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Brown shrimp abundance in northwest European coastal waters from 1970 to 2010 and potential causes for contrasting trends

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ABSTRACT: We investigated long-term trends in abundance of the NE Atlantic population of brown shrimp *Crangon crangon* based on data collected in annual autumn surveys carried out along the coasts of the North Sea in The Netherlands, Germany and Denmark. Surveys covered some estuaries and intertidal areas, as well as shrimp fishery grounds. The 40 yr period showed distinct regional trend differences, but only in estuarine areas: the Western Dutch Wadden Sea (increase), the Eastern Dutch Wadden Sea (decrease) and the Oosterschelde (decrease). The decrease in the Oosterschelde coincided with the closure of this sea arm from fresh water inflow. Increases in the Western and Eastern Dutch Wadden Sea were driven primarily by increased abundance of small shrimp, suggesting that the causative mechanism likely affected younger shrimp. Trends in potential causes were examined in the 2 regions. Of all abiotic factors investigated, only water clarity decreased significantly in the west but not in the east. Mean abundance of potential predators (cod, whiting, shore crab and swimming crab) was used as an indicator of predation pressure. Shore crab showed similar increases in both areas. In the other 3 species, predator abundance in the east was generally initially higher than in the west, but declined towards similar densities in recent years. Shrimp fishing pressure in NW Europe has increased strongly since the 1990s. Preliminary, spatially resolved logbook data show that shrimp landings from the Western Wadden Sea followed this increase, but those from the Eastern Wadden Sea remained stable. Apart from mechanisms related to fishing pressure and water clarity, a candidate cause of differences in abundance may be differences in food condition or competition for food. Generally biomass of benthos, a primary food for shrimp, increased in the west and remained stable in the east. However, because brown shrimp are omnivorous, quantification of changing fractions of food available to them is difficult.

KEY WORDS: Benthic community · *Crangon crangon* · Epibenthos · Predators · Shore crab · Swimming crab · Gadoids · Wadden Sea

INTRODUCTION

Brown shrimp *Crangon crangon* is a very common crustacean that inhabits the shallow waters along the east coast of the Atlantic Ocean from Norway to Morocco, the Baltic Sea, The Mediterranean and the Black Sea (Campos & Van der Veer 2008). It also represents a valuable resource for the North Sea and Wadden Sea fisheries (ICES 2010). As a predator of larvae and juvenile stages of several fish and benthic species, brown shrimp fulfil a key role in the ecosystem and locally may even dominate the benthic community (Hamerlynck et al. 1993). Brown shrimp is omnivorous and feeds on meiofauna and endobenthic macrofauna, including infaunal organisms (bivalves, cumaceans, foraminiferans, harpacticoids,

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nematodes, oligochaetes), epifaunal organisms (amphipods, isopods, gastropods) and demersal organisms (mysids, shrimps and fishes) (Pihl & Rosenberg 1984, Jensen & Jensen 1985, Pihl 1985, Nilsson et al. 1993, Oh et al. 2001). It is also an important prey species for fishes such as gobies, gadoids, several flatfish and demersal roundfish species, and several crab species (Ansell & Gibson 1990, Del Norte-Campos & Temming 1994, Van der Veer et al. 1998, Amara & Paul 2003). Because of its complicated population dynamics (almost continuous reproduction with 2 main reproduction periods, short lifespan of 2 to 3 yr, high production:biomass [$P:B$] ratio) it is difficult to quantify the structure of the population (Kuipers & Dapper 1984, Henderson & Holmes 1987). Therefore, until now it has not been possible to carry out a formal stock assessment of the kind that is performed for many commercial fish and crustacean species (van der Hammen & Poos 2010). Given the attention currently being paid to stock status in the context of the application by European shrimp fishers for a Marine Stewardship Council (MSC) label, information on the status of the population is urgently needed. In addition, shrimp fishing grounds overlap to a great extent with Natura2000 sites, so regionally stratified information is also required for management purposes.

Reproduction of brown shrimp occurs offshore at depths of 10 to 20 m (Tiews 1954, Henderson & Holmes 1987). During the egg stage, eggs are carried by females. After hatching, the free-floating planktonic larvae migrate to shallow nursery areas, such as estuaries, where they develop and settle to become demersal. The mechanisms determining recruitment of juveniles to the adult stock are not clearly understood. Correlates of recruitment that have been identified are food availability, predation pressure and environmental conditions such as water temperature, salinity, light intensity or day length and dissolved oxygen (Kuipers & Dapper 1984, Henderson & Holmes 1987, Beukema 1992, Aarnio & Bonsdorff 1993, Del Norte-Campos & Temming 1994, Cattrijsse et al. 1997, Attrill et al. 1999). Previous time series analyses identified predation pressure as the most important source of shrimp mortality (Boddeke 1968, Driver 1976, Henderson & Holmes 1987, Attrill et al. 1999, Welleman & Daan 2001, Campos et al. 2010), though predation alone seems insufficient to explain recruitment variation. River inflow, winter water temperature and the winter North Atlantic Oscillation index have also been identified as important drivers, although the directions of the effects differ among studies, locations and seasons (Siegel et al. 2005, Henderson et al. 2006). Genetically the NE Atlantic can be separated from Mediterranean populations but there are no genetic distinctions among NE Atlantic locations (Luttikhuizen et al. 2008). Therefore gene flow between NE Atlantic populations is large.

All previous time series studies have focused on a specific area within the distribution range. This study is the first to explore the time series over a large part of the species' distribution range from the Netherlands to Denmark in an integral way. It covers estuarine areas as well as shallow coastal habitats, based on a long-term survey dataset starting in 1970. We analysed the data to explore regional variation in time trends, and tried to interpret opposing regional trends by searching for contrasts in potential influencing factors.

MATERIALS AND METHODS

Sampling

The Dutch Demersal Fish Survey (DFS) covers the coastal waters (up to 25 m depth) from the southern border of the Netherlands to Esbjerg, including the Wadden Sea, the outer part of the Ems-Dollard estuary, the Westerschelde and the Oosterschelde (van Beek et al. 1989). This survey has been carried out in September–October since 1970. Areas are delineated according to tidal basins or other geographic features defined in the original survey design (Boddeke et al. 1972) Sampling along the German and Danish coast started more recently, in 1979 (Table 1). We analysed data from 10 distinct regions (delineated areas), 5 along the coast (from South to North: Voordelta, Southern Dutch coast, Dutch Wadden coast, Southern German coast, German-Danish coast) and 5 in inner waters or estuaries (from South to North: Westerschelde, Oosterschelde, Western Dutch Wadden Sea, Eastern Dutch Wadden Sea, Ems-Dollard) (Fig. 1). This division is in accordance with the Trilateral Monitoring and Assessment program (Bolle et al. 2009, Jager et al. 2009). The estuaries all have natural borders. We split the Dutch Wadden Sea into a western side and an eastern side, each consisting of 3 tidal basins. The Voordelta is distinct from the remaining coastline because of the very dynamic underwater relief characterised by sandbanks and gullies. Because all these regions are open and connected, shrimp can potentially move between them, and regional divisions do not represent natural discontinuities in all cases.

Table 1. Number of hauls sampled per year and per region along the coasts of the Netherlands, Germany and Denmark. See Fig. 1 for location of regions. –: no data

	Voordelta	Westerschelde	Oosterschelde	Southern Dutch coast	Western Dutch Wadden Sea	Eastern Dutch Wadden Sea	Dutch Wadden coast	Ems-Dollard	Southern German coast	German-Danish coast	Total
1970	6	26	31	22	47	38	22	20	–	–	212
1971	8	30	29	22	49	29	19	21	–	–	207
1972	8	28	29	26	42	30	20	20	–	–	203
1973	8	31	30	17	44	29	19	22	–	–	200
1974	8	31	32	27	49	33	19	21	–	–	220
1975	8	26	29	19	53	33	19	21	–	–	208
1976	0	26	30	0	53	33	0	21	–	–	163
1977	10	27	27	25	54	34	23	21	–	–	221
1978	1	28	29	25	54	33	23	21	8	34	256
1979	0	28	28	23	47	30	13	19	7	37	232
1980	9	29	27	17	54	33	26	21	7	39	262
1981	10	27	28	18	53	33	24	21	10	10	234
1982	18	27	28	17	54	32	28	21	14	27	266
1983	18	27	27	19	53	32	15	21	8	27	247
1984	22	27	27	20	54	31	29	21	15	25	271
1985	17	27	26	21	54	30	27	20	14	27	263
1986	17	27	26	22	54	32	28	21	15	25	267
1987	16	28	30	21	54	31	27	23	15	27	272
1988	18	27	23	22	47	30	29	22	14	27	259
1989	25	29	38	22	47	31	28	23	10	27	280
1990	25	29	33	22	46	31	28	23	15	27	279
1991	16	31	30	22	53	33	28	24	15	26	278
1992	25	28	36	29	55	18	25	28	15	25	284
1993	21	27	24	29	50	33	28	28	14	26	280
1994	19	33	31	29	50	28	28	25	15	24	282
1995	17	33	34	22	54	34	25	26	14	27	286
1996	17	33	43	22	62	34	29	27	14	27	308
1997	17	34	43	22	55	35	28	27	13	0	274
1998	9	34	42	18	62	35	0	26	0	0	226
1999	17	35	35	22	57	36	14	22	1	0	239
2000	14	43	42	9	68	36	17	26	10	25	290
2001	0	48	45	18	53	35	28	26	15	22	290
2002	21	41	42	21	53	33	26	26	14	0	277
2003	16	35	37	22	55	31	28	26	15	24	289
2004	17	30	35	17	61	32	19	25	14	22	272
2005	17	36	41	28	60	33	30	33	15	23	316
2006	15	36	41	23	62	32	28	29	15	23	304
2007	16	36	41	28	64	31	30	25	14	22	307
2008	16	36	34	19	61	30	19	27	11	10	263
2009	16	36	35	27	58	30	29	27	15	22	295
2010	16	36	41	25	57	28	29	26	15	22	295
Total	574	1286	1359	879	2212	1305	954	973	406	729	10677

Between 1979 and 2010 a total of 230 to 310 hauls yr^{-1} were taken over the whole area (Table 1). The number of hauls per area was kept as constant as possible. In several years not all sampling points were sampled due to adverse weather and, in a few years, whole regions were omitted (1976: Dutch coastal areas; 1979 and 2001: Voordelta; 1998: German-Danish coast). For each haul, the position, date, time of day and depth were recorded. The Westerschelde, Oosterschelde and Wadden Sea were sampled with a 3 m beam trawl, while along the coast a 6 m beam was used. In both cases, the beam trawls were rigged with 1 tickler chain, a bobbin rope, and a fine-meshed cod-end (20 mm). The reason for the choice of a different size is that a 3 m beam is more manoeuvrable in the estuaries, where sampling often took place in narrow gullies, whereas the 3 m beam would be

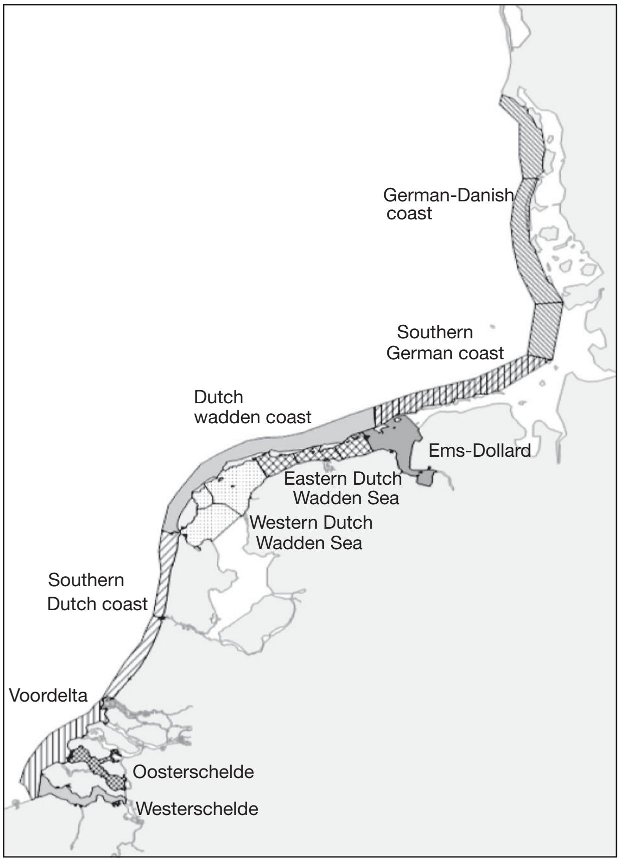

Fig. 1. Survey areas for brown shrimp *Crangon crangon* abundance in 10 regions along North Sea coasts of The Netherlands, Germany and Denmark

too light in the less sheltered, generally deeper waters along the coast. The expectation is that densities (expressed as number of individuals per 10 000 m^{-2}) derived from both these gears do not differ, although they have never been formally compared. For the calculations of indices as input for stock assessments the data from both 3 and 6 m beams are treated in a similar combined way (ICES 2011). Fishing was restricted to the tidal channels and gullies deeper than 2 m because of the draught of the research vessel. The combination of low fishing speed (2 to 3 knots) and fine mesh size results in selection of brown shrimp > 20 mm, small fish species, younger year classes of large fish, and other epibenthos. Sample locations were stratified by depth (5 × 5 m depth strata). Shrimp were separated from the fish and other epibenthos and measured to the nearest millimetre. The mean abundance per area was calculated for all regions in the period 1970 to 2010, weighted by surface area of the 5 depth strata (taken from ICES 2011). Densities of potential shrimp predators (gadoids and 2 species of crabs, only available from 1994 onwards) were derived from the DFS survey (Tulp et al. 2008).

Data analyses

Time series of individual species were analysed using TrendSpotter, a computer program based on structural time-series analysis (Harvey 1989) in combination with the Kalman filter (Visser 2004). The Kalman filter algorithm operates recursively on streams of noisy input data to produce a statistically optimal estimate of the underlying system state (Kalman 1960). The program is used to identify periods with significant increases or decreases beyond annual fluctuations, by estimating smoothed population numbers for a time series with N equidistant measurements over time. TrendSpotter also estimates the standard deviations (SDs) of the smoothed population numbers. Finally, it estimates the SDs of the differences between consecutive time points and any time point with respect to the last. The estimation of confidence intervals (CIs) is based on the deviations of time point values from the smoothed line. The output also produces autocorrelation functions. A more detailed description of the method can be found in Visser (2004) and Soldaat et al. (2007). This method accounts for serial correlation and provides confidence limits (CLs) to test for changes in abun-

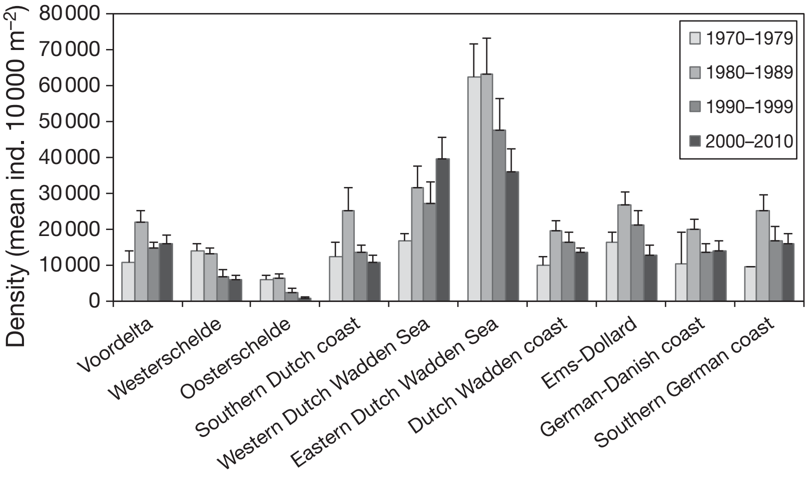

Fig. 2. Densities (mean ind. 10000 m^{-2} + SE) of brown shrimp along North Sea coasts compared across regions and periods. See Fig. 1 for locations of regions

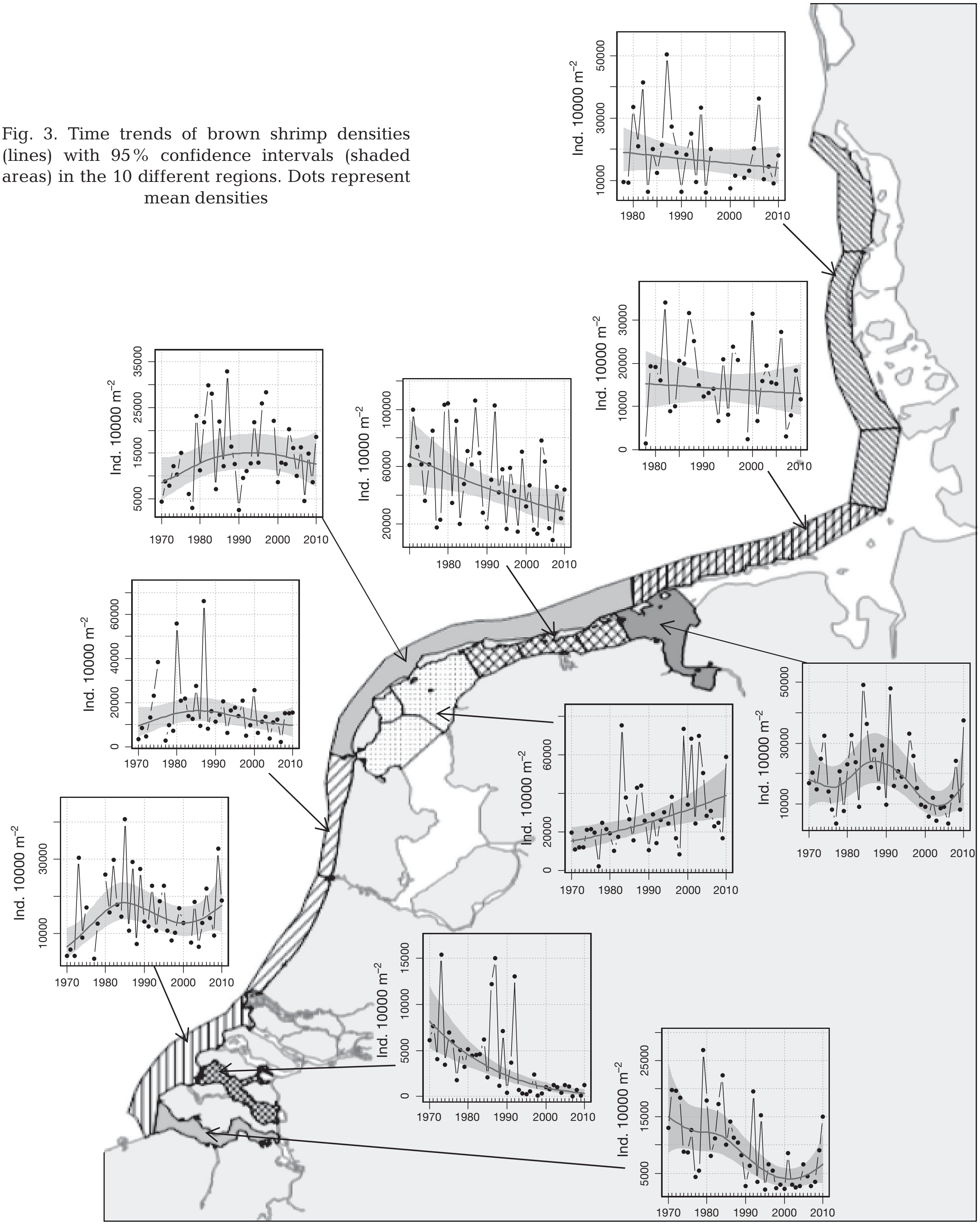

Fig. 3. Time trends of brown shrimp densities (lines) with 95% confidence intervals (shaded areas) in the 10 different regions. Dots represent mean densities

dance. The classification of trends in the last decade was based on the 95% CI of the yearly change rate method presented in Soldaat et al. (2007). We distinguished among strong increase, moderate increase, stable, moderate decline, steep decline and uncertain. A yearly change rate of 1.00 indicates no change. A strong increase is defined as a yearly change rate > 1.05 (5% increase yr^{-1}), based on the value of the lower CL (>1.05). Similarly a steep decline is characterised by a yearly change rate ≤0.95, based on the value of the upper CL (<0.95). A moderate increase has a lower CL between 1.00 and 1.05 and a moderate decline has an upper CL between 0.95 and 1.00. In stable trends the CI includes 1.00, and the lower CL ≥0.95 and upper CL ≤ 1.05. An uncertain trend is defined as having a CI that includes 1.00, and the lower CL < 0.95 or upper CL > 1.05. Apart from a classification by year an overall classification of the last decade was made. Densities were 4th root transformed before analyses because of non-normality. Trend analyses were based on density in numbers and carried out separately for 2 size classes determined by the commercial size in the shrimp fisheries (small <54 mm, large ≥54 mm).

RESULTS

Mean densities varied greatly among regions with highest values in the Dutch Wadden Sea (Fig. 2). At the start of the monitoring series densities in the Eastern Wadden Sea were the highest and at least twice as high compared to all other regions. Currently, densities in the Eastern and Western Wadden Sea are very similar but these are still twice as high as neighbouring areas. In all open coastal areas maximum densities were recorded in the 1980s (Fig. 2).

Time trends showed great variations between regions (Fig. 3). Periods with significant yearly declines occurred in the Westerschelde, Oosterschelde and the Eastern Dutch Wadden Sea. Only in the Voordelta and Western Dutch Wadden Sea were periods with significant increases were identified (Fig. 4). The last decade showed a steep increase for the Western Dutch Wadden Sea, a steep decrease in the Eastern Wadden Sea and a steep decline in the Oosterschelde. In all other areas trends in the last decade were uncertain.

The Wadden Sea regions each contain 3 tidal basins (Fig. 1). To find out if there is a specific tidal basin dominating this trend we looked at trends within these basins. Partial trends show a moderate increase throughout the whole period in the Western Wadden Sea areas 610 and 616. In the last decade these increases were moderate (area 610) and strong (616). In the Eastern Wadden Sea the decline was moderate in the period 1977 to 1983 in area 619 (Fig. 5). The trends for the final decade in all 3 areas were identified as uncertain.

The total rate of change in the last decade, calculated as the smoothed population number in the last year compared with the smoothed population number in the first year (where >1 indicates an increase and <1 a decrease of population), was 1.24 in the Western Wadden Sea, 0.79 in the Eastern Dutch Wadden Sea, and 0.35 in the Oosterschelde (Fig. 6). Size-structured time trends show that small individuals drive the increase in the Western Dutch Wadden Sea (Fig. 7). In the Voordelta the increase in the last decade showed up in both size classes, but it was only significant in the larger size class. Regions with significant declines (Oosterschelde and Eastern Dutch Wadden Sea) showed declines in both size classes, but declines were significant only in the small size class (with stable trends in large individuals). For 1986 to 1995 only, the decline in the Oosterschelde was also significant for large individuals. We found periods with significant increase in large individuals in the Voordelta (1971 to 1980) and the Southern Dutch coast (1973

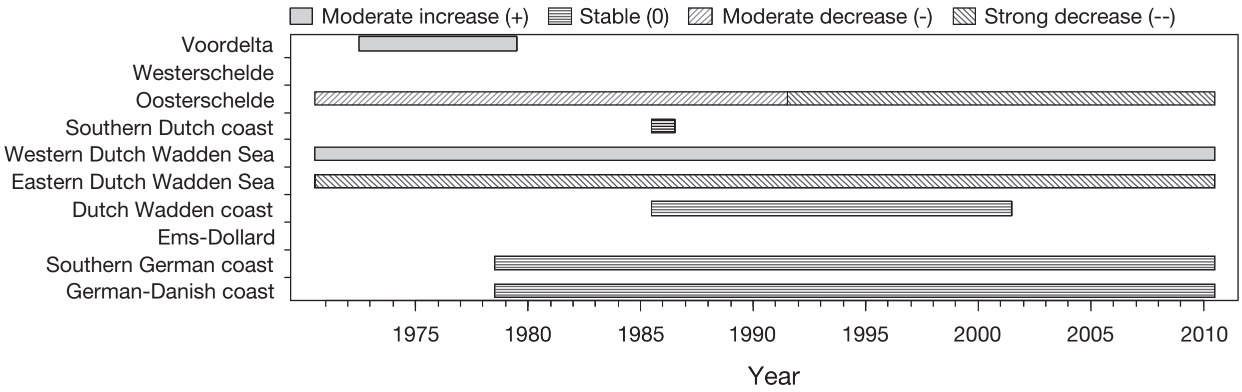

Fig. 4. Summary of trends in densities of brown shrimp (ind. 10 000 m^{-2}) in the 10 regions. Only periods with significant changes or stable trends are indicated

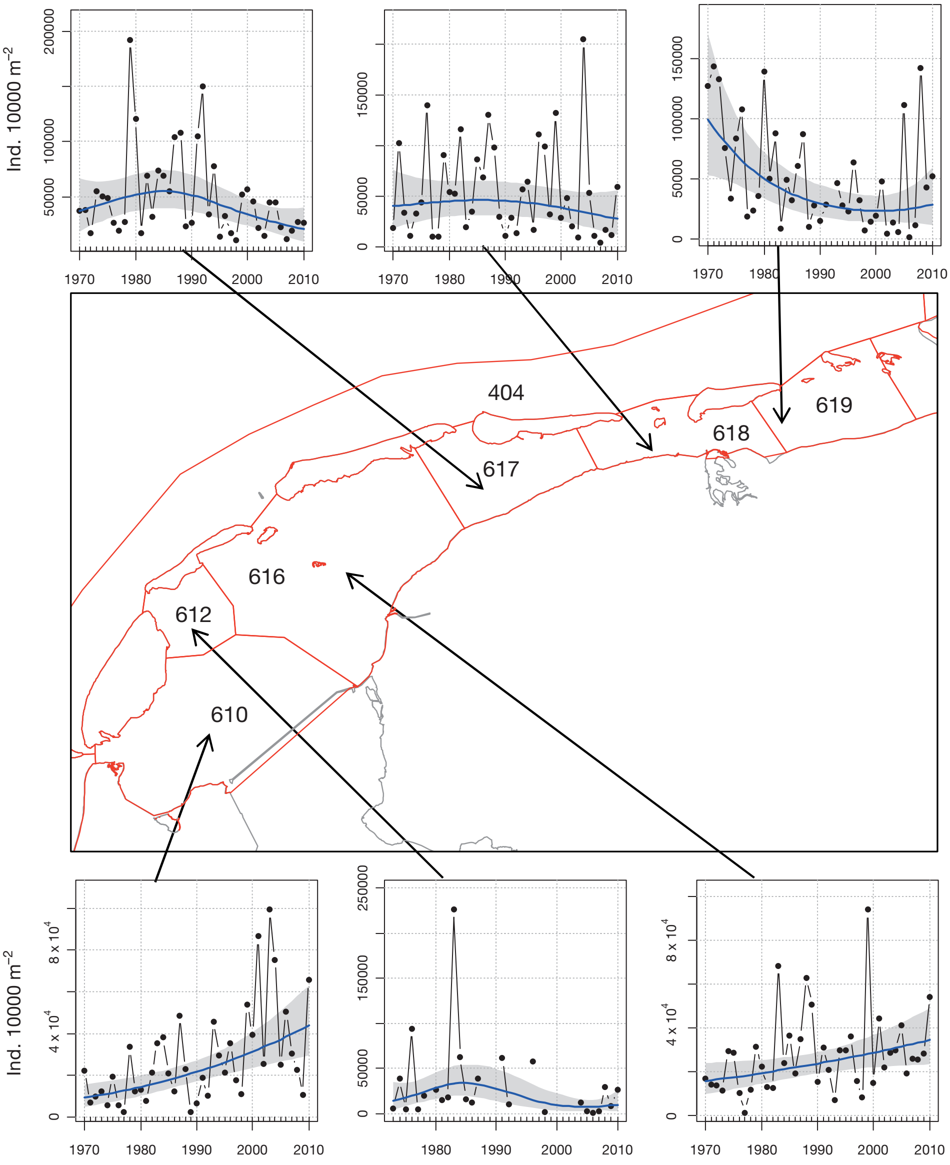

Fig. 5. Time trends and 95% confidence intervals of brown shrimp densities (ind. 10000 m^{-2}) in the subregions within the Dutch Wadden Sea. See Fig. 3 legend for explanation of lines and shading

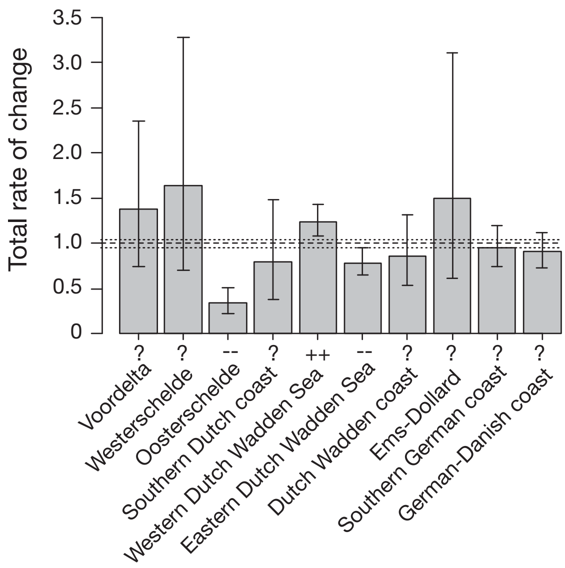

Fig. 6. Total rate of change (median ± 95% confidence intervals) in the last decade (2000 to 2010) in the 10 regions. Symbols below the *x*-axis show the classification of trends (as per Soldaat et al. 2007): ++ strong increase, –– strong decrease, ? uncertain

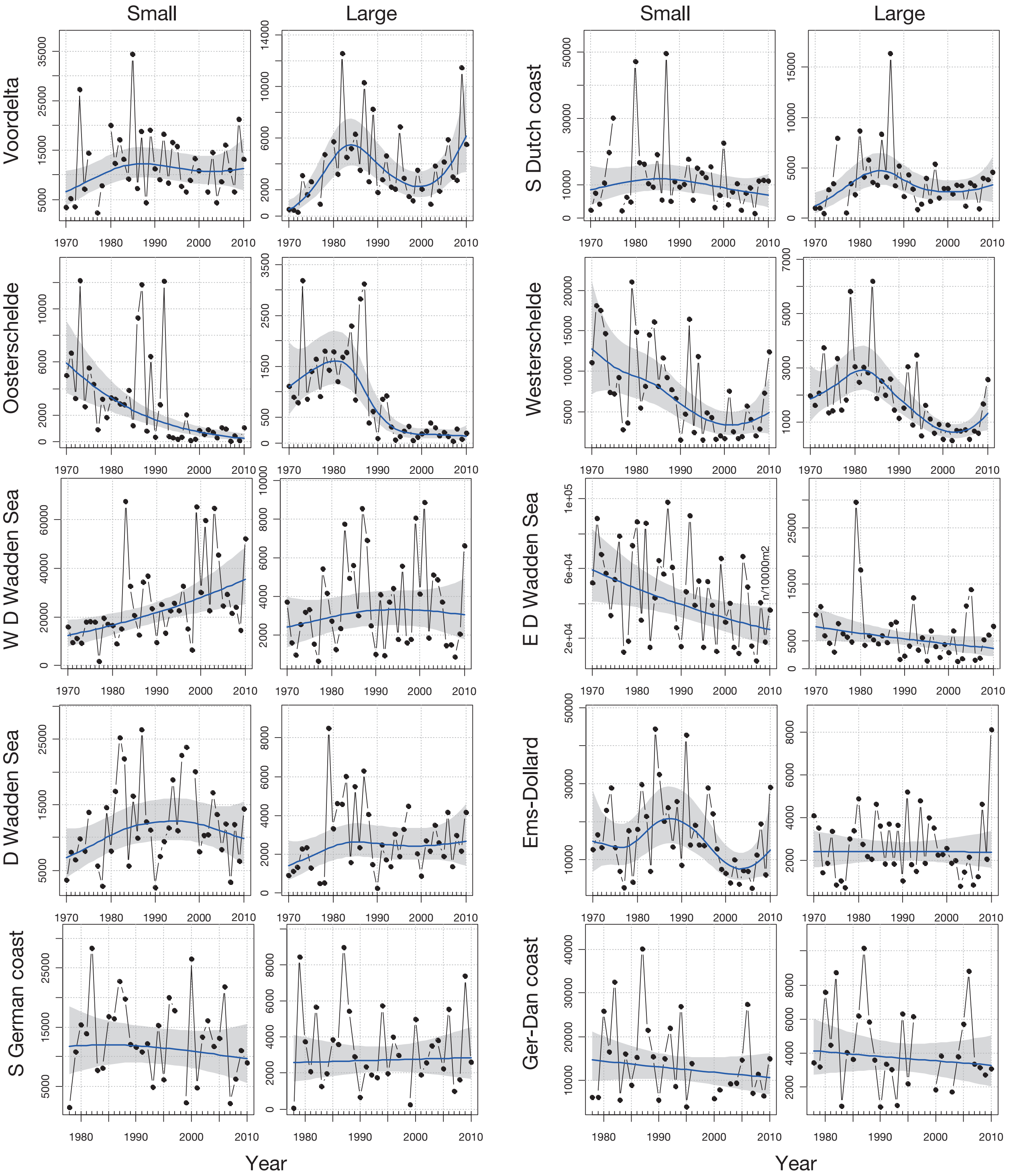

Fig. 7. Time trends of densities and 95% confidence intervals in small (<54 mm) and large (≥54 mm) brown shrimp in the regions with significant changes. See Fig. 3 legend for explanation of lines and shading

to 1978), but no significant declines or increases in other regions or either size class.

Autocorrelation functions (ACFs) showed a significant correlation between densities in years with a time lag of 1 to 5 yr for the regions Westerschelde and Oosterschelde (Fig. 8), indicating that data from one year correlated significantly with the previous and following 5 yr. None of the other regions showed significant ACFs, indicating no correlation between a given observation and the previous or subsequent

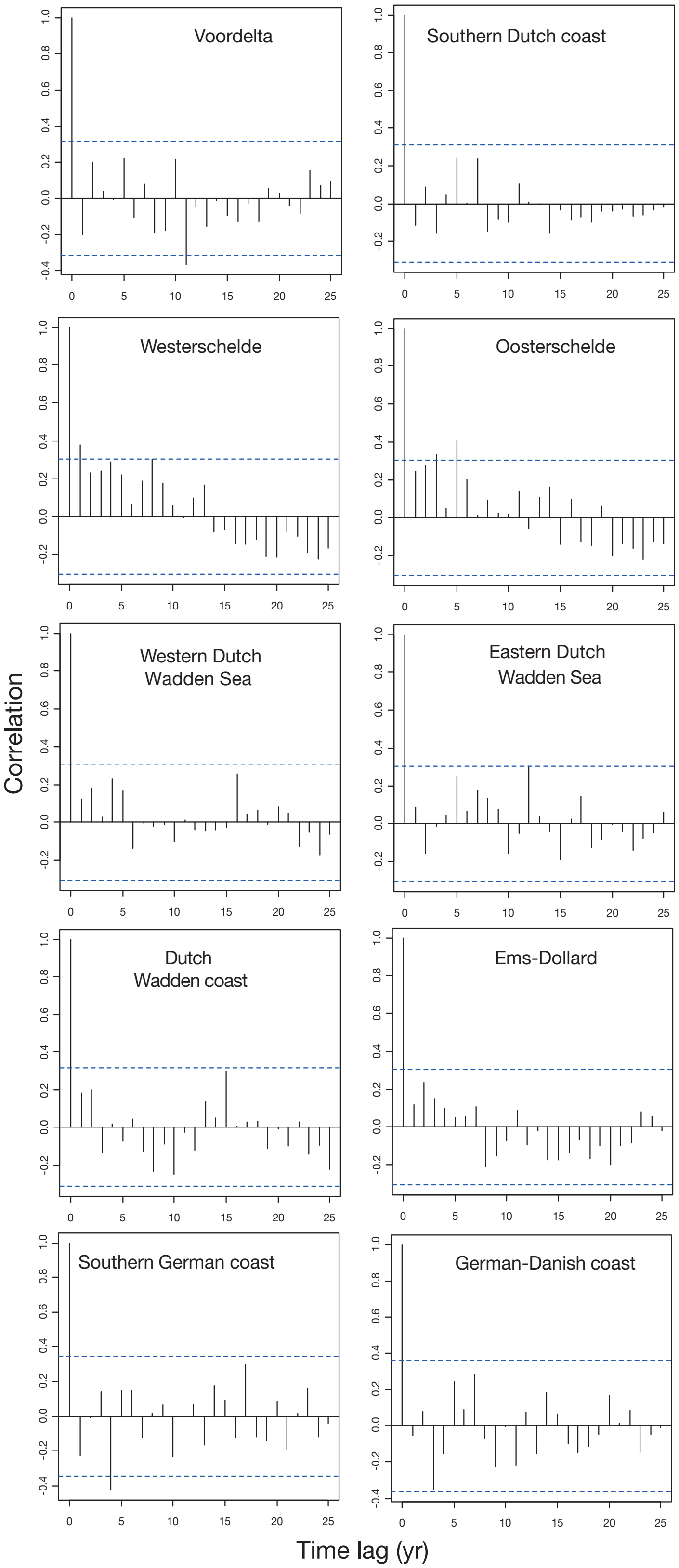

Fig. 8. Serial correlation in the different regions. The auto-correlation function shows the Pearson correlation of a time series

year. However, within areas (Fig. 5), the smaller size class in area 610 showed significant serial correlation. In the Oosterschelde, the ACF was mainly determined by large individuals, whereas both size classes contributed to the ACF in the Westerschelde (although only the small sizes showed a significant ACF for a lag of 1 yr).

The opposing trends in the Western and Eastern Dutch Wadden Sea triggered a search for contrasting trends in other parameters that might explain this contrast. Abundance of likely fish predators (cod *Gadus morhua* and whiting *Merlangius merlangus*) declined in both areas, with a stronger decline in the Eastern Dutch Wadden Sea. Other potential fish preying on brown shrimp did not show contrasting trends either (not shown). The most abundant potential epibenthic predators were the shore crab *Carcinus maenas* and the swimming crab *Liocarcinus holsatus*. The shore crab increased significantly in both areas. The swimming crab declined significantly in the last decade in the Eastern Dutch Wadden Sea, while the trend is uncertain in the Western Dutch Wadden Sea (Fig. 9).

DISCUSSION

Long-term trends in abundance

Given the complicated population dynamics and possibilities for migration between the regions, we had not expected to find trends, or year-to-year correlation, or regional variation. The regions where we did find significant, long-term time trends in densities (Western Dutch Wadden Sea, Eastern Dutch Wadden Sea, Oosterschelde) and serial correlation (Oosterschelde and Westerschelde) were mainly estuarine areas. In a few regions periods with significant changes were identified: increases throughout the 40 yr period in the Western Dutch Wadden Sea, a decrease throughout in the Eastern Dutch Wadden Sea and the Oosterschelde and an increase in the period 1973 to 1979 in the Voordelta. The decrease in the Oosterschelde strongly parallels the timing of the building of the storm surge barrier and the closure of the sea arm from freshwater input in 1986 (Nienhuis et al. 1994), and confirms previous studies (Hostens & Hamerlynck 1994). The final decade showed a strong increase in the Western Wadden Sea and a steep decrease in the Eastern Dutch Wadden Sea and the Oosterschelde. While population dynamics in both the Eastern and Western Dutch Wadden Sea were mainly driven by the small individuals, the recent increase in the Voordelta was mainly due to an increase in large individuals.

A similar increase for the Western Wadden Sea was recorded by Campos et al. (2010) for brown shrimp caught at the southern end of Dutch island Texel (1973 to 2008) and for juvenile shrimp in the Balgzand intertidal area at the western end of the Wadden Sea (1973 to 2002) (Beukema & Dekker 2005). Increased recruitment (though not adults) was also reported for Bristol Channel (1981–2005) (Henderson et al. 2006).

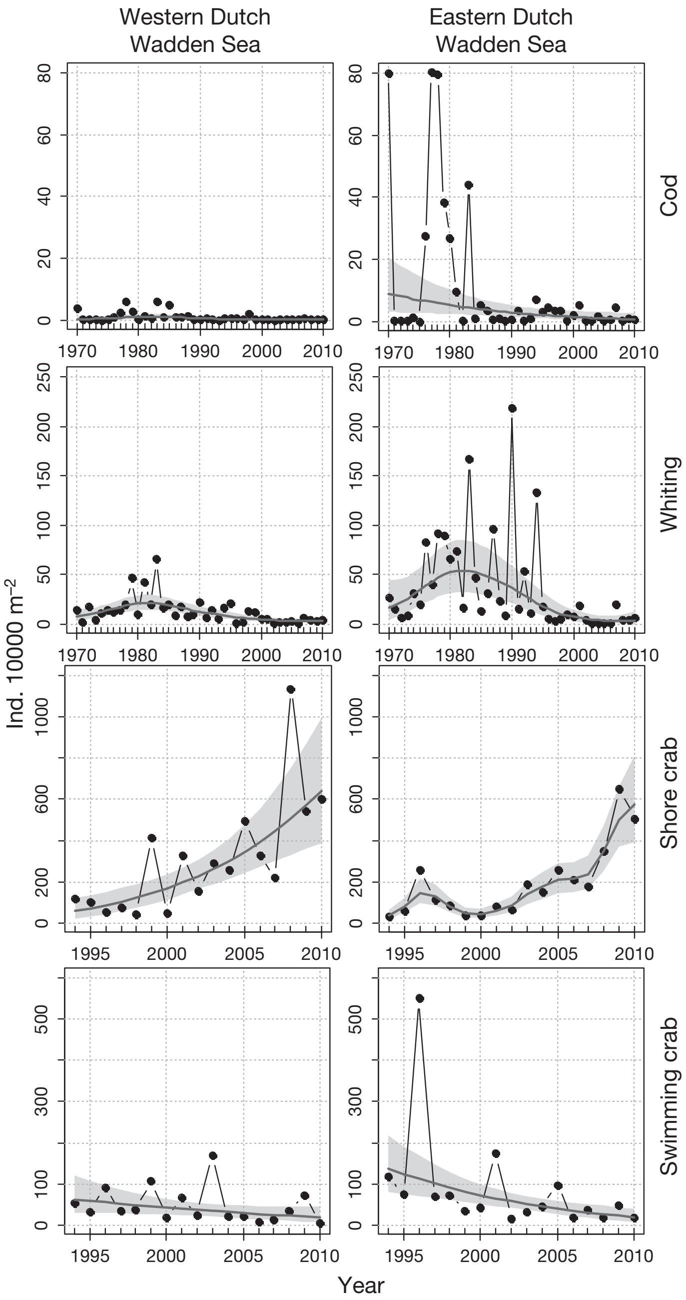

Fig. 9. Time trends of the most important predators of brown shrimp in the Western and Eastern Dutch Wadden Sea. See Fig. 3 legend for explanation of lines and shading

Opposing trends in the Dutch Wadden Sea: possible mechanisms

Small individuals determined trends in the Dutch Wadden Sea, suggesting that the driving mechanism acted on smaller rather larger individuals. Possible candidates causing these opposing trends include: differences in abiotic variables, predation pressure, food availability, or human impacts. We examined 4 of the most likely predators but found no strong differences in time trends between the 2 regions. Fishing pressure (on cockles, mussels and brown shrimp) has changed since the 1990s (Taal et al. 2004, ICES 2010). We derived the few geographically resolved data available from a selection of logbook data of fishermen with Wadden Sea permits and that landed shrimp in Dutch Wadden Sea harbours. (It is possible however that some of these landed shrimp were not actually caught inside the Wadden Sea). These data indicate that since 1999 shrimp landings taken from the Western Wadden Sea have increased while those from the Eastern Wadden Sea have remained stable (Fig. 10).

Available abiotic time series include water temperature, salinity, and water clarity. Temperature and salinity (affected by river runoff) are known to affect brown shrimp ecophysiology and migration and indirectly influence the stock through changes in productivity. Mean temperatures in the survey season (Sept–Oct) over the study period increased similarly

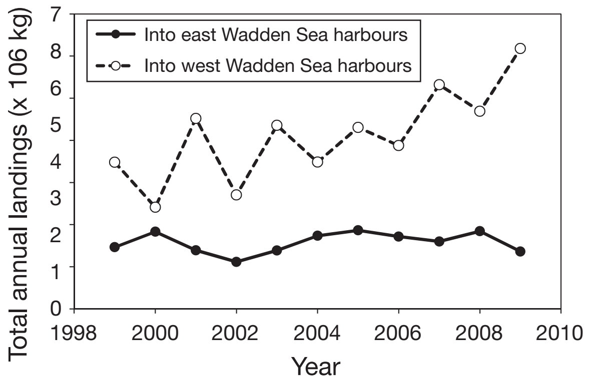

Fig. 10. Development of brown shrimp landings at Western and Eastern Wadden Sea harbours by Dutch fishermen holding Wadden Sea licenses, based on logbook data (source: VISSTAT, Agricultural Economics Research Institute [LEI])

in the Western (Marsdiep) and Eastern Wadden Sea (Zoutkamp) (www.waterbase.nl; Fig. 11). The observed temperatures in the area are all well within the species' temperature tolerance range (optimal temperature 23°C, maximum 30°C; Freitas et al. 2007). Winter temperatures are known to influence local brown shrimp stocks (Siegel et al. 2005), but this variable also shows similar trends in both areas. Salinity data from the in the Eastern (Zoutkamp) and Western Wadden Sea (Blauwe Slenk Oost) show consistently higher mean annual salinity in the East compared to the West and a decreasing trend in both areas probably related to an increase in river runoff (www.waterbase.nl, Fig. 9). The outflow from the IJsselmeer into the Western Wadden Sea causes the salinity difference between east and west. Salinity tolerance is temperature and age dependent, but generally brown shrimp are found at salinities between 7 and 40 PSU (McLusky et al. 1982). In spring tide periods, shrimp are exposed to tidal salinity fluctuations ranging from 25 to 25 PSU in summer and from 14 to 34 PSU in winter (Regnault 1984). Egg development can occur at salinities >15 PSU, (Broekema 1942) and temperatures between 6 and 21°C (Wear 1974). However, successful larval development requires temperatures between 9 and 18°C and salinities >16; development slows below 25 PSU (Criales & Anger 1986). Though temperature and salinity patterns in the study area include long periods with suboptimal conditions for development, growth and reproduction, neither salinity nor temperature seem to be critical in structuring brown shrimp populations in the Wadden Sea. However, differences in bathymetry between the regions may result in temperatures and salinity extremes in shallow areas, but we lack the data to investigate this possibility.

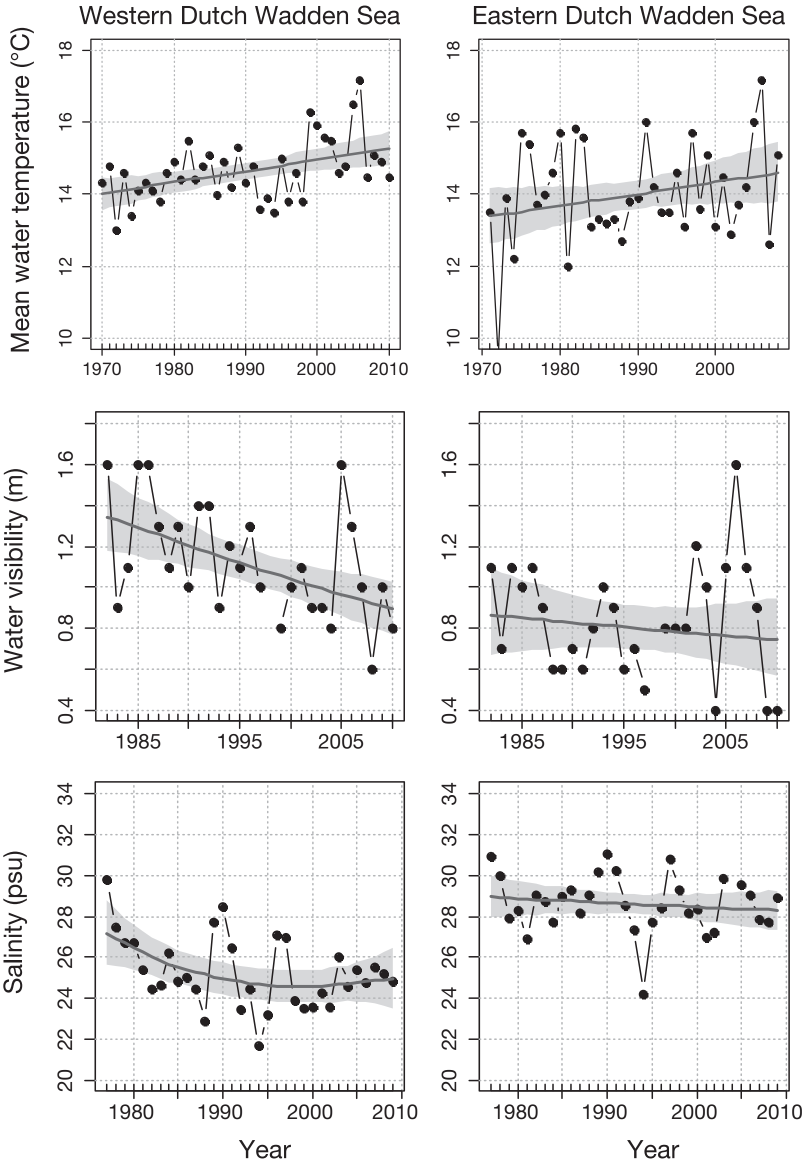

Fig. 11. Mean seawater temperature (Sep–Oct), water clarity (Secchi measurements) and salinity (annual means) in the Western and Eastern Dutch Wadden Sea. Data on temperature and salinity from Waterbase (www.waterbase.nl); on water clarity from the Dutch Demersal Fish Survey (DFS). See Fig. 3 legend for explanation of lines and shading

Besides temperature and salinity, water clarity may play a role both in shrimp abundance and in their catchability. Secchi disc observations during the DFS (data only available for 1982 to 2010) show that water clarity is generally lower in the Eastern (0.84 ± 0.28 m) than in the Western Dutch Wadden Sea (1.13 ± 0.28 m), and shows a significant decline over this period in the Western Wadden Sea, but an uncertain trend in the Eastern Wadden Sea (Fig. 11). Catches of fish and crustaceans are known to vary with turbidity (Stoner 1991, Beyst et al. 2002). Maximum catch rates of dab *Limanda limanda* that occur in the same habitat as brown shrimp occurred in water with a clarity of 1 to 1.5 m (Bolle et al. 2001). It is unknown how brown shrimp catchability varies with water clarity, but presumably there is an optimum. In a dynamic area such as the Wadden Sea the bathymetry has undoubtedly changed throughout the period, possibly influencing shrimp densities (given that densities vary strongly with depth), but we lack spatially resolved time series.

Since brown shrimp are trophic generalists, quantifying their food resources is difficult. The diet of brown shrimp includes both meiofauna and endobenthic macrofauna, depending on season (Pihl & Rosenberg 1984, Pihl 1985, Nilsson et al. 1993). Modelled trends in production rates of benthic food are available for the Western Wadden Sea only, and indicate an increase from the 1970s to the mid-1980s followed by an ongoing decrease (B. Brinkman pers. comm.). The reduction in nutrients from the early 1980s onwards has been stronger in the Western than the Eastern Wadden Sea (Brinkman 2008). For the Balgzand area, a general increase in benthic biomass has been observed since the early 1980s (Philippart et al. 2007), largely because of drastic increases in large macrofauna such as *Mya arenaria*. Shellfish filtering activity decreased, however, and followed the nutrient loading pattern. Although time series for the Eastern Wadden Sea are shorter, evidence for a biomass increase is lacking (van der Graaf et al. 2009). A correlation with food availability would be expected only if food is limiting for brown shrimp. Density-dependent regulation of brown shrimp has been reported for the Bristol Channel (Henderson et al. 2006) and on Balgzand in the Western Wadden Sea (Kuipers & Dapper 1981). Growth reduction due to food limitation was reported by Amara & Paul (2003) for the French coast of the eastern English Channel. Food limitation in brown shrimp has been shown to occur in the German Wadden Sea from November until April, when up to 75% of the population exhibited signs of starvation or food limitation (Hufnagl et al. 2010). Nonetheless, Hufnagl et al. (2010) conclude that food limitation has only limited direct effects on mortality and instead impairs growth performance.

Given the complexity and dynamics of the area, the scale at which processes act are likely to be crucial. The Eastern and Western Dutch Wadden Sea are very different in their morphology and hydrodynamics. But these 2 regions also exhibit large variations in several parameters, and a mechanistic approach aimed at integrating food availability, energetic needs and mortality is probably the most promising way forward to understand trends in brown shrimp populations.

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