reiss and Kröncke, 2004; Neumann *et al.*, 2008b). The objectives of our study were to (i) investigate whether the epifauna community shift in 2002 was a large-scale phenomenon in the southeastern North Sea, and (ii) assess the differences in response of the epifauna to hydroclimatic forcing in different areas of the southeastern North Sea.

Material and methods

Samples of epibenthos were analysed from 2-m beam trawl catches taken during surveys with the RV “Walther Herwig III” during the periods 1998–2000 and 2003–2008. The surveys were part of the IBTS and covered 24 ICES rectangles (30 × 30 miles) from 53°30′ to 56°N and 3 to 8°E (Figure 1a). The study area included the inner German Bight with its shallow West and North Frisian coasts, the deeper Oyster Ground, and the shallow northeastern Dogger Bank. The depth generally increased from the coast towards the north-western rectangles, except Dogger Bank, and varied in depth

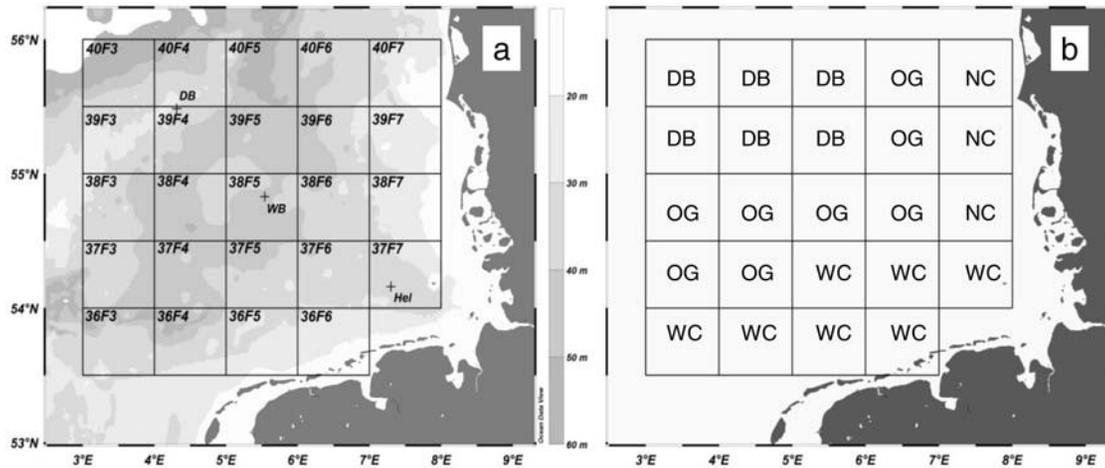


Figure 1. Location of the 24 rectangles in the southeast North Sea with (a) depth contours and temperature stations at Helgoland (Hel), White Bank (WB), and Dogger Bank (DB), and (b) the corresponding regions referred to here as West Frisian coast (WC), North Frisian coast (NC), Dogger Bank (DB), and Oyster Ground (OG).

from 18 m (Rectangle 38F7) to 55 m (Rectangle 40F5). Mud content ($<63 \mu\text{m}$) was highest in the inner German Bight (Rectangle 37F7; up to 40%) and around the Frisian Front (Rectangles 36F4–36F5 and 37F4–37F5; 10–25%), and lowest at the Dogger Bank ($<1\%$; Rectangle 39F3) and along the North Frisian coast (38F7–39F7; $<1\%$).

Sampling and sample treatment

Epibenthos was sampled in July/August of 1998–2000 and 2003–2008. Sampling did not take place in the study area in 2001 and 2002. Generally, beam trawls sample semi-quantitatively (Eleftheriou and Moore, 2005). However, the construction of the 2-m beam trawl and the sampling protocol followed standardizations described by Jennings *et al.* (1999), and sampling and data analysis were evaluated on different spatial scales in the North Sea (Zühlke *et al.*, 2001; Callaway *et al.*, 2002; Hinz *et al.*, 2004; Neumann *et al.*, 2008b). The beam trawl was fitted with a net of 20 mm mesh and a codend of 4 mm mesh. A SCANMAR depth sonar was attached to its top just behind the steel beam to determine the exact time and position of contact with the seabed. From the moment of contact with the seabed, the beam was towed at a speed of ~ 1.5 –2 knots for 5 min. One sample was taken per rectangle, and 6–13 replicates were taken per year only in Rectangle 37F7. Additional replicates were used just for the GIS analysis. In all, 306 samples were taken during the study period.

Samples were sieved over a 5-mm mesh, and epibenthic fauna were separated from the remains. Most species were identified on board ship. Unidentified species were preserved in a 4% seawater formalin solution for identification in the laboratory. Abundance and wet weight of the epifauna were determined using a motion-compensated marine scale (Pols) to an accuracy of 1 g, and all animals were identified to the lowest possible taxon.

Temperature data

The Federal Maritime and Hydrographic Agency of Germany (BSH) provides weekly sea surface temperature (SST) data at fixed stations in the North Sea. Monthly standardized temperature

anomalies were calculated from stations at Helgoland (Hel; $54^{\circ}9.6'N$ $7^{\circ}18.0'E$), White Bank (WB; $54^{\circ}49.8'N$ $5^{\circ}32.4'E$), and Dogger Bank (DB; $55^{\circ}29.4'N$ $4^{\circ}18.6'E$; Figure 1a), based on the 1968–2007 mean. To attribute the rectangles to specific regions in the study area, winter (December–February) and summer (June–August) bottom temperature data from the database of the Federal Research Institute for Rural Areas, Forestry and Fisheries were gridded over the study area using the programme “Ocean Data View” (Schlitzer, 2006).

Data analysis

The selection of species incorporated in the analysis was based on studies of catching efficiency (e.g. Kaiser *et al.*, 1994; Reiss *et al.*, 2006a) to provide the best possible quantitative results. Abundance and biomass data were standardized to a tow length of 250 m (area sampled = 500 m^2). The Shannon–Wiener index H' was calculated to assess diversity during the study period. Abundance, biomass, and the Shannon–Wiener index were given as mean values for the corresponding regions and years, respectively. Non-metric multidimensional scaling (MDS) in the PRIMER v6 package (Plymouth Marine Laboratory) was used based on square-root-transformed abundance data. Similarities were calculated using the Bray–Curtis coefficient. ANOSIM randomization tests were performed to test the differences in the community composition between areas and years (H_0 : no differences in community composition). Additionally, the RELATE routine in PRIMER was used to measure how closely related two sets of multivariate data were by calculating the Spearman rank correlation coefficient (H_0 : no agreement in multivariate pattern).

The extension Spatial Analyst from ArcGIS 9.0 was used to create a surface grid of the spatial variability of the brittlestar *O. albida* in the study area. The calculations were performed for 1998–2000 and 2003–2008. The deterministic interpolation method inverse-distance weight, which is based on the similarities between datapoints, was applied to predict the values of cells that lacked sampled points (Childs, 2004).

An empirical model proposed by Brey (2001) was applied to predict individual annual somatic production P ($\text{kJ m}^{-2} \text{ year}^{-1}$):

$$\log\left(\frac{P}{B}\right) = 7.947 + [-2.294 \times \log(M)] + \left[-2409.856 \times \frac{1}{T+273}\right] + 0.168 \times \frac{1}{D} + 0.194 \times \text{SubT} + 0.18 \times \text{InEpi} + 0.277 \times \text{MoEpi} + 0.174 \times \text{AnnCrust} + (-0.188 \times \text{Ech}) + 582.851 \times \log(M) \times [1/(T+273)] \quad (1)$$

The variables biomass (B ; kJ m^{-2}), mean individual body mass (M ; kJ), water temperature (T ; $^{\circ}\text{C}$), and water depth (D ; m) were used as continuous variables, whereas the other parameters were transformed to categorical binary variables (1 or 0): subtidal (SubT: yes, 1; no, 0), infauna or epifauna (InEpi: infauna, 1; epifauna, 0), mobile epifauna (MoEpi: yes, 1; no, 0), Annelida or Crustacea (AnnCrust: yes, 1; no, 0), Echinodermata (Ech: yes, 1; no, 0). Taxon-specific conversion factors were used to calculate secondary production (Brey, 2001). Production was given as the mean value for the community in the corresponding region and year.

Results

Spatial variability of abiotic data

Spatial patterns of mean summer and winter bottom temperature (Figure 2) and the depth contours (Figure 1a; Table 1) correspond to the areas West Frisian coast (WC), North Frisian coast (NC), Dogger Bank (DB), and Oyster Ground (OG; Figure 1b). The North and West Frisian coasts and the Oyster Ground largely cover depths of 20–30, 30–40, and 40–50 m, respectively (Figure 1a). Depth at the Dogger Bank ranged from 28 to 52 m (Table 1). Temperature variation between summer and winter was less pronounced at the Dogger Bank and increased towards the coast. Lowest mean and minimum winter bottom temperatures (6.8 and 1.9°C) and highest mean and maximum summer bottom temperatures (15.2 and 18.4°C) were recorded at the North Frisian coast. In general, the four regions follow an increasing gradient of bottom temperature in winter and a decreasing one in summer, from the coast to offshore (Figure 2; Table 1).

1995–2007 temperature anomalies

Standardized SST revealed similar trends at the Helgoland, White Bank, and Dogger Bank stations, except the first quarter of 2001, which showed negative anomalies at Dogger Bank and positive anomalies at Helgoland and White Bank (Figure 3). The cold winter of 1995/1996 is clearly reflected in strong negative SST anomalies from the start of 1996, which persisted until May 1997 at all stations. In subsequent years, anomalies were mainly above the long-term mean (1968–2007) at each station. Highest anomalies were in April 2007 at Helgoland and White Bank (2.14 and 2.19, respectively), and in October 2006 at Dogger Bank (2.02). Since 2002, positive SST anomalies often persisted throughout the year and were exceptionally high during winter and spring (Figure 3).

Community characteristics

The ANOSIM randomization test revealed that the epibenthic communities of the four areas were significantly different in each year, except 1999 ($R = 0.429$, $p < 0.001$; Table 2). In all, we found 132 free-living species of epifauna in 306 samples. Characteristic species of the four areas are listed in Table 3. The seastar *Asterias rubens* and the hermit crab *Pagurus bernhardus* were common to all areas. Species such as the goby *Pomatoschistus minutus* and the brittlestar *O. albida* (WC), as well as the dragonet *Callionymus lyra* (NC), the sea urchin *Echinocardium cordatum* (OG), and the masked crab *Corystes casivelaunus* (DB), were more common in single areas. Some species were only found in one area. The whelk *Neptunea antiqua*, the crab *Hyas coarctatus*, and the snail *Colus gracilis* were only recorded at Dogger Bank, and the sea squirt *Asciidiella scabra* was characteristic of the North Frisian coast. In general, common species were more abundant in coastal areas (WC and NC) than offshore (OG and DB).

Temporal variability in community structure

ANOSIM analyses revealed significantly different community structure between the periods 1998–2000 and 2003–2008 in the area of the West Frisian coast ($R = 0.88$, $p < 0.01$) and the North Frisian coast ($R = 0.74$, $p < 0.01$), coinciding with the shift found by Neumann *et al.* (2008a) in a small area of the German Bight. The dissimilarity of the communities was 42%

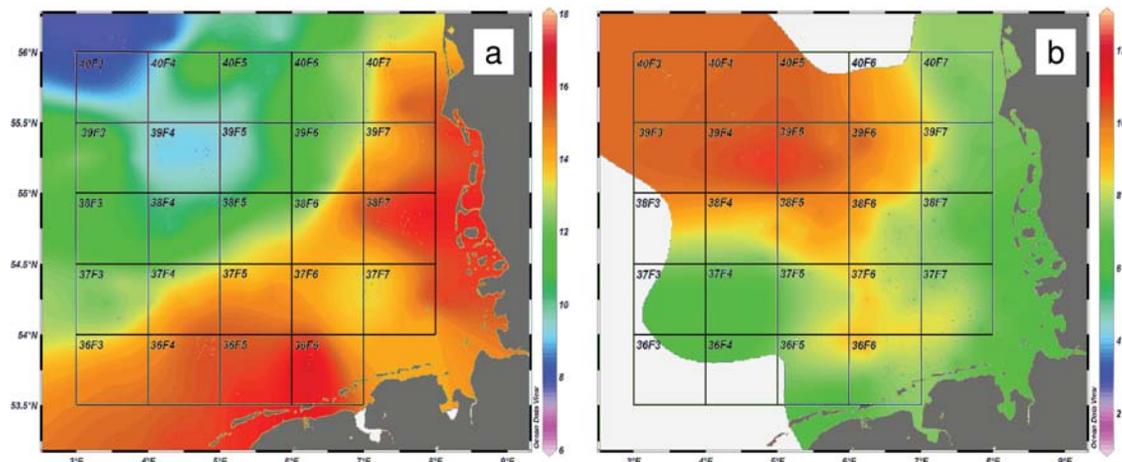
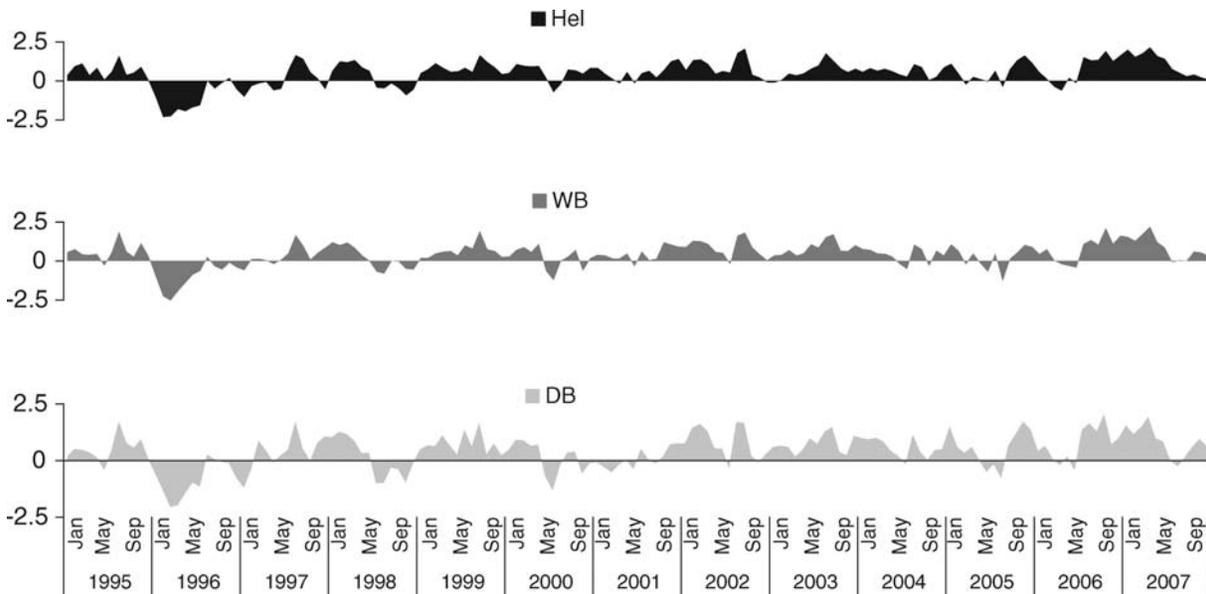


Figure 2. Mean (a) summer and (b) winter bottom temperatures ($^{\circ}\text{C}$) in the study area from 1998 to 2007.

Table 1. Mean, minima, and maxima of depth, and summer and winter bottom temperature at the West Frisian coast (WC), the North Frisian coast (NC), the Oyster Ground (OG), and Dogger Bank (DB).

Area	Depth (m)			Summer bottom temperature (°C)			Winter bottom temperature (°C)		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum
WC	38	27	43	14.7	11.7	17.9	7.3	2.4	11.4
NC	27	20	30	15.2	10.6	18.4	6.8	1.9	11.5
OG	44	40	49	12.2	8.0	17.5	8.5	4.8	12.2
DB	41	28	52	9.7	5.8	15.5	10.4	8.1	12.3

**Figure 3.** Anomalies in SST (°) at the Helgoland (Hel), White Bank (WB), and Dogger Bank (DB) stations, based on the 1968–2007 mean.**Table 2.** Results of the ANOSIM analysis to test the differences in species composition between the areas West and North Frisian coasts, Oyster Ground, and Dogger Bank.

	1998	1999	2000	2003	2004	2005	2006	2007	2008
R statistic	0.694	0.429	0.615	0.615	0.653	0.568	0.592	0.592	0.636

All R values are given at $p < 0.001$.

at the West Frisian coast and 56% at the North Frisian coast. No significant change in community structure was observed in deeper areas such as the Oyster Ground and the Dogger Bank. Figure 4 shows the results of MDS analyses for the four areas from 1998 to 2008. There was a similar temporal pattern at the West and North Frisian coasts, which was confirmed by the RELATE analysis ($R = 0.68$, $p < 0.005$). Despite the data gap in 2001 and 2002, it became obvious that the differences in community structure between the periods 1998–2000 and 2003–2008 were larger at the West and North Frisian coasts than on the Oyster Ground and Dogger Bank (Figure 4). Temporal variability of diversity (H') supported the differences between both periods at the West and North Frisian coasts (Figure 5). Diversity was < 3 between 1998 and 2001 and > 3 between 2003 and 2008, in both areas. Generally, diversity increased during the study period, with values lowest in 1998 at the West Frisian coast (2.7) and in 2000 at the North Frisian coast (2.7). Diversity was greatest at the

West Frisian coast in 2006 (3.8) and at the North Frisian coast in 2008 (3.7). The shift in community structure at the West and North Frisian coasts was mainly caused by changes in abundance of some typical species (Table 4). Changes in brittlestar *O. albida* presence were most prominent from 1998 to 2008 (Figure 6). This species was extremely abundant in 1998, especially along the West Frisian coast, but decreased continuously in subsequent years. The decrease in *O. albida* was most pronounced from 1998 to 2000, but it persisted right up to 2008. The mean abundance of *O. albida* was considerably lower from 2003 to 2008 at the West and North Frisian coasts than in earlier years (Figure 6, Table 4). Additionally, the abundance of *Ophiura ophiura*, *P. bernhardus*, and *A. scabra* decreased in the later period (Table 4). From 2003 to 2008, the mean abundance of *A. rubens* was lower at the West Frisian coast, but higher along the North Frisian coast, mainly through the large numbers of juveniles in 2007. Small benthic fish such as *P. minutus*, *Buglossidium luteum*, *Arnoglossus laterna*,

and *C. lyra*, and also the swimming crab *Liocarcinus holsatus*, were very abundant from 2003 to 2008 in both areas (Table 4).

In contrast to the changes in species abundance and diversity at the West and North Frisian coasts, the secondary production of

Table 3. Frequency of occurrence (expressed as the percentage of samples) and mean abundance of dominant species in the communities at the West Frisian coast (WC), the North Frisian coast (NC), the Oyster Ground (OG), and Dogger Bank (DB).

Area	Species	Frequency (%)	Abundance (numbers 500 m ⁻²)
WC	<i>Asterias rubens</i>	99	183
	<i>Buglossidium luteum</i>	97	44
	<i>Pomatoschistus minutus</i>	96	110
	<i>Liocarcinus holsatus</i>	96	42
	<i>Pagurus bernhardus</i>	96	10
	<i>Ophiura albida</i>	92	903
NC	<i>Asterias rubens</i>	100	216
	<i>Buglossidium luteum</i>	96	46
	<i>Pagurus bernhardus</i>	96	5
	<i>Limanda limanda</i>	89	6
	<i>Liocarcinus holsatus</i>	85	6
	<i>Callionymus lyra</i>	81	8
OG	<i>Astropecten irregularis</i>	97	27
	<i>Asterias rubens</i>	86	12
	<i>Buglossidium luteum</i>	83	7
	<i>Pagurus bernhardus</i>	83	3
	<i>Limanda limanda</i>	81	3
	<i>Echinocardium cordatum</i>	75	13
DB	<i>Asterias rubens</i>	98	14
	<i>Pagurus bernhardus</i>	98	11
	<i>Astropecten irregularis</i>	94	15
	<i>Limanda limanda</i>	80	3
	<i>Corystes cassivelaunus</i>	74	2

epifauna was generally greater in all four areas after 2003 than earlier (Figure 7). Production was highest at the West Frisian coast in 2004 (168 kJ m⁻² year⁻¹), at the North Frisian coast in 2006 (35 kJ m⁻² year⁻¹), and at the Oyster Ground and Dogger Bank in 2005 (23 and 12 kJ m⁻² year⁻¹, respectively). Secondary production was also high in 1998 at the West Frisian coast. There, the trends in production coincided with those of mean abundance, largely reflecting the abundance and production of *O. albida*, whereas in the other areas, trends in abundance were different from those of secondary production.

Discussion

Spatial variability of epifaunal communities

Many large-scale studies have identified water depth as important in separating epifaunal communities in the North Sea. The most conspicuous boundary is at the 50-m depth contour, which separates the central–northern epifaunal communities from the southern communities (Jennings *et al.*, 1999; Callaway *et al.*, 2002; Neumann *et al.*, 2008b). Based on presence/absence transformed data, Callaway *et al.* (2002) identified two epibenthic communities in the southeastern North Sea. The most widespread was characterized by the crustaceans *C. cassivelaunus*, *L. holsatus*, and *P. bernhardus*, the starfish *A. rubens* and *Astropecten irregularis*, the brittlestars *O. ophiura* and *O. albida*, and small, benthic fish such as *B. luteum* and *C. lyra*. The second community along the continental coast had a similar species composition, but the number of species was less (Callaway *et al.*, 2002). Epifaunal communities in the current study were also separated by water depth, resulting in spatial separation along the North and West Frisian coasts and in the deeper offshore areas of Dogger Bank and Oyster Ground. The characteristic species found in our study coincide with those found by Callaway *et al.* (2002). However,

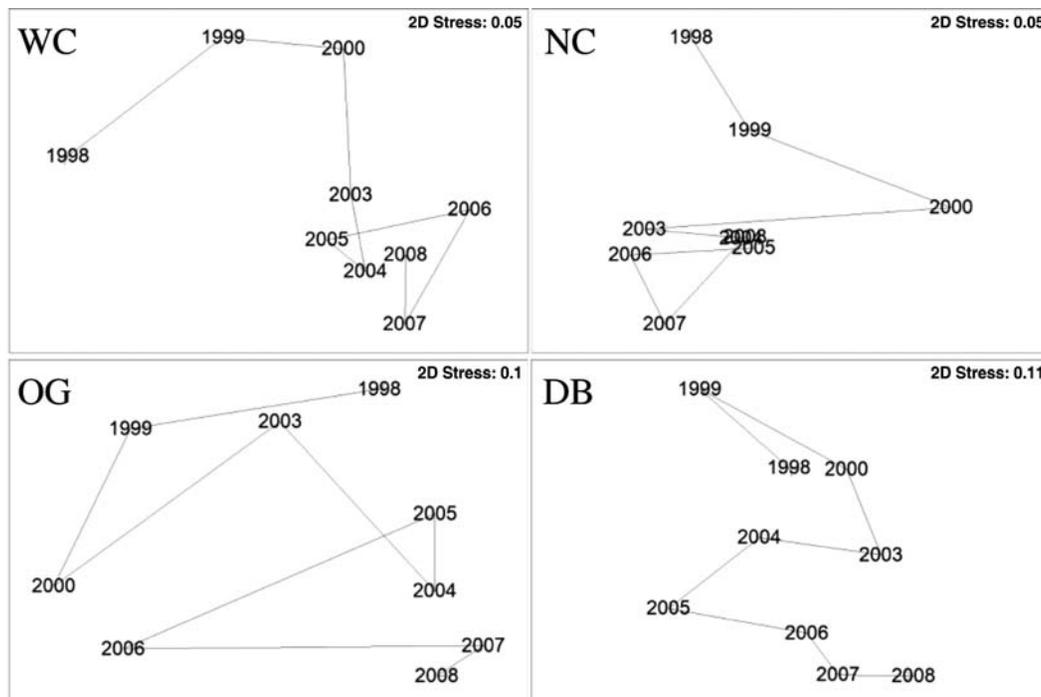


Figure 4. MDS plots of the communities in the southeastern North Sea from 1998 to 2008. Abundance data were square-root-transformed. WC, West Frisian coast; NC, North Frisian coast; OG, Oyster Ground; DB, Dogger Bank.

the differences in the abundance of species, neglected in the presence/absence analysis of Callaway *et al.* (2002), resulted in further subdivisions of communities in the southern North Sea. The coastal communities in our study were characterized by greater abundance of species than in the offshore communities.

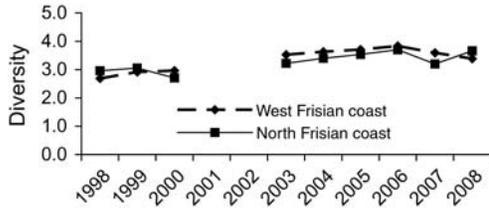


Figure 5. Shannon–Wiener diversity index (H') at the West and North Frisian coasts from 1998 to 2008.

The depth contours correspond to differences in temperature, primary production, and hydrographic factors such as stratification and circulation patterns (Duineveld *et al.*, 1991; Callaway *et al.*, 2002; Reiss and Kröncke, 2004; Neumann *et al.*, 2008b). The coastal areas in our study were characterized by a mixed water column throughout the year, whereas there was summer stratification on the Oyster Ground and Dogger Bank (Becker *et al.*, 1992), resulting in lower seasonal temperature variation in the deeper than in the coastal areas (Figure 2). Our areas were also affected by differences in water masses. Central North Sea water was found at Dogger Bank and Oyster Ground. This water mass is not directly influenced by coastal river run-off and is characterized by medium salinity, medium nutrient concentrations, and thermal stratification in summer (Laevastu, 1963). Total oxygen concentration and chlorophyll *a* content decreased from the German Bight to the Dogger Bank probably as a

Table 4. Mean abundance of species which increased (left) and decreased (right) from 1998 to 2008 at the West (WC) and North (NC) Frisian coasts.

Area	Species that increased	Abundance (numbers 500 m ⁻²)		Species that decreased	Abundance (numbers 500 m ⁻²)	
		1998–2000	2003–2008		1998–2000	2003–2008
WC	<i>Pomatoschistus minutus</i>	43	114	<i>Ophiura albida</i>	1 942	244
	<i>Buglossidium luteum</i>	20	46	<i>Asterias rubens</i>	113	51
	<i>Liocarcinus holsatus</i>	12	62	<i>Ophiura ophiura</i>	98	12
	<i>Turritella communis</i>	6	32	<i>Pagurus bernhardus</i>	21	5
NC	<i>Asterias rubens</i>	44	353	<i>Ophiura albida</i>	52	0
	<i>Buglossidium luteum</i>	11	70	<i>Ophiura ophiura</i>	42	0
	<i>Callionymus</i> spp.	1	14	<i>Ascidella scabra</i>	28	3
	<i>Arnoglossus laterna</i>	0	16	<i>Pagurus bernhardus</i>	6	2

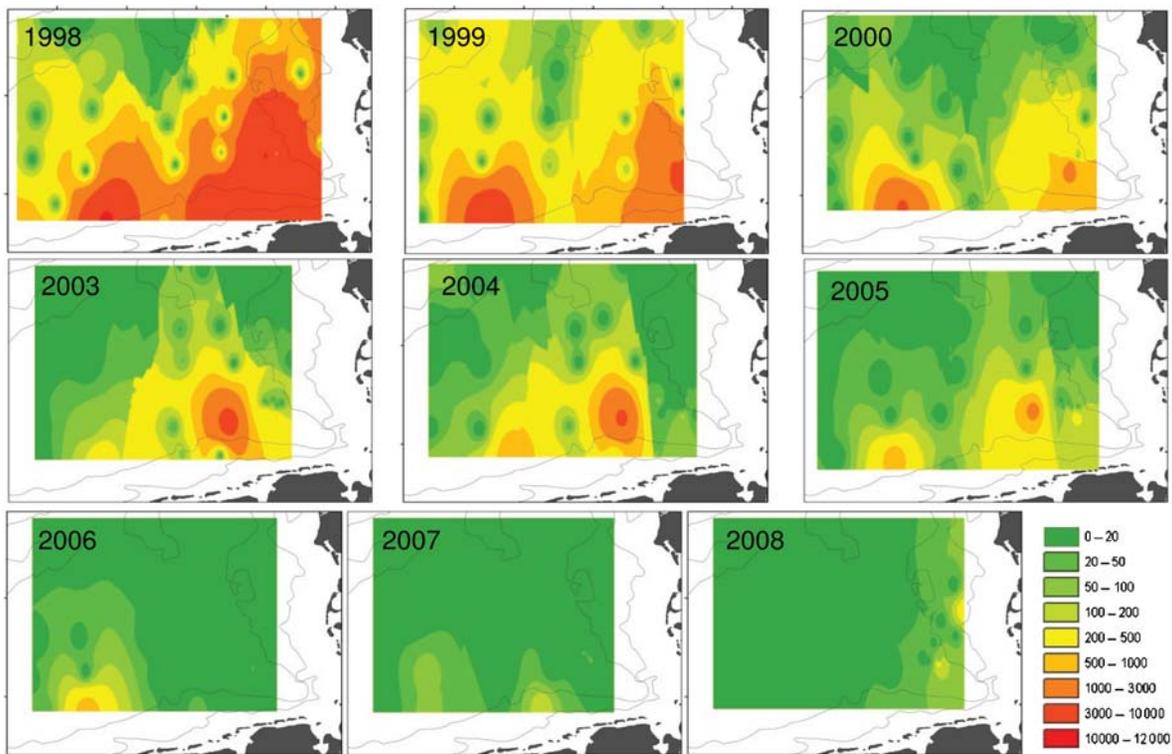


Figure 6. Mean abundance (numbers 500 m⁻²) of the brittlestar *O. albida* in the southeastern North Sea from 1998 to 2000, and from 2003 to 2008.

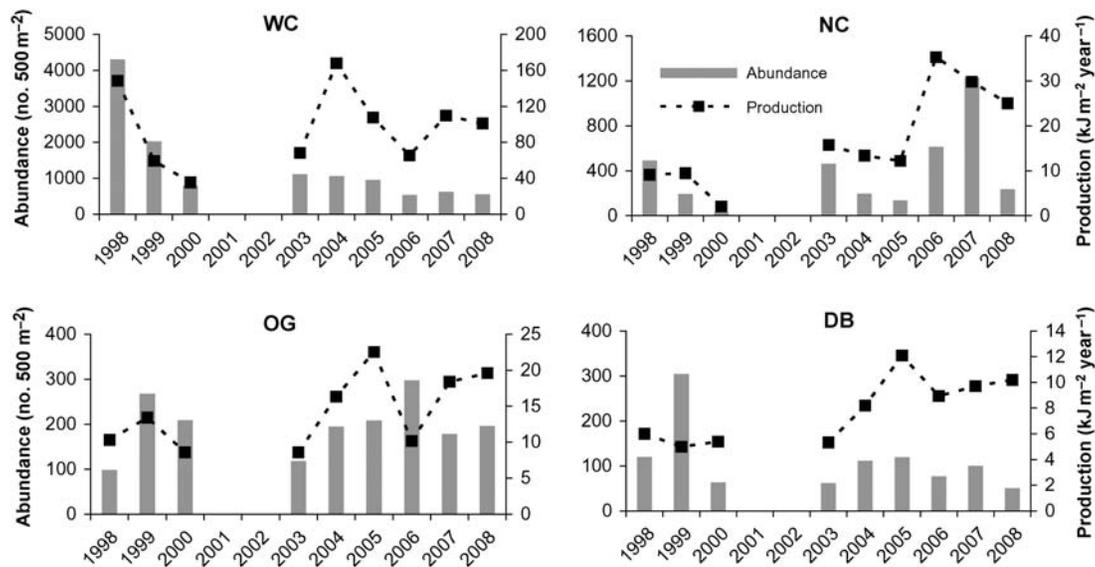


Figure 7. Mean abundance (numbers 500 m⁻²) and secondary production (kJ m⁻² year⁻¹) at the West Frisian coast (WC), North Frisian coast (NC), Dogger Bank (DB), and Oyster Ground (OG), from 1998 to 2008.

consequence of the summer stratification, which inhibited sedimentation of organic matter and the input of nutrients from bottom waters into upper layers (Kröncke *et al.*, 2004; Reiss and Kröncke, 2005). This indicates a decreasing food supply to the benthic system from the southern coastal areas towards the Dogger Bank, which might result in a generally decreasing trend in secondary production from south to north in our study (Figure 7). The water masses at the West and North Frisian coasts (continental coastal water) are influenced largely by freshwater run-off from rivers, resulting in low salinity and high nutrient input (Becker *et al.*, 1992). Together with a relatively long residence time of the water masses, the high nutrient input could result in intense algal blooms and, therefore, in enhanced food supply for benthic fauna (Dauwe *et al.*, 1998; Stoeck and Kröncke, 2001). Hence, greater abundance of species such as *O. albida* and *A. rubens* in coastal areas and a high secondary production, especially at the West Frisian coast, might be explained by the enhanced food supply.

Only a few species were found exclusively in one of our areas. Nevertheless, the goby *P. minutus* and the dragonet *C. lyra* were characteristic of shallow coastal areas (Callaway *et al.*, 2002). The gastropods *N. antiqua* and *C. gracilis*, which were found only on the Dogger Bank in this study, were characteristic of epifaunal communities inhabiting a transitional area between the southern and the central–northern North Sea (Neumann *et al.*, 2008b). In contrast, species such as *A. rubens* and *P. bernhardus*, which were common to all four areas, were widespread across the entire North Sea (Zühlke *et al.*, 2001).

The 1998–2000 period, following the cold winter of 1995/1996

Our results confirm the changes in community structure on a large spatial scale found by Neumann *et al.* (2008a) on a small spatial scale in the German Bight. Changes in community structure were only significant in the shallow areas of the West and North Frisian coasts despite the data gap in 2001 and 2002. This indicated a greater impact of cold winters in nearshore than in offshore

(more stable) environments, a result also found for benthic infauna (Reiss *et al.*, 2006b). Cold winters influenced benthic infauna dramatically through direct (enhanced mortality) and indirect (reduced reproduction and production) effects on species (Reiss *et al.*, 2006b). For example, one-third of the infaunal species on tidal flats of the Dutch Wadden Sea die during cold winters (Beukema, 1992), and macrofauna communities of the UK's Northumberland coast show reduced diversity and increased survival of dominant species after cold winters (Buchanan and Moore, 1986). Additionally, periods after cold winters are characterized by highly successful recruitment of *r*-selected opportunistic species such as the polychaetes *Spiophanes bombyx* and *Scoloplos armiger* (Kröncke *et al.*, 1998; Schröder, 2005). High abundance of *S. bombyx* was also recorded by Ziegelmeier (1970) after the severe winter of 1963/1964 near the island of Sylt. He explained the increase in abundance after that cold winter by the absence of the mussel *Fabulina fabula*, which feeds on polychaete larvae.

Similar to the results of Neumann *et al.* (2008a), the brittlestar *O. albida* was the dominant species, especially in the coastal areas during the years 1998–2000. *Ophiura albida* is a small, short-lived (3–9 years), fast-growing opportunist, with high annual productivity (Dahm, 1993). Data on the temporal variability of *O. albida* following oxygen deficiency demonstrate that it is a typical *r*-selected species that recolonizes a habitat faster than other species after catastrophic events (Dethlefsen and von Westernhagen, 1983; Dyer *et al.*, 1983; Niermann *et al.*, 1990). Therefore, it is reasonable to assume that the abundance of *O. albida* from 1998 to 2000, especially at the West and North Frisian coasts, was a direct effect of the cold winter of 1995/1996 because of its high tolerance of low temperature (Ursin, 1960), which resulted in lower mortality. This assumption was confirmed by Reiss *et al.* (2006b), who found only a slight decrease in *O. albida* after the cold winter of 1995/1996 in the German Bight in contrast to the strong decrease in other species. Additionally, the absence of predators of *O. albida* larvae and post-larvae in cold winter temperatures could favour its recruitment success. The reproduction of *O. albida* follows a well-defined

annual cycle: initiation of gametogenesis between October and December, first spawning in late May and early June, and spent adults and planktonic larvae up to early October (Tyler, 1977). The absence of predators of larvae and post-larvae in October 1995 seems to have resulted in the recruitment success of *O. albida* in 1996, which was confirmed by IK (unpublished), who found unusual abundance of juvenile ophiurids (1240 m⁻²) in summer 1996 in the sublittoral zone of Norderney.

However, the abundance of *O. albida* at the West Frisian coast was quite different from the situation at the North Frisian coast. The ophiurid was extremely abundant at the West Frisian coast from 1998 to 2000, as found by Neumann *et al.* (2008a), indicating that the West Frisian coast was the focus of its distribution. Additionally, *O. albida* and *O. ophiura* completely disappeared from the North Frisian coast during the period 2003–2008, whereas both species were still found at the West Frisian coast. However, the temporal variability of *O. albida* and the mean abundance, secondary production, and diversity during the years 1998–2000 coincided with the succession of benthic infauna communities after catastrophic events (Arntz and Rumohr, 1982). These communities at the so-called “ecotone point” were defined by Pearson and Rosenberg (1978) as transitional communities, which were poor in species, abundance, and biomass. Therefore, the communities at the West and North Frisian coasts during the years 1998–2000 were at a characteristic succession stage between the opportunistic period and the development of an established community (Arntz and Rumohr, 1982).

2003–2008

Weekly measured SST at the Helgoland, White Bank, and Dogger Bank stations revealed a warming of surface water in the southeastern North Sea, especially in winter, after 2002 (Figure 3). This coincides with generally increasing SST and a significant increase in the length of the warming season in the North Sea (Hughes and Holliday, 2007). The area-averaged SST of the North Sea in September 2002 was the highest since 1971. Also, the SST in winter and spring 2002 was above normal, missing much of the cooling usually observed in February and March (Hughes and Lavin, 2003). The area-averaged SST for August 2003 (>18°C) was the highest since 1968, and for August 2004, the second highest (Hughes and Lavin, 2004, 2005). In October and November 2005, the SST was the highest since 1971, resulting in SST values 2°C warmer than normal in autumn/winter (Hughes and Holliday, 2006). The area-averaged SST in October 2006 even exceeded the SST in October 2005. Together with those in December 2006, both were 2.4 and 1.7°C, respectively, above the climatological means (1971–1993). Additionally, winter bottom temperature increased by some 3°C from 2000 to 2007 in the southern German Bight (Neumann *et al.*, 2008a). These increases in temperature were accompanied by a persisting decrease in *O. albida* abundance and an increase in abundance of other species and diversity at the West and North Frisian coasts, resulting in significant changes in community structure. Other community shifts, which were related to increasing temperature, were found in North Sea plankton communities in 2000 and attributed to an increasing prevalence of warm-water copepods (Edwards *et al.*, 2008) as well as in the benthic infauna communities off Norderney in 2002 (IK, unpublished).

Secondary production in all four areas was higher in 2003–2008 than in 1998–2000. Hughes and Holliday (2007) found that the increase in SST resulted in a much longer period of

primary production than normal in the North Sea. Enhanced primary production, which probably starts earlier in the year, might result in greater food supply for benthic fauna (Kröncke *et al.*, 1998, 2001; Reid *et al.*, 1998). Temperature and food availability were considered to be major factors affecting benthic communities on a temporal scale (Clarke and Frid, 2001; Beukema *et al.*, 2002; Kröncke *et al.*, 2004). Beukema *et al.* (2002) hypothesized that algal food largely determines the abundance, biomass, and growth rate of zoobenthos. They found significant correlations between annual mean values of chlorophyll concentrations and zoobenthos abundance and biomass, as well as between annual growth rates of *Macoma baltica* and food supply. We hypothesized that the increase in secondary production at the West and North Frisian coasts, the Oyster Ground, and Dogger Bank might be the result of enhanced primary production from which, for instance, suspension-feeding species such as the tower shell *Turritella communis* (which increased at the West Frisian coast) benefit directly. However, production, which can be defined as the part of the assimilated matter turned into body mass, depends on many biotic variables (e.g. recruitment, mortality, food supply) and environmental conditions (e.g. temperature, depth; Brey, 2001). Many variables were not taken into account in this study. However, as described above, temperature largely influences species life history including variables such as mortality, recruitment, and food supply, which have a strong impact on secondary production (Cusson and Bourget, 2005).

Mortality during the mild winters from 2003 to 2008 might have been less and reproduction higher than in cold winters, but benthic communities seem to be more influenced by predation (Beukema, 1992). It was obvious to us that a greater abundance of potential predators on *O. albida* corresponded to a decrease in the numbers of ophiurids, indicating greater predation pressure on the species. The benthic fish *B. luteum*, *A. laterna*, and *P. minutus*, which were more abundant in the period 2003–2007, are generalists that feed on a varied diet (Hesthagen, 1978; Nottage and Perkins, 1983; Aarnio and Bonsdorff, 1993; Darnaude *et al.*, 2001; Amara *et al.*, 2004). Additionally, Fonds (1973) attributed the increasing abundance of *P. minutus* after the cold winter of 1962/1963 to increased food supply. Epibenthic invertebrates such as *L. holsatus* also feed on ophiurids (Choy, 1986). Aronson (1989) found that *L. holsatus* (increased at the West Frisian coast) and *A. rubens* (increased at the North Frisian coast) feed intensively on beds of brittlestars around the British Isles. As larval development of *L. holsatus* is faster with higher temperature (Choy, 1991), the increased abundance during the years 2003–2008 in contrast to 1998–2000 might be related to enhanced recruitment success. Similar results were documented by Kirby *et al.* (2007) for the sea urchin *Echinocardium cordatum*. They showed that a stepwise increase in the North Sea temperature after 1987 favoured the reproduction and survival of that species, resulting in alternations in the trophodynamics of the summer pelagic ecosystem through competition between its larvae and holoplankton taxa.

Increasing water temperature, especially in winter, also favours the survival of introduced or invasive species (Gollasch and Nehring, 2006), and some findings coincided with the timing of the changes observed in this study. The angular crab *Goneplax rhomboides*, which occurs normally around the western parts of the British Isles and in the English Channel (Skewes, 2008), was found for the first time on our survey in 2008 (on the West

Table 5. Fishing effort (days at sea) of large and small Dutch beam trawlers at the West Frisian coast (WC), the North Frisian coast (NC), the Oyster Ground (OG), and the Dogger Bank (DB) from 1998 to 2007.

Area	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
WC	7 016	7 472	6 506	6 874	5 489	5 004	5 163	5 466	4 814	5 414
NC	119	179	339	379	263	178	99	158	208	155
OG	4 362	4 889	4 710	3 376	2 672	2 348	1 344	1 560	1 732	1 683
DB	779	814	1 043	675	455	684	276	341	325	67

Data were derived from automated position registration (APR) data between 1998 and 1999 and vessel monitoring through satellite (VMS) data between 2000 and 2007.

Frisian coast and the Oyster Ground). First records of this species in the southeastern North Sea were reported by fishers in 2003 and 2004 off the Netherlands, followed by records in 2006 and 2007 from scientific surveys at stations located in our Oyster Ground area (T. Neudecker and G. C. A. Duineveld, pers. comm.). As the increasing water temperatures in winter coincide with the first occurrence of that species, our opinion is that the increase in temperature likely enhances its survival in the southeastern North Sea. Coincident with this has been the exceptional abundance of the snake pipefish *Entelurus aequoreus* and its larvae since 2003, which were recently reported from the Northeast Atlantic and the North Sea (Kirby *et al.*, 2006; Lindley *et al.*, 2006; Harris *et al.*, 2007). Harris *et al.* (2007) and Fleischer *et al.* (2007) found a dramatic increase in the abundance of that species starting around 2003 and a range expansion northwards to Spitsbergen and the Barents Sea. Increased SST, linked to global warming, was the proposed cause, probably a result of greater reproductive success of the species (Kirby *et al.*, 2006; Fleischer *et al.*, 2007).

The southern North Sea is one of the most heavily trawled areas of the North Sea, and many studies have described the effects of fishing (especially beam trawling) on benthic communities (e.g. Kaiser *et al.*, 1998; Rijnsdorp *et al.*, 1998; Frid *et al.*, 2000; Jennings *et al.*, 2001a, b). Therefore, we might reasonably expect trawling disturbance to affect the temporal variability of epifauna in our study area. Kaiser *et al.* (2000) showed that benthic communities dominated by sessile and high-biomass species shifted to communities dominated by small opportunistic species under chronic fishing disturbance. Moreover, Reiss *et al.* (in press) found significant negative correlations between total biomass, species richness, and secondary production and trawling intensity in the southern North Sea. Table 5 lists the days at sea of Dutch beam trawlers, the most active fleet in our study area (van Keeken *et al.*, 2007). Generally, effort of that fleet was greater at the West Frisian coast (4814–7472 days at sea) and the Oyster Ground (1344–4889 days at sea), and low along the North Frisian coast (99–379 days at sea) and on Dogger Bank (67–1043 days at sea). Further, fishing effort decreased remarkably at the West Frisian coast and the Oyster Ground from 1998 to 2007 (Table 5), giving basis to the hypothesis that the increase observed in secondary production in these areas (Figure 7) might be attributed to decreasing fishing disturbance at least as a synergistic effect of increasing temperature. However, Jennings *et al.* (2001a) investigated large-scale trawling effects on benthic production (infauna and epifauna) across quantified gradients of trawling disturbance and concluded that changes in biomass and production were related to increasing primary production driven by warming rather than trawling disturbance.

The most critical issue in interpreting the impact of fishing disturbance on benthic fauna is the spatial patchiness of fishing effort. Rijnsdorp *et al.* (1998) demonstrated that fishing effort within ICES rectangles was highly aggregated and estimated that, on average, 29% of the surface area in eight of the most heavily fished rectangles was trawled less than once per year. As our samples were taken at random within the ICES rectangles, we sampled with relatively high probability in intensively fished and relatively undisturbed areas of the rectangles. Hence, it seems unlikely that the variability we observed, especially the continuous changes found for *O. albida* (Figure 6), and the diversity (Figure 5) could be attributed to fishing disturbance. Moreover, both the total fishing effort and the temporal variability of the fishing effort at the West and North Frisian coasts provide no explanation for the significantly different community structure in those areas between the periods 1998–2000 and 2003–2008. Therefore, we assume that temperature anomalies such as cold winters or increasing temperature seem to have had a greater impact on the variability of epifaunal communities in this study than fishing effort.

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