ELSEVIER

In Collaboration with the Royal Netherlands Institute for Sea Research

Journal of Sea Research 60 (2008) 54–73

JOURNAL OF SEA RESEARCH

www.elsevier.com/locate/seares

# Signals from the shallows: In search of common patterns in long-term trends in Dutch estuarine and coastal fish

Ingrid Tulp *, Loes J. Bolle, Adriaan D. Rijnsdorp

*Wageningen IMARES, Institute for Marine Resources and Ecosystem Studies, P.O. Box 68 IJmuiden, 1970 AB, The Netherlands*

Received 7 March 2008; received in revised form 29 April 2008; accepted 29 April 2008
Available online 10 May 2008

**Abstract**

Shallow waters along the North Sea coast provide nursery areas for juveniles of commercially exploited species and natural habitat for resident species and seasonal visitors. The areas have gone through major changes in the last decades due to climate change and human activities such as fishing and eutrophication and changes in abundance of apex predators. Using a long-term dataset we present trends from 1970 to 2006 in 34 fish species in three coastal areas in the Netherlands: the Dutch Wadden Sea, the Westerschelde and the Dutch coastal zone. The patterns varied widely among individual species as well as between the three areas. Total fish biomass showed a dome shape pattern with an increase from 1970 to 1985 and a subsequent decline until the early 2000s. Based on multivariate and time series analyses we explore possible correlations of fish density with a predefined set of three categories of environmental variables: abiotic, biotic and fisheries related variables. Dynamic factor analysis (DFA) identified one common trend for every area: for the Wadden Sea and Westerschelde increasing from the 1970s to the early 1980s followed by a steep decrease until the mid 1990s, a temporary period (until 2002) of increase for the Wadden Sea, and a continuing increase for the Westerschelde. The common trend in the Dutch coastal zone shows a similar increase but a time lag compared to the estuarine areas, while the distinct decline was absent here. The species that showed the strongest correlation with this common trend differed between the areas, and explains the difference between the common trend in the coastal zone with that in the estuarine areas. Common trends were best described by models containing variables from all categories of environmental variables (only maximum 2 tested at a time).


*Keywords:* Fish; Biomass; Wadden Sea; Dutch coast; Westerschelde; Time series analyses; Dynamic factor analysis

## 1. Introduction

Shallow coastal areas in the Netherlands such as the Wadden Sea and Westerschelde have long been regarded important nursery areas for the juveniles of many North Sea fishes (Zijlstra, 1976; Bergman et al., 1989; van Beek et al., 1989). Nurseries are areas where juveniles aggregate and where survival and growth are enhanced through better feeding conditions, refuge opportunities and high connectivity with other habitats. After they have reached a certain size or age, they leave the nursery area and recruit to the (sub)adult populations (Pihl et al., 2002). Other species visit these shallow areas only seasonally. In addition to marine juveniles and seasonal migrants there are also several resident species

* Corresponding author.
*E-mail address:* ingrid.tulp@wur.nl (I. Tulp).

1385-1101/$ - see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.seares.2008.04.004

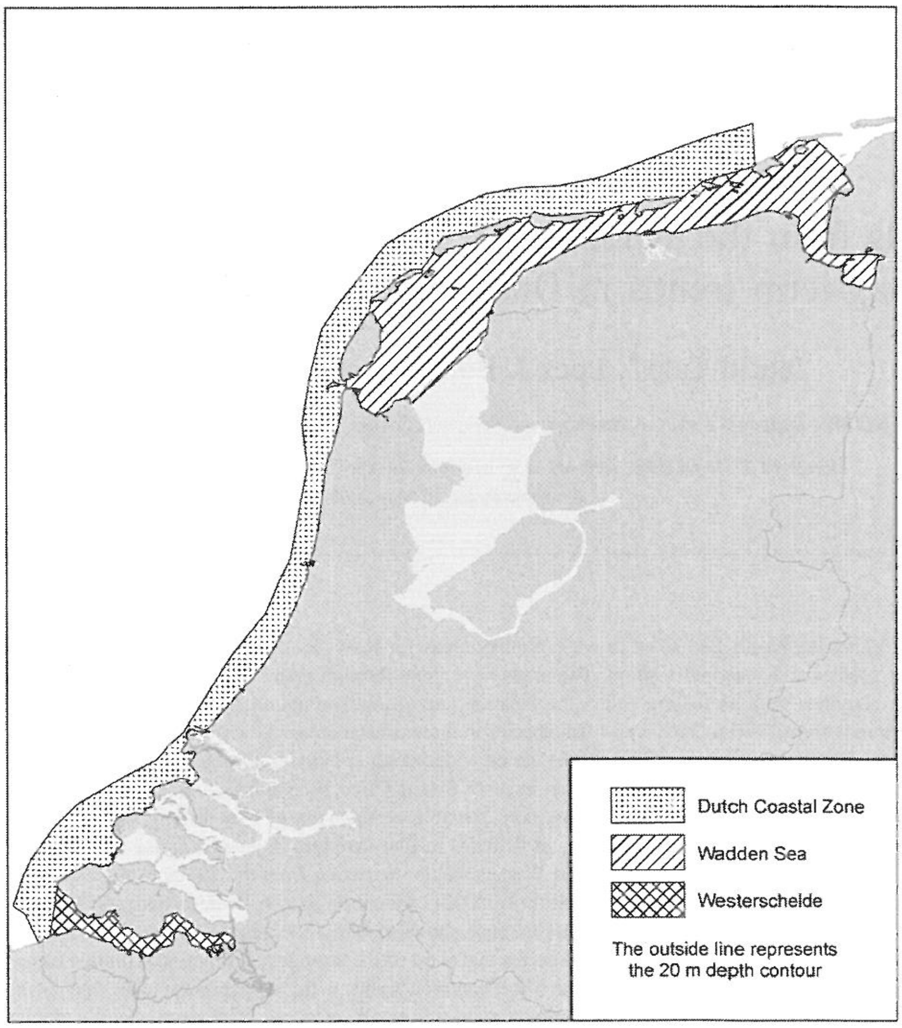



Fig. 1. The three coastal areas in the Netherlands used in this study.

that inhabit the Wadden Sea and Westerschelde year round. They entirely depend on the estuarine environment in all life stages. Most non-resident species leave in autumn and migrate to the deeper waters of the North Sea and return again in spring.

In addition to its natural dynamics, environmental characteristics in the coastal areas have changed considerably in the past decades. Long-term data series have shown that water temperature has increased (van Aken, 2003), a phenomenon that has been observed at North Sea scale as well (Becker and Pauly, 1996). Nutrient loads showed a peak in the seventies of the last century and decreased subsequently (Van Raaphorst and De Jonge, 2004). Especially in shallow areas such strong changes in environmental factors are expected to impact the ecosystem. Changes in primary production and bivalve recruitment (Cadee and Hegeman, 2002; Philippart et al., 2003; Philippart et al., 2007) and a change in the composition of the benthic community has been shown (Ens et al., 2004). Fish are in the middle of the food web, they feed on zooplankton and benthos and are eaten by predatory fish, birds and sea mammals. Depending on whether the abundance of fish is controlled top-down or bottom-up, they are likely to respond to changes in either food availability or predator abundance.

On top of changes in environmental conditions, also human activities such as shellfish fishing have impacted coastal waters (Piersma et al., 2001; van Gils et al., 2006). Until 1990 the cockle *Cerastoderma edule* fisheries was not limited by quota, between 1990 and 2003 it was more or less regulated and by 2005 it was expelled from the Wadden Sea. Mussel fisheries take place on mussel cultivation lots in the Wadden Sea. Shrimp fisheries has traditionally been an important fisheries in the Wadden Sea and adjacent coastal waters. Although brown shrimp *Crangon crangon* is the target species of this fisheries, young fish are caught as well and discarded. Due to the fact that brown shrimp is a non-quota species, there is very little information on the magnitude and variations in shrimp fisheries. The impact of this type of fisheries on the ecosystem is poorly known, but bycatch is substantial (van Marlen et al., 1998; Polet, 2003; Doeksen, 2006; Catchpole et al., 2008). Offshore fisheries will also directly and indirectly impact the coastal fish assemblage through the offshore species that utilize coastal waters as nurseries or seasonal feeding areas (Zijlstra, 1976; van Beek et al., 1989).

The above changes in physical (man-induced or not) and biological factors will likely result in changes in the abundance and species composition. Long-term trends in the fish assemblage of the Wadden Sea, Westerschelde and the shallow part of the Dutch coastal zone (Fig. 1) since 1970 are explored using data of the Demersal Fish Survey (DFS). By comparing trends in the Wadden Sea and Westerschelde to those in the shallow part of the Dutch coast (Fig. 1) we attempt to identify patterns among species and species groups sharing similar characteristics that could give rise to the hypotheses on the causes of observed trends. The objective of this contribution is twofold: (a) to present long-term trends in total fish densities together with trends on individual fish species, (b) to explore the effect of environmental variables, food availability and predator populations on patterns in changes in the fish community using time series analyses.

## 2. Methods

### 2.1. Time series fish

The Dutch Demersal Fish Survey (DFS) is part of an international inshore survey carried out by the Netherlands, England, Belgium and Germany (van Beek et al., 1989). The Dutch survey covers the coastal waters from the southern border of the Netherlands to Esbjerg, including the Wadden Sea, the outer part of the Eems-Dollard estuary, the Westerschelde and the Oosterschelde. This survey has been carried out in September–October since 1970. For the purpose of this paper data from three distinct areas were analysed: the Dutch Wadden Sea (including the outer part of the Eems-Dollard estuary), the Dutch coastal zone and the Westerschelde (Fig. 1). Each year ca 120, 65, and 40 hauls are taken in the three areas, respectively. Sampling effort has been constant over the years, although in a few years not all sampling points were sampled due to adverse weather (e.g. 1976 Dutch coastal area). For each haul, the position, date, time of day, depth and surface water temperature were recorded. The Westerschelde and Wadden Sea are sampled with a 3 m-beam trawl, while along the Dutch coast a 6 m beam is used. The beam trawls were rigged with one tickler chain, a bobbin rope, and a fine-meshed cod-end (20 mm). Fishing is restricted to the tidal channels and gullies

Table 1

List of species for which trend data are presented and their classification in food groups and biogeographic guild

| Species | Scientific name | Food | Biogeographic guild |
|---|---|---|---|
| River lamprey | *Lampetra fluviatilis* | Parasitic | Boreal |
| Eel | *Anguilla anguilla* | Benthivore | Atlantic |
| Twaite shad | *Allosa fallax* | Planktivore | Lusitanian |
| Herring | *Clupea harengus* | Planktivore | Boreal |
| Sprat | *Sprattus sprattus* | Planktivore | Lusitanian |
| Smelt | *Osmerus eperlanus* | Planktivore | Boreal |
| Cod | *Gadus morhua* | Shrimp/fish | Boreal |
| Poor cod | *Trisopterus minutus* | Benthivore | Lusitanian |
| Bib | *Trisopterus luscus* | Shrimp/fish | Lusitanian |
| Whiting | *Merlangius merlangus* | Shrimp/fish | Lusitanian |
| Five-bearded rockling | *Ciliata mustela* | Shrimp/fish | Boreal |
| Eelpout | *Zoarces viviparous* | Benthivore | Boreal |
| Pipefishes | *Syngnathus sp.* | Planktivore | Lusitanian |
| Tub gurnard | *Trigla lucerna* | Shrimp/fish | Lusitanian |
| Grey gurnard | *Eutrigla gurnardus* | Shrimp/fish | Lusitanian |
| Bull rout | *Myoxocephalus scorpius* | Shrimp/fish | Boreal |
| Hooknose | *Agonus cataphractus* | Shrimp/fish | Boreal |
| Sea snail | *Liparis liparis* | Shrimp/fish | Boreal |
| Lumpfish | *Cyclopterus lumpus* | Jellyfish | Boreal |
| Sea bass | *Dicentrarchus labrax* | Shrimp/fish | Lusitanian |
| Lesser weever | *Echiichthys vipera* | Benthivore | Lusitanian |
| Butterfish | *Pholis gunnellus* | Benthivore | Boreal |
| Sandeel | *Ammodytes* sp. | Planktivore | Boreal |
| Greater sandeel | *Hyperoplus lanceolatus* | Planktivore | Boreal |
| Dragonet | *Callionymus lyra* | Benthivore | Lusitanian |
| Gobies | *Pomatoschistus* sp. | Shrimp/fish | Lusitanian |
| Turbot | *Psetta maxima* | Benthivore | Lusitanian |
| Brill | *Scophthalmus rhombus* | Benthivore | Lusitanian |
| Scaldfish | *Arnoglossus laterna* | Benthivore | Lusitanian |
| Dab | *Limanda limanda* | Benthivore | Boreal |
| Flounder | *Platichthys flesus* | Benthivore | Lusitanian |
| Plaice | *Pleuronectes platessa* | Benthivore | Boreal |
| Sole | *Solea solea* | Benthivore | Lusitanian |
| Solenette | *Buglossidium luteum* | Benthivore | Lusitanian |

The classifications are derived from www.fishbase.nl for food types and Yang (1982) for biogeographic guild.

deeper than 2 m because of the draught of the research vessel. The combination of low fishing speed (2–3 knots) and fine mesh size results in selection of mainly the smaller species and younger year classes. Sample locations are stratified by depth. Fish are sorted and measured to the cm below. The mean abundance per area was calculated for 34 species in the period 1970–2006 weighed by surface area for each depth stratum. Species were classified according to food types: planktivore, shrimp/fish-eating, benthivore and parasitic; and biogeographical guilds: Lusitanian (preferring warm water), boreal (preferring cold water) and Atlantic (Table 1). Only species caught in at least one third of all years were analysed. This means that the selection of species may differ slightly between the three areas.

### 2.2. Time series abiotic variables and data on food, predators and fisheries

We used several time series of explanatory variables comprising abiotic variables, biotic variables and variables related to fisheries. Naturally any choice of parameters is arbitrary and partly driven by the availability of the data. That is also the reason why we sometimes used different datasets for different areas (Table 2). In this exploratory phase we focused on variables potentially impacting fish densities directly, but did not consider indicators of water quality such as pollutants. We did include nutrients given the recent discussions on the effect of these on the carrying capacity of the marine system, even though we are aware that nutritional links between nutrients and fish are still not well understood and only partly proven (Philippart et al., 2007; Kuipers and van Noort, 2008). So besides the direct links in the food web, be it as predator or prey, we included the NAO winter index, temperature, river runoff, salinity, total phosphate and nitrate.

#### 2.2.1. Abiotic series

The NAO winter index (December–March) was taken from the Internet http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao_index.html. During the DFS sea surface temperature is recorded at haul level. For the Wadden Sea we used salinity data collected by NIOZ on Texel, for the other areas, series were taken from www.waterbase.nl (mean for September/October).

Table 2
Abiotic and biotic parameters used in the time series analyses in the three different areas

| Explanatory variable | Wadden Sea | Dutch coastal area | Westerschelde |
|---|---|---|---|
| *Abiotic* | | | |
| Temperature (°C) | DFS | DFS | DFS |
| Salinity (Texel: practical salinity scale of 1978, other areas:‰) | NIOZ: Texel, 't Horntje | www.waterbase.nl: average 2 stations* | www.waterbase.nl: average 2 stations** |
| River runoff ($m^3/s$) | www.waterbase.nl: Kornwerderzand | www.waterbase.nl: IJmuiden | www.waterbase.nl: Schaar van ouden Doel |
| Total phosphate (mg/l) | www.waterbase.nl: Marsdiep | www.waterbase.nl: Noordwijk | www.waterbase.nl: average 2 stations*** |
| Total nitrate (mg/l) | www.waterbase.nl: Marsdiep | www.waterbase.nl: Noordwijk | www.waterbase.nl: average 2 stations*** |
| *Biotic* | | | |
| Piscivorous fish North Sea coast (kg/ha) | SNS: gadoids>20 cm, within 30 m depth | SNS: gadoids>20 cm within 30 m depth | SNS: gadoids>20 cm within 30 m depth |
| Cormorants (*n* or *n* breeding pairs) | SOVON non-breeding birds | Breeding birds (M. Leopold pers.) | SOVON non-breeding birds |
| seals (*n*) | IMARES common and grey seals | IMARES common and grey seals | DELTARES: common and grey seals |
| Brown shrimp densities (kg/ha) | DFS: Wadden Sea | DFS: Dutch coast | DFS: Westerschelde |
| *Fishing pressure* | | | |
| Brown shrimp effort (see text) | ICES WGCRAN: total Dutch landings corrected for brown shrimp densities | ICES WGCRAN: total Dutch landings corrected for brown shrimp densities | ICES WGCRAN: total Dutch landings corrected for brown shrimp densities |
| Cockle landings (million kg meat) | Ministry LNV: Wadden Sea | Ministry LNV: North Sea coast | Ministry LNV: Westerschelde |
| Beam trawl effort North Sea (hp days) | Rijnsdorp et al., 2008 | Rijnsdorp et al., 2008 | Rijnsdorp et al., 2008 |

* North of Terschelling and off Goeree mean for September; ** Hansweert geul and Vlissingen boei SSVH; *** Vlissingen boei SSVH and Terneuzen boei 20.

River runoff was also taken from the same source and was measured at all major outflows, and we used the annual mean of the series at Kornwerderzand for the Wadden Sea, at IJmuiden for the North Sea coast and at the Schaar van Ouden Doel for the Westerschelde. These runoff series are all highly correlated. Total phosphate and nitrate was taken from www.waterbase.nl (annual means). Missing values were interpolated based on correlations between local values and concentrations in the Rhine discharge (Van Raaphorst and De Jonge, 2004).

Mean temperature during the survey period has increased in all three areas, but stronger in the Wadden Sea and Westerschelde than along the Dutch coast (Fig. 2). Besides a slow increase in salinity along the Dutch coast, no long-term trend seems apparent in salinity in the other areas. River runoff has shown great annual fluctuations and an increase in all three areas, but steepest in the Wadden Sea. Total phosphate showed a maximum in the period 1975–1985, and declined subsequently. Nitrate showed a similar pattern in the Westerschelde and Dutch coastal zone, while concentrations in the Wadden Sea concentrations were more stable after an initial decline.

### 2.2.2. Biotic series

For biotic series we used data on predators and prey. The most common (non-fish) predators are cormorant *Phalacrocorax carbo*, common *Phoca vitulina* and grey seals *Halichoerus grypus*. For cormorants in the Wadden Sea we used number of non-breeding birds, because these numbers are usually larger than the breeding numbers and the period corresponds better with the fish sampling period. For the Dutch coastal zone only breeding numbers were available and compiled from different sources (M. Leopold pers. comm.). Seals are counted several times per year by airplane and total populations are estimated (monitoring program IMARES). Because of their larger numbers the harbour porpoise *Phocoena phocoena* has probably been a more important fish predator in recent times than seals in the Dutch coastal zone. However, the time series has the same signal as that for seals with a steep increase from the early 1990s onwards (Camphuysen, 2005) and therefore we used seal time series for all three areas. As a measure of predation pressure by fish we have included gadoid densities (in kg/ha within the 30 m depth contour, between 52°N and 55°30′N and east of 3°E from the Sole Net Survey (SNS) survey) as explanatory variables for the three areas. Gadoids are piscivorous already from lengths of 4 cm onwards (Bromley et al., 1997), but since they generally eat prey about 4 times smaller than their own size we used a lower size limit of 20 cm (Daan, 1973). In the Wadden Sea the number of non-fish predators has shown a steep increase since 1980 (Fig. 2). Populations of both common and grey seals have increased, although grey seals only appeared in 1979 for the first time in this period. Although common seals still outnumber grey seals, by 2006 the ratio common to grey seals has decreased to 2:1. In the Westerschelde the numbers have shown a similar increase although total numbers are an order of magnitude lower. For the Dutch coast no separate line is presented as the seals from both Wadden Sea and Westerschelde visit the North Sea to feed and the Dutch coast does not provide haul out sites. Cormorants increased both in the Wadden Sea and Westerschelde, but stabilized recently. The densities of piscivorous fish in the North Sea has shown variable densities over the years, with an overall decrease from the early 1990s onwards.

Fish feed on zooplankton, buried benthic and epibenthic prey. The only food source for which information is available (for all areas and the full time series) is brown shrimp abundance. However the role of brown shrimp is complicated as brown shrimp can also predate on juvenile fish (van der Veer and Bergman, 1987; Amara and Paul, 2003). No time series on other benthic prey or zooplankton are available for the study period and study area. Brown shrimp densities are overall highest in the Wadden Sea and show strong annual variation and a long-term decline in the Westerschelde but no clear trend in the Wadden Sea or Dutch coastal zone (Fig. 2).

## 2.3. Fishing pressure

The most important fisheries within the three areas include brown shrimp fisheries and shellfish fisheries (Verver et al., 2005). These fisheries are likely to have the biggest impact on small fish, because of the bycatch, bottom disturbance and removal of possible prey. Because no detailed information on fishing pressure per area is available, we estimated brown shrimp trawl effort by dividing total shrimp landings in the Netherlands by mean brown shrimp densities in the autumn DFS survey. Cockle fisheries pressure was estimated as the cockle landings per area. Fishing effort in the offshore waters bordering our study area was estimated from the Dutch beam trawl effort which dominates the fishing effort in this area (Jennings and Cotter, 1999). Brown shrimp trawl effort has been constant throughout the 1970s and 1980s but has shown a steep increase since the early nineties. Cockle fishing started in the Wadden Sea in the mid 1980s and lasted until 2005,

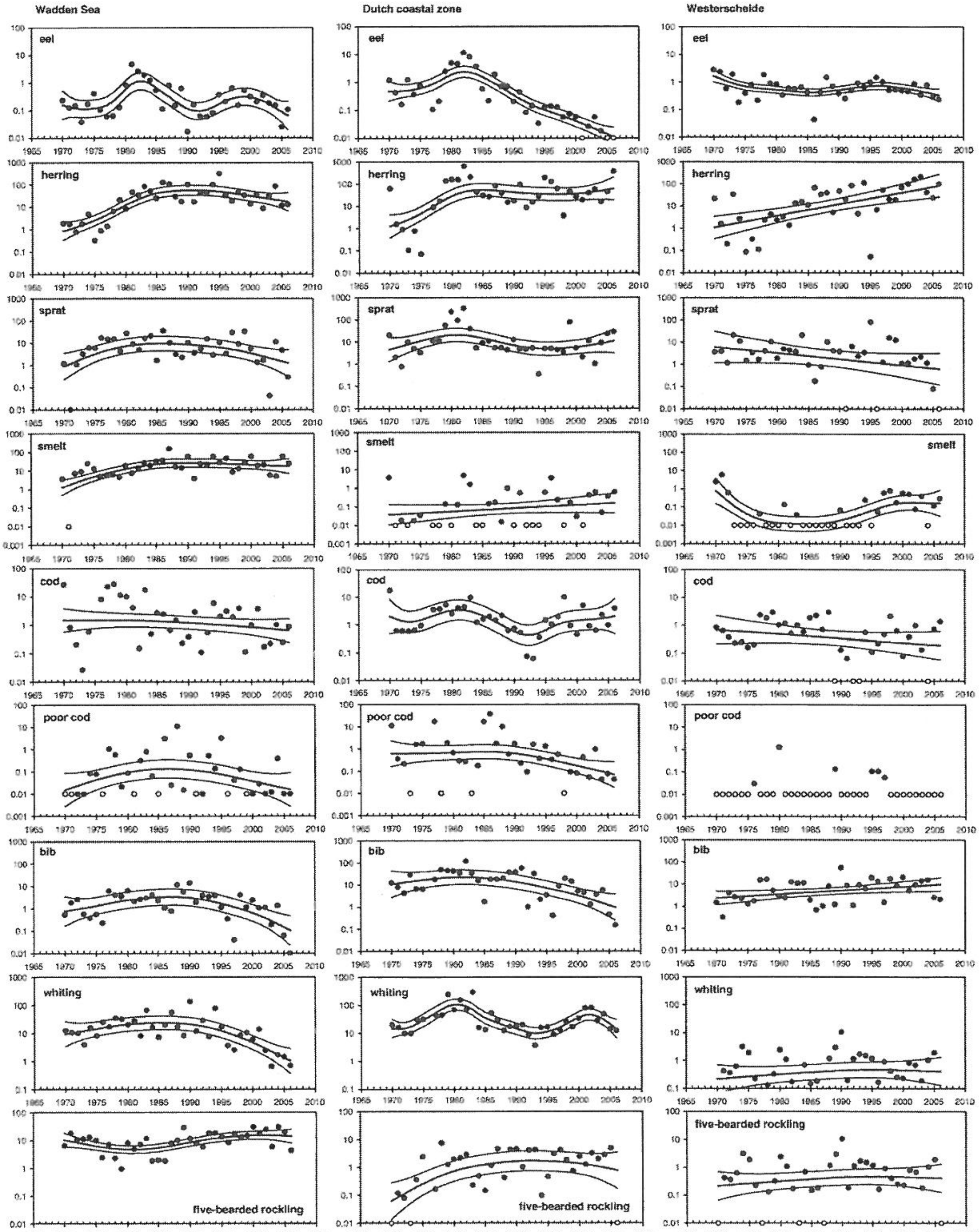



Fig. 4. Time series analysis of the mean density of 32 species in three different areas between 1970 and 2006. The dots indicate the mean densities (n/ha) per year. Twaite shad and river lamprey are not presented because of their occurrence in only one of the areas and their very low numbers in the other. The black line is the smoothed mean number as estimated by Trendspotter. The thin black lines indicate the upper and lower limits of the 95% confidence interval. Zero values are indicated with open dots.

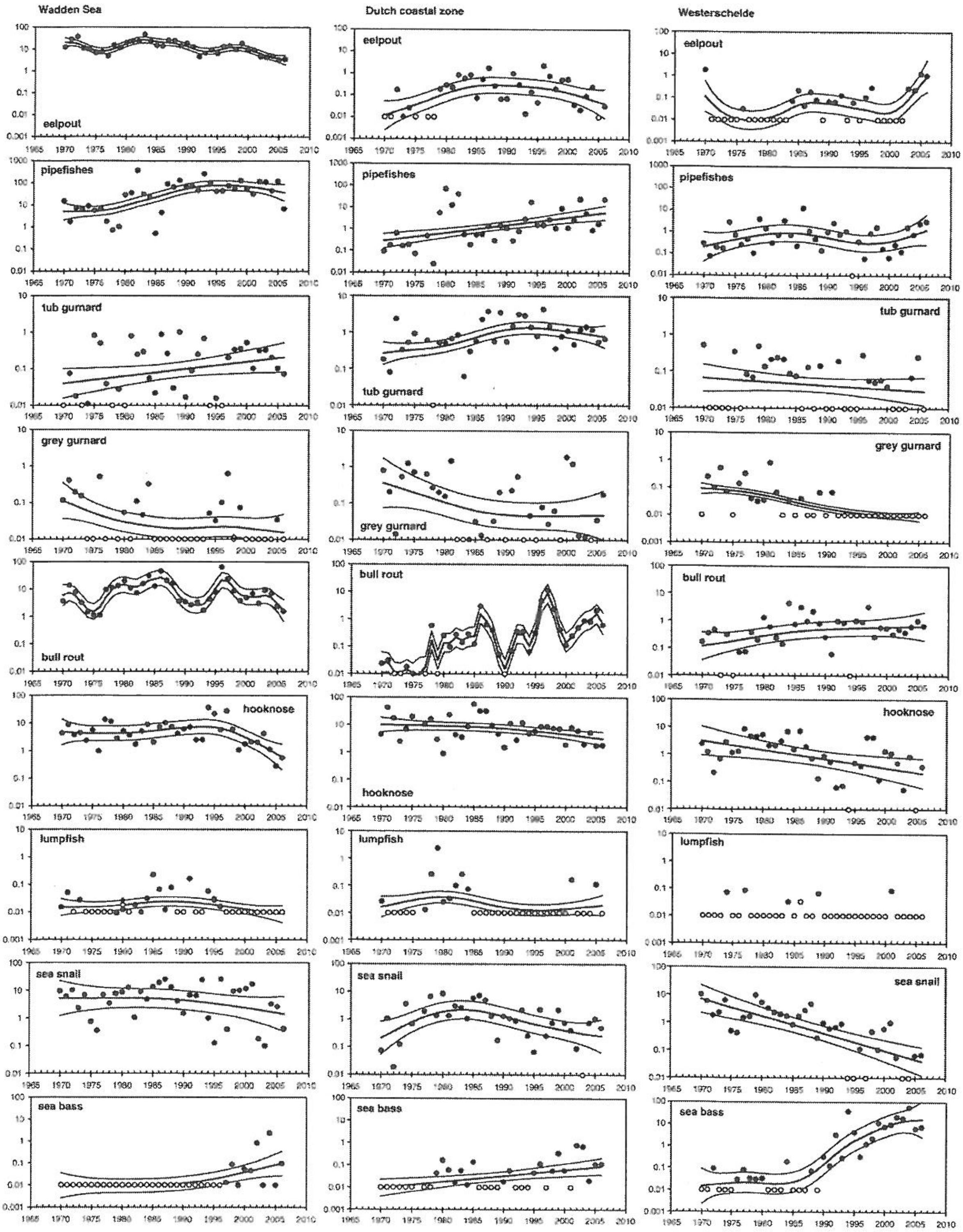



Fig. 4 (*continued*).

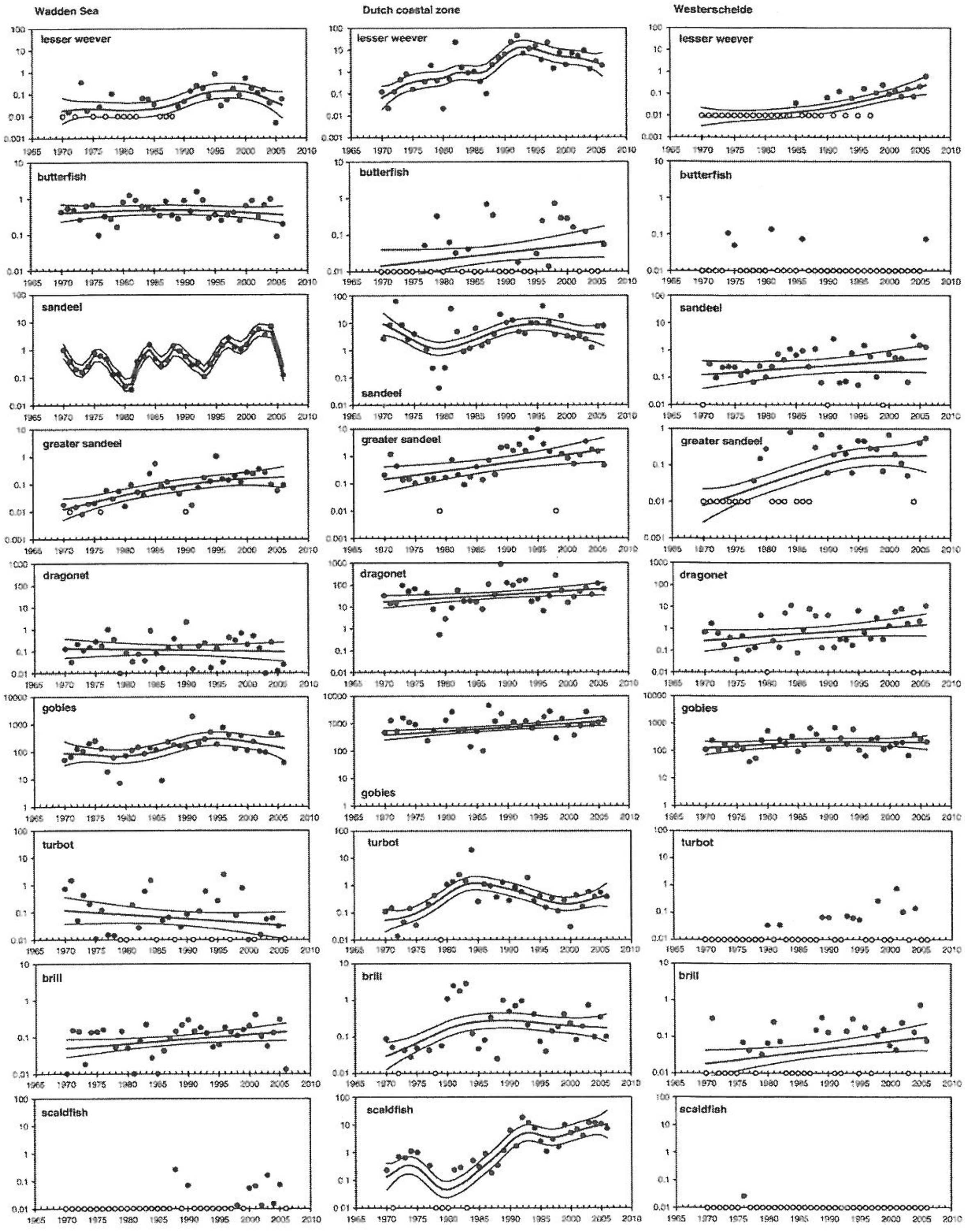



Fig. 4 (*continued*).

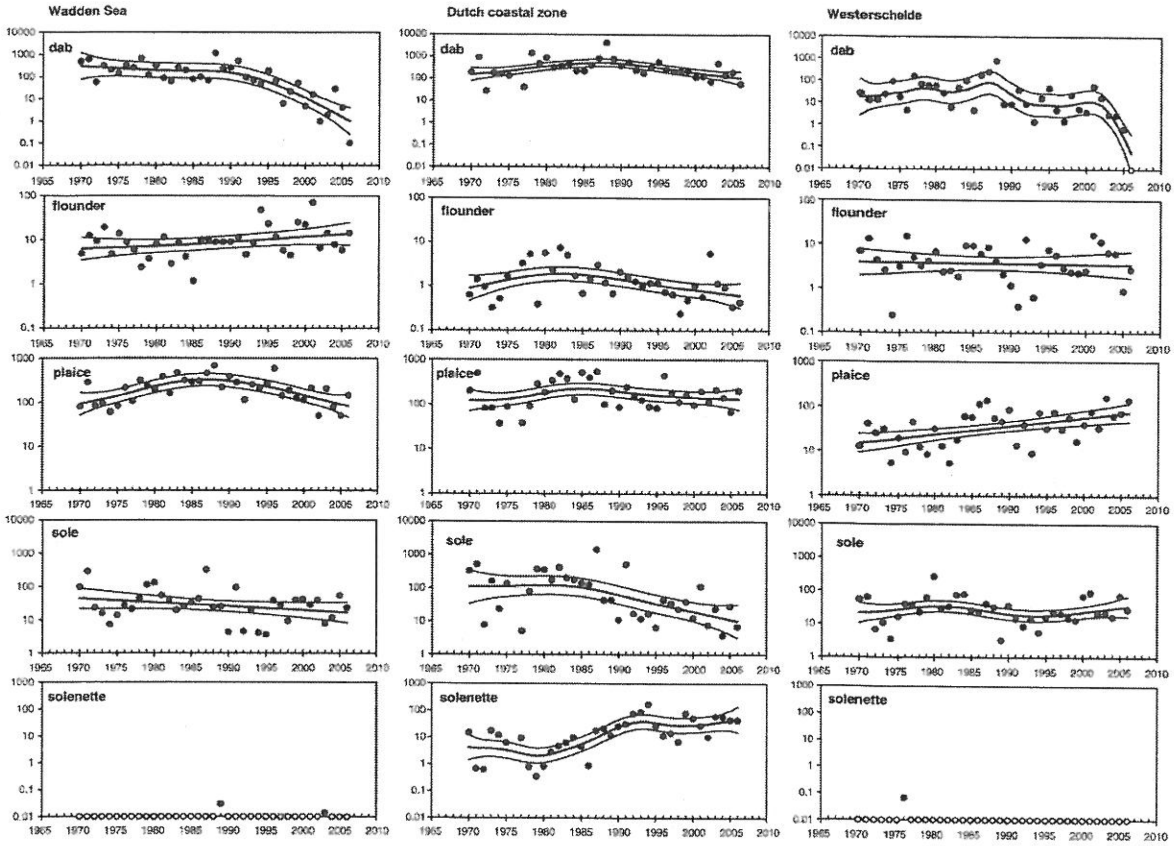



Fig. 4 (*continued*).

whether there are any underlying common patterns in different time series, whether there are interactions between the response variables, and identify the effects of explanatory variables. The aim of DFA is to set the number of common trends as small as possible but still have a reasonable model fit. The magnitude and sign of the factor loadings determine how these trends are related to the original time series.

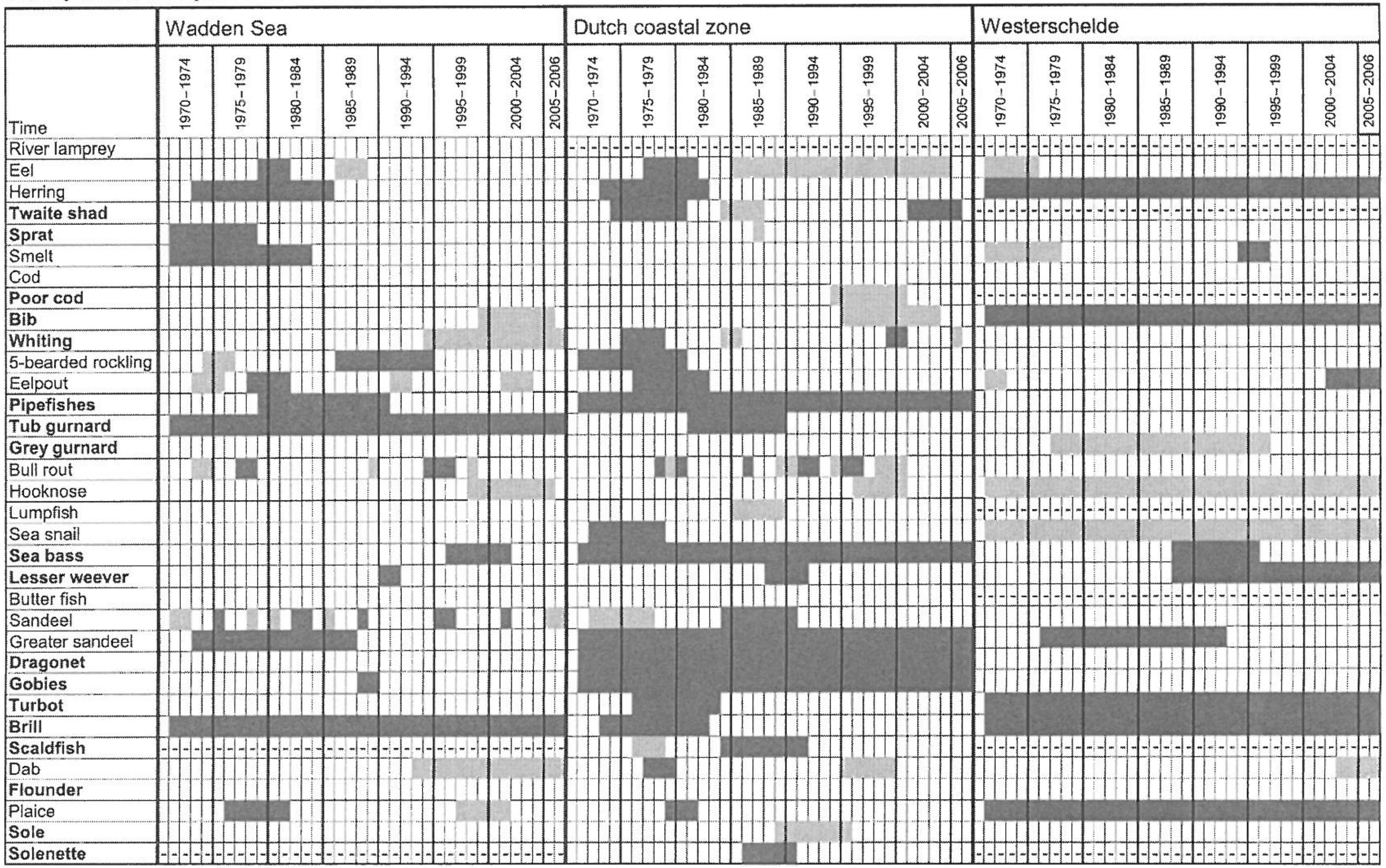
One problem with this analysis is that we model fish density as a function of biotic variables. This approach assumes that the number of fish is a function of the explanatory variables used. But for some of the explanatory variables, i.e. number of seals, the relationship might also be reversed, that the number of seals is a function of fish densities. This endogeneity is of course a difficult problem and we cannot assume that it does not occur in this set.

Only DFA models with a symmetric, non-diagonal error covariance matrix could be used, fitted for 1 and 2 common trends and with no, 1 or 2 explanatory variables (with 12 possible explanatory variables this results in 92 models to be tested for every number of common trends and area). Analyses were performed on log-transformed and standardized time series. Explanatory variables were standardized if they contained large values (in order to arrive at interpretable regression estimates). Model selection was based on Akaike's information criterion (AIC). Canonical correlations are presented to illustrate correlations between common trends and original series. Model validation was carried out by comparing the time trends of the individual species with the original data. Results were obtained with the software package Brodgar (http://www.brodgar.com).

In summary, in DFA, the trends are the common signal in the 34 time series that are not related to the explanatory variables. The common trend can be interpreted as a partial, common effect. The trends calculated by Trendspotter are real trends that capture the pattern of the data, without taking the effect of explanatory variables into account.

Data exploration indicated strong collinearity (correlation of >0.80) between the variables cormorants and seals, cormorants and phosphate, and phosphate and nitrate in the Dutch coastal zone, between seals and cormorants, and cormorants and phosphate in the

Table 3
Summary of trends in 34 species in the Wadden Sea, Dutch coastal zone and Westerschelde




Years with significant increases are indicated with a dark grey panel, years with significant decreases with a light grey panel, years without significant changes with no shading. Species that do not (or very rarely) occur in the area (but do occur in the other two coastal areas) are indicated with –. Lusitanian species are printed bold.

Table 4
Selection of five best models for the common trend in the three areas

| Area | Number model | Model | AIC |
|---|---|---|---|
| Wadden Sea | 1 | Seals+beam trawl effort | 2874.92 |
| | 2 | Runoff+beam trawl effort | 2892.73 |
| | 3 | Seals+runoff | 2924.66 |
| | 4 | Brown shrimp+beam trawl effort | 2930.25 |
| | 5 | Beam trawl effort+nitrate | 2932.04 |
| Dutch coastal zone | 1 | Brown shrimp+runoff | 2638.79 |
| | 2 | Seals+cockle landings | 2667.40 |
| | 3 | Temp+seals | 2678.39 |
| | 4 | Runoff+phosphate | 2698.37 |
| | 5 | Shrimp effort+phosphate | 2702.13 |
| Westerschelde | 1 | Beam trawl effort+phosphate | 2683.60 |
| | 2 | Cormorants+beam trawl effort | 2695.61 |
| | 3 | Seals+salinity | 2710.19 |
| | 4 | Cormorants+phosphate | 2710.85 |
| | 5 | Cormorants+seals | 2717.53 |

All models included one common trend only.

Wadden Sea and between seals and phosphate, phosphate and nitrate, and seals and beam trawl effort in the Westerschelde. Because of the almost similar pattern in the seal and cormorant population for Wadden Sea and Dutch coastal zone and the fact that the cormorant series had one missing value, we excluded cormorants from the analyses for these areas. The choice to exclude any other variables would be very arbitrary. Instead we included all variables in the analyses to see which ones resulted in the best model, keeping the collinearity in mind and not selecting models that contained two collinear variables.

## 3. Results

### 3.1. Trends total fish numbers and biomass

Mean total fish biomass per haul shows a dome-shaped pattern in all three areas with an increase from 1970 to 1985 and a subsequent fivefold decline (Fig. 3). However this dome shape seems most pronounced in the Wadden Sea. The decline in the Westerschelde sets in a few years later and the decline levels off since 2000. For the Wadden Sea and the Westerschelde the pattern in densities reflects the same patterns as found in total biomass. Along the Dutch coast there is no clear trend in densities. Overall the Westerschelde has the lowest densities of these three areas.

### 3.2. Individual species trends

Absolute densities of many species differ up to one order of magnitude between areas (Fig. 4, plaice, flounder, gobies, dragonet). Some species are only common in the Wadden Sea (e.g. bull rout, butter fish) or common along the Dutch coast but rare in the Wadden Sea and Westerschelde (dragonet, scaldfish, solenette). Individual species show great variation in trends (Fig. 4). Some species show different trends in the three sub-areas (e.g. plaice, sea snail). Trends and confidence limits calculated by Trendspotter are highly influenced by zero catches (taken as log(0.01) values in the analyses). Species that have colonized the Dutch coastal waters recently include sea bass, lesser weever and greater sandeel (Westerschelde).

Species that show significant recent declines (since 1985) in the Wadden Sea include eel, eelpout, bib, whiting, hooknose, dab and plaice (Table 3), while periods with significant increases occurred in five-bearded rockling, pipefishes, tub gurnard, sea bass, greater sandeel and brill. In general the periods with decreases occurred later than the periods of increases. Along the Dutch coast eight species (twaite shad, pipefishes, tub gurnard, sea bass, sandeel, greater sandeel, dragonet and gobies) show recent extensive periods of significant increase and seven (eel, poor cod, bib, hooknose, lumpfish, dab and sole) with periods of significant decrease (Table 3). In the Westerschelde herring, bib, eelpout, sea bass, lesser weever, greater sandeel, turbot, brill and plaice show long continuous periods of significant increase, while grey gurnard, hooknose, sea snail and dab show recent significant decreases (Table 3).

### 3.3. Common trends

The best DFA fit for all three areas was obtained for one common trend (smallest AIC). For every area the five best models are presented (Table 4). The main common trend for the Wadden Sea and Westerschelde shows an increase from the mid 1970s to the early 1980s followed by a steep decrease in the late 1980s, with a

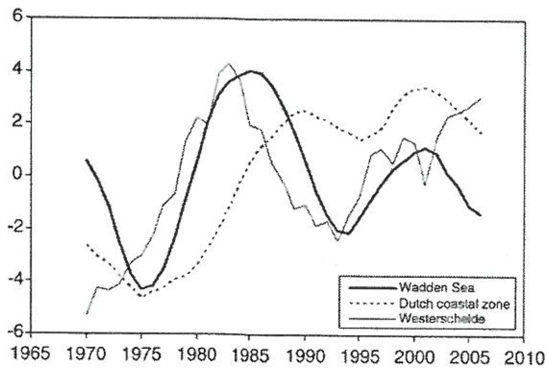



Fig. 5. Common trends as results of DFA analyses in the three areas.

second much smaller peak in the Wadden Sea around 2000 and a subsequent decline (Fig. 5). The pattern for the Dutch coastal zone is different in that the increase started years later, followed by a moderate decline in the mid 1990s and stabilization in the recent decade (Fig. 5). The environmental variables involved in the best five models for the Wadden Sea included seals, beam trawl effort, runoff, brown shrimp densities and total nitrate. The model with the best fit included seals and beam trawl effort (Table 4). For the Dutch coastal zone the

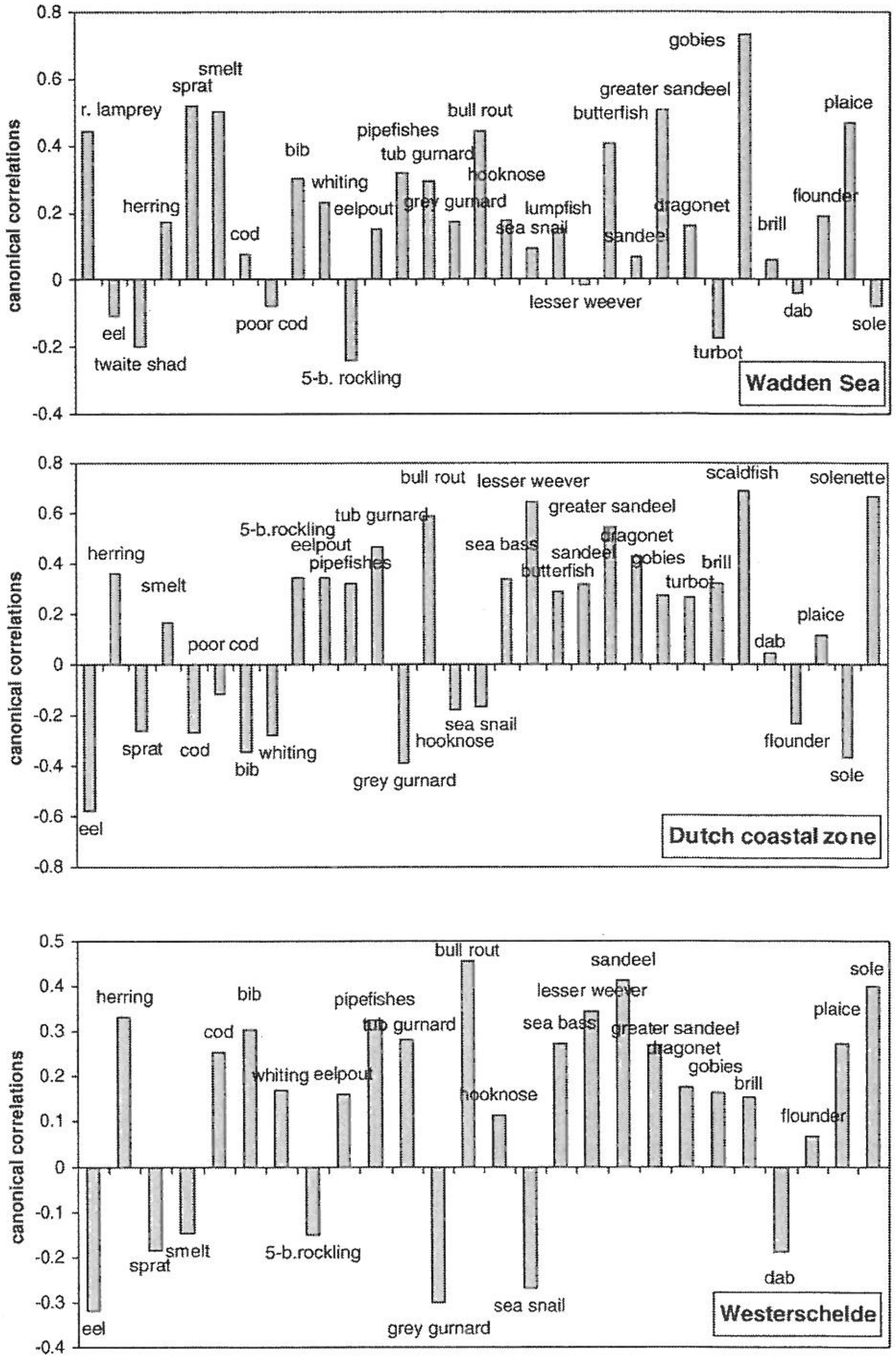



Fig. 6. Canonical correlations (= correlation between trends and original series) of every species with the DFA common trend for the three areas.

Table 5
Estimated regression parameters, standard errors (se) and *t*-values for the explanatory variables for the best model in each of the three areas

Wadden Sea

| Species | Seals | | | Beam trawl effort | | |
|---|---|---|---|---|---|---|
| | Estimate | se | *t*-value | Estimate | se | *t*-value |
| River lamprey | 0.61 | 0.12 | **4.85** | 0.32 | 0.12 | **2.54** |
| Eel | −0.09 | 0.18 | −0.48 | −0.16 | 0.17 | −0.96 |
| Twaite shad | −0.01 | 0.17 | −0.07 | −0.11 | 0.17 | −0.64 |
| Herring | 0.26 | 0.14 | 1.78 | 0.43 | 0.14 | **3.17** |
| Sprat | −0.20 | 0.15 | −1.37 | 0.36 | 0.15 | **2.45** |
| Smelt | 0.25 | 0.14 | 1.85 | 0.50 | 0.13 | **3.73** |
| Cod | −0.17 | 0.16 | −1.05 | −0.14 | 0.16 | −0.88 |
| Poor cod | −0.22 | 0.15 | −1.50 | 0.33 | 0.15 | **2.22** |
| Bib | −0.50 | 0.14 | **−3.57** | 0.14 | 0.14 | 0.99 |
| Whiting | −0.66 | 0.12 | **−5.69** | 0.19 | 0.12 | 1.61 |
| 5-bearded rockling | 0.40 | 0.15 | **2.67** | 0.27 | 0.15 | 1.84 |
| Eelpout | −0.55 | 0.16 | **−3.49** | −0.21 | 0.14 | −1.47 |
| Pipefishes | 0.38 | 0.14 | **2.76** | 0.40 | 0.14 | **2.98** |
| Red gurnard | 0.26 | 0.16 | 1.63 | 0.13 | 0.16 | 0.81 |
| Grey gurnard | −0.22 | 0.16 | −1.37 | −0.15 | 0.16 | −0.93 |
| Bull rout | −0.15 | 0.18 | −0.81 | −0.12 | 0.17 | −0.69 |
| Hooknose | −0.49 | 0.13 | **−3.74** | 0.35 | 0.13 | **2.72** |
| Sea snail | −0.29 | 0.16 | −1.76 | −0.12 | 0.16 | −0.78 |
| Lumpfish | −0.25 | 0.16 | −1.56 | 0.16 | 0.15 | 1.04 |
| Lesser weever | 0.33 | 0.14 | **2.34** | 0.55 | 0.14 | **4.00** |
| Butterfish | −0.15 | 0.17 | −0.91 | −0.01 | 0.16 | −0.05 |
| Sandeel | 0.56 | 0.13 | **4.23** | 0.27 | 0.13 | **2.06** |
| Greater sandeel | 0.54 | 0.12 | **4.51** | 0.44 | 0.12 | **3.81** |
| Dragonet | −0.09 | 0.16 | −0.59 | 0.30 | 0.16 | 1.88 |
| Turbot | −0.22 | 0.16 | −1.35 | −0.04 | 0.16 | −0.23 |
| Gobies | 0.19 | 0.15 | 1.32 | 0.53 | 0.15 | **3.62** |
| Brill | 0.18 | 0.16 | 1.14 | 0.36 | 0.15 | **2.34** |
| Dab | −0.87 | 0.08 | **−10.84** | 0.01 | 0.08 | 0.17 |
| Flounder | 0.30 | 0.16 | 1.90 | 0.30 | 0.15 | 1.94 |
| Plaice | −0.34 | 0.15 | **−2.31** | 0.25 | 0.14 | 1.77 |
| Sole | −0.09 | 0.16 | −0.54 | −0.61 | 0.15 | **−4.05** |

Dutch coastal zone

| Species | Brown shrimp density | | | Runoff | | |
|---|---|---|---|---|---|---|
| | Estimate | se | *t*-value | Estimate | se | *t*-value |
| Eel | 0.37 | 0.13 | **2.96** | −0.09 | 0.13 | −0.70 |
| Flounder | 0.33 | 0.15 | **2.28** | 0.23 | 0.15 | 1.54 |
| Butterfish | 0.11 | 0.15 | 0.69 | 0.24 | 0.15 | 1.57 |
| Poor cod | 0.04 | 0.16 | 0.27 | −0.06 | 0.17 | −0.39 |
| Solenette | 0.07 | 0.13 | 0.54 | −0.07 | 0.13 | −0.52 |
| Grey gurnard | −0.20 | 0.15 | −1.34 | 0.14 | 0.15 | 0.93 |
| Brill | 0.40 | 0.14 | **2.87** | 0.10 | 0.14 | 0.74 |
| Gobies | 0.35 | 0.13 | **2.63** | −0.45 | 0.14 | **−3.30** |
| Herring | 0.32 | 0.13 | **2.38** | 0.28 | 0.14 | **2.09** |
| Hooknose | 0.03 | 0.16 | 0.17 | −0.22 | 0.16 | −1.40 |
| Cod | −0.08 | 0.16 | −0.48 | 0.18 | 0.16 | 1.13 |
| Lesser weever | 0.07 | 0.13 | 0.51 | 0.09 | 0.14 | 0.65 |
| Dragonet | −0.05 | 0.14 | −0.35 | −0.35 | 0.14 | **−2.39** |
| Eelpout | 0.46 | 0.14 | **3.35** | −0.02 | 0.14 | −0.18 |
| Red gurnard | 0.31 | 0.14 | **2.29** | −0.13 | 0.14 | −0.93 |
| Dab | 0.25 | 0.16 | 1.55 | 0.03 | 0.16 | 0.20 |
| Plaice | 0.49 | 0.14 | **3.46** | −0.22 | 0.14 | −1.53 |
| Scaldfish | −0.10 | 0.12 | −0.80 | −0.20 | 0.13 | −1.53 |
| Sea snail | 0.19 | 0.15 | 1.28 | 0.33 | 0.15 | **2.19** |
| Greater sandeel | 0.24 | 0.13 | 1.85 | −0.20 | 0.14 | −1.45 |
| Smelt | 0.39 | 0.15 | **2.69** | −0.25 | 0.15 | −1.71 |
| Sprat | 0.23 | 0.15 | 1.53 | 0.29 | 0.15 | 1.93 |
| Bib | −0.01 | 0.16 | −0.07 | 0.10 | 0.16 | 0.60 |
| Turbot | 0.25 | 0.15 | 1.61 | 0.06 | 0.16 | 0.38 |
| Sole | 0.40 | 0.14 | **2.86** | −0.16 | 0.14 | −1.13 |
| 5-bearded rockling | 0.22 | 0.14 | 1.63 | 0.36 | 0.14 | **2.63** |
| Whiting | 0.07 | 0.14 | 0.46 | 0.41 | 0.15 | **2.84** |
| Sandeel | 0.09 | 0.14 | 0.68 | −0.49 | 0.14 | **−3.55** |
| Bull rout | 0.24 | 0.13 | 1.88 | 0.02 | 0.13 | 0.12 |
| Pipefishes | 0.40 | 0.13 | **3.09** | 0.33 | 0.13 | **2.52** |
| Sea bass | 0.12 | 0.15 | 0.79 | 0.15 | 0.15 | 0.97 |

Westerschelde

| Species | Beam trawl effort | | | Total phosphate | | |
|---|---|---|---|---|---|---|
| | Estimate | se | *t*-value | Estimate | se | *t*-value |
| Eel | −0.09 | 0.17 | −0.55 | −0.06 | 0.16 | −0.36 |
| Herring | −0.03 | 0.15 | −0.17 | −0.47 | 0.15 | **−3.24** |
| Sprat | 0.22 | 0.16 | 1.40 | 0.33 | 0.16 | **2.11** |
| Smelt | −0.42 | 0.13 | **−3.26** | −0.60 | 0.13 | **−4.66** |
| Cod | −0.25 | 0.16 | −1.64 | 0.30 | 0.15 | 1.97 |
| Bib | 0.21 | 0.16 | 1.30 | −0.06 | 0.16 | −0.37 |
| Whiting | 0.22 | 0.15 | 1.48 | 0.49 | 0.15 | **3.33** |
| 5-bearded rockling | 0.27 | 0.16 | 1.64 | −0.07 | 0.16 | −0.41 |
| Eelpout | −0.20 | 0.16 | −1.27 | −0.35 | 0.16 | **−2.25** |
| Pipefishes | −0.17 | 0.17 | −1.02 | 0.05 | 0.16 | 0.28 |
| Tub gurnard | −0.19 | 0.16 | −1.21 | 0.32 | 0.15 | **2.08** |
| Grey gurnard | −0.28 | 0.14 | −1.98 | 0.40 | 0.14 | **2.94** |
| Bull rout | 0.04 | 0.17 | 0.24 | −0.09 | 0.16 | −0.54 |
| Hooknose | −0.08 | 0.14 | −0.57 | 0.53 | 0.14 | **3.76** |
| Sea snail | −0.11 | 0.12 | −0.93 | 0.65 | 0.12 | **5.47** |
| Sea bass | −0.02 | 0.11 | −0.22 | −0.77 | 0.10 | **−7.44** |
| Lesser weever | −0.19 | 0.13 | −1.54 | −0.71 | 0.12 | **−5.95** |
| Sandeel | −0.03 | 0.17 | −0.16 | −0.04 | 0.16 | −0.26 |
| Greater sandeel | 0.24 | 0.14 | 1.74 | −0.43 | 0.14 | **−3.14** |
| Dragonet | 0.07 | 0.16 | 0.41 | −0.22 | 0.16 | −1.36 |
| Gobies | 0.12 | 0.17 | 0.73 | −0.10 | 0.17 | −0.63 |
| Brill | −0.12 | 0.16 | −0.76 | −0.29 | 0.16 | −1.80 |
| Dab | 0.36 | 0.13 | **2.75** | 0.65 | 0.13 | **5.07** |
| Flounder | −0.08 | 0.17 | −0.45 | 0.08 | 0.17 | 0.48 |
| Plaice | 0.09 | 0.16 | 0.54 | −0.32 | 0.16 | **−2.03** |
| Sole | −0.36 | 0.16 | **−2.28** | 0.13 | 0.15 | 0.84 |

Significant parameters are in bold.

variables in the five best models were brown shrimp density, runoff, seals, cockle landings, temperature, phosphate and shrimp effort with the best model including brown shrimp density and runoff. The common trend for the Westerschelde was best explained by models including beam trawl effort, phosphate, cormorants, beam trawl effort, seals and salinity. The best model included beam trawl effort and phosphate.

In the Wadden Sea, river lamprey, sprat, smelt, bull rout, butterfish, greater sandeel, gobies and plaice show strong positive correlations (>0.4) with the common trend (Fig. 6), while no species show strong negative correlations. The remaining species are moderately or poorly correlated to the common trend. The Dutch coastal zone shows strong positive correlations with the common trend for tub gurnard, bull rout, lesser weever, greater sandeel, scaldfish and solenette and strong negative correlations for eel and grey gurnard. All other species show moderate or poor correlation with the common trend (Fig. 6). In the Westerschelde, bull rout, sandeel and sole are the only three species strongly positively correlated to the common trend, while none show strong negative correlations (Fig. 6). The remaining species have weaker correlations. Overall the strongest correlations were found for Wadden Sea and the Dutch coastal zone while in the Westerschelde the correlations with the common trend were less strong.

The estimated regression parameters for the explanatory variables in the best models are given in Table 5 for every area. Significant *t*-values indicate strong relationships with the explanatory variables. For the Wadden Sea, river lamprey, bib, whiting, five-bearded rockling, eelpout, pipefishes, hooknose, lesser weever, greater sandeel, sandeel, dab and plaice had relatively large *t*-values for the first explanatory variable (seals), of which river lamprey, five-bearded rockling, pipefishes, lesser weever, sandeel and greater sandeel increased with the number of seals and the other species decreased. River lamprey, herring, sprat, smelt, poor cod, pipefishes, hooknose, lesser weever, sandeel, greater sandeel, gobies, brill and sole had relatively large *t*-values for the second explanatory variable (beam trawl effort). Of these the coefficients were all positive except for sole. Regression parameters for fish in the Dutch coastal zone were significant and positive for the first explanatory variable (brown shrimp density) for eel, flounder, brill, gobies, herring, eelpout, red gurnard, plaice, smelt, sole and pipefishes indicating an increase in densities with brown shrimp density. Herring, sea snail, five-bearded rockling, whiting and pipefishes showed significant, positive estimates for the regression coefficients of the second explanatory variable (runoff). For gobies, dragonet and sandeel these regression coefficients were negative. The regression parameters for fish in the Westerschelde showed significant correlations with the first explanatory variable (beam trawl effort) for smelt, dab and sole. These were negative for smelt and sole, pointing at decreasing densities with increasing beam trawl effort. Significant negative coefficients for the second variable (total phosphate) were found for herring, smelt, eelpout, sea bass, lesser weever, greater sandeel and plaice. Sprat, whiting, tub gurnard, grey gurnard, hooknose, sea snail and dab showed increases with total phosphate.

## 4. Discussion

### *4.1. Observed patterns*

Although the trend analyses for individual species showed large variation, there are several large scale patterns that emerge from these 37 year time series. Firstly total fish densities expressed both in numbers and biomass have decreased strongly from the mid-1980s after an initial increase between 1970 and 1980. This dome-shaped pattern was apparent in all three areas (Fig. 3). The DFA allowed to investigate the common signal in the series of 34 species densities, after correction for the two most dominant explanatory variables. Densities showed similar common trends for the two estuarine areas. The common trend for the Dutch coastal zone showed a time lag compared to the Wadden Sea and Westerschelde. The canonical correlations (Fig. 6) indicate which species contribute most to the common trend and although the common trend was similar for Westerschelde and Wadden Sea, the species contributing most to this trend differed. For the Dutch coastal zone mainly the recently increasing species as solenette, scaldfish and lesser weever contributed to the common trend (Fig. 6). This explains why the common trend differs from that in the estuarine areas, where all these species are less predominant.

Apart from differences in absolute densities the same species sometimes showed different trends in the three areas (e.g. bib, pipefishes, sandeel, plaice). Of these plaice is the only species that shows significant opposite trends (decrease in Wadden Sea and increase in Westerschelde, stable in Dutch coastal zone). The trends in the Wadden Sea and the coastal zone are consistent with the offshore movement of juvenile plaice (van Keeken et al., 2007). Species that showed a decreasing trend in all three areas were hooknose and dab, although the rate of decrease differed. Lesser weever and greater sandeel increased in all areas. The number of species showing recent declines was highest in the Wadden Sea and in the Dutch coastal zone (Table 3). The Dutch coastal zone is characterized by a number of species with recent strong increases, part of which can be attributed to relatively new species colonizing the area such as lesser weever and sea bass. Solenette and scaldfish show sudden increases since the late 1980s, but inhabited the coastal waters from the start of the series in low densities. They are completely absent from the estuarine areas because they avoid low-salinity waters (Amara et al., 2004). The recent increases has been assumed to be related to the increase in seawater temperature, however Amara et al. (2004) showed that small scale solenette distribution was not influenced by temperature. Species that are practically absent from the Westerschelde but are relatively common in the other two areas include poor cod, butterfish and turbot.

### 4.2. Possible causes of observed patterns

The interpretation of the variables that explained a significant part of the variation in the time trends of the individual species in the DFA is complicated by the collinearity between the variables. In the interpretation, a significant effect of a variable may reflect the role of another collinear variable. For example, for the Wadden Sea there was strong collinearity between seals and cormorants, and between cormorants and phosphate. Therefore we must keep in mind that any effect found might be explained by one of these variables, or even some other variable not incorporated but related to all of these. Other problems with variables used is that short term variation can be large and is not captured in overall means. Also variables that may be relevant such as turbidity (Bolle et al., 2001) and other food groups such as zooplankton and benthos were not available and could not be included. Furthermore the analyses do not give an explanation for patterns observed, they merely indicate correlative relations.

Temperature was significant in explaining part of the variations in the time trends among individual species in the Dutch coastal zone but not in the Wadden Sea or Westerschelde, while the NAO winter index was not significant in any of the five best DFA models. Recently a large volume of publications has attributed changes in fish densities and distributions to climate change and rise of sea water temperature (Roessig et al., 2004; Rose, 2005; Harley et al., 2006; Portner and Knust, 2007). Let us first look if we find indications that species with a warm water preference (Lusitanian) show different trends from species with a cold water preference (boreal) (Table 1). Recent (since 1985) increases (in any of the three areas) were observed more often in Lusitanian (11; 65%) than in boreal species (7; 47%). Recent declines occurred in 5 Lusitanian (29%) and 8 boreal (53%) species (based on the fact that the series consist of 16 boreal and 18 Lusitanian species). This suggests that Lusitanian species show a stronger response than boreal species. The decline in eelpout in the Wadden Sea observed since 1985 corroborates the decline in the coastal waters in Germany that was caused by the increase in temperature above the thermal maximum of the species (Portner and Knust, 2007).

Another option is to explore if patterns can be detected in species with different food preferences. As before, we scored the number of species of each food group that showed recent in- or decreases in any of the areas (combination of Tables 1 and 3): 0% of planktivores showed a recent decrease, while 57% increased, equal numbers (45%) of shrimp/fisheaters in- and decreased and 43% of benthivores decreased while 57% increased (based on 7 planktivores, 11 shrimp/fisheaters and 14 benthivores). In conclusion the recent significant in- and decreases seem to have occurred in all food groups, but relatively more planktivores and benthivores showed increases than the other groups. It should be noted however that the majority of Lusitanian species is also benthivore.

Naturally food and temperature preferences are only two of the possible variables that might explain differences in trends between areas and species. Alternative possibilities can be sought in functional guilds (whether species inhabit the area permanently or only part of the year (Elliott and Dewailly, 1995)), age-groups, thermal tolerance (range of their distribution), longevity of species, whether or not the species is commercially exploited and whether or not it concerns species with strong preferences for bottom structures such as mussel beds. Separate DFA analyses on any of these species subgroups may come up with different common trends and allow better interpretations of observed patterns.

The fact that a similar dome-shaped pattern occurred in the two intertidal areas would suggest similar mechanisms. Also on individual species level, there are more species declining in the Wadden Sea and Westerschelde than in the Dutch coastal zone. Explanations can be sought in factors related to bottom-up processes (food), top-down processes (predation, fishing) or changes in habitat suitability. In all three areas, DFA showed a significant contribution of variables related to bottom-up (phosphate, run off) and top-down processes (fishing effort, seals).

The significant effect of river run off, phosphate and nitrate in the DFA may reflect the effect of eutrophication of the coastal waters. In the 1960s and 1970s, eutrophication has likely resulted in an increase in primary and secondary production (Beukema and Cadee, 1988; Colijn et al., 2002) and may explain the observed increase in fish biomass (Fig. 3). Also the growth rate of plaice is positively related to eutrophication (Rijnsdorp and van Leeuwen, 1996; Teal et al., 2008). It is still debated whether the recent decrease in nutrients resulted in a decrease in the productivity of the coastal waters (Cadee and Hegeman, 2002; Philippart et al., 2007). However, Kuipers and van Noort (2008) recently showed that shortly after 2000 the persistently high primary production under low P-discharge of the Rhine seem to have come to an end, with a time lag of more than 10 years.

Because fish are ectoterms, food intake (and also growth) is temperature sensitive (Fonds and Saksena, 1978). This complicates the discussion whether observed changes relates to decreased carrying capacity or increased temperature. To understand the interplay between these, we need temperature sensitivity of growth for each species and information on food conditions to evaluate whether they are able to fill in this growth potential (e.g. Teal et al., 2008). Not only may the fish themselves be temperature sensitive, but also potential predators and prey. Crustaceans (brown shrimp and crab) have higher temperature sensitivity and tolerance range than their predators and their bivalve prey (Freitas et al., 2007). Since mortality of 0-group plaice over the season is mainly attributed to predation by brown shrimp (van der Veer and Bergman, 1987; Amara and Paul, 2003), an increase in temperature could potentially lead to overall higher predation pressure by crustaceans with negative impacts on flatfish and bivalve recruitment (Freitas et al., 2007).

The significant effect of fishing effort (beam trawl, shrimping) may reflect the impact of fishing on the size structure and species composition of the North Sea fish assemblage (Daan et al. 2005). Due to the fisheries removal of larger predatory fish, both the abundance of small fish and small sized fish species has increased over the last 30 years. As several species inhabiting the coastal waters spent part of their life in offshore areas where they are directly or indirectly exposed to fisheries, the changes in the fish assemblage in offshore waters may affect the coastal fish assemblage as well. It is striking that shrimping effort did not show any significant relation to the time series analysis. Shellfish fisheries did not significantly affect the time series analysis in the Wadden Sea or Westerschelde, although it did in the Dutch coastal zone. These fisheries will possibly influence the fish assemblage by removal of benthic prey for fish and by the influence on benthic habitats (Piersma et al., 2001; Hiddink, 2003; Kraan et al., 2007).

The increase in fish predators over time (notably seals and cormorants) coincides with the recent decrease in total fish densities, but whether this correlation reflects a causal relationship is not clear at all. Cormorants are known to feed on juvenile flatfish in the Wadden Sea (Leopold et al., 1998) and seals feed on a variety of fish species (Brasseur et al., 2004). More quantitative information on predation mortality and selectivity of fish predators is needed to get more insight in the nature of the correlation.

The current analyses provides a first attempt to describe the major changes in the fish community in intertidal and coastal areas in the Netherlands and identify possible causal processes. At this stage the causes for these changes only remain speculative. Our study showed that no single or simple set of environmental variables can be found to explain the observed patterns. It is likely that more detailed analyses are needed that are focused on specific hypotheses and the interaction of the main environmental drivers (increase in temperature, decrease in nutrients and the effects of fishing).

## Acknowledgements

Data on predators were obtained from Kees Koffijberg (SOVON, cormorants), Peter Reijnders (seals), and Bas van de Boogaard (seal data Westerschelde). We are grateful to Niels Daan and Henk Heessen for discussions on the approach. Jenny Cremer prepared Fig. 1. Over the years Marcel de Vries, Gerrit Rink, Peter Groot, Simon Rijs and many other field assistants carefully carried out the monitoring activities during which the data for this paper were collected. This study was funded through the FP6 project RECLAIM (Contract no. 044133—FISH REG/A3(2006)D/14751) and the program BSIK Klimaat en Ruimte: "Climate-related shifts in the NCP ecosystem, and consequences for future spatial planning". We thank two anonymous referees and Alain Zuur for critical comments on an earlier version of this manuscript.

## References

Amara, R., Paul, C., 2003. Seasonal patterns in the fish and epibenthic crustaceans community of an intertidal zone with particular reference to the population dynamics of plaice and brown shrimp. Estuarine Coastal and Shelf Science 56, 807–818.

Amara, R., Mahe, K., LePape, O., Desroy, N., 2004. Growth, feeding and distribution of the solenette *Buglossidium luteum* with particular reference to its habitat preference. Journal of Sea Research 51, 211–217.

Becker, G.A., Pauly, M., 1996. Sea surface temperature changes in the North Sea and their causes. Ices Journal of Marine Science 53, 887–898.

Bergman, M.J.N., Van der Veer, H.W., Stam, A., Zuidema, J.J., 1989. Transport mechanisms of larval plaice (*Pleuronectes platessa* L.) from the coastal zone into the Wadden Sea nursery area. Rapports et Procès-verbaux des Réunions du Conseil international pour l'Exploration de la Mer 191, 43–49.

Beukema, J.J., Cadee, G.C., 1988. Zoobenthos responses to eutrophication of the Dutch Wadden Sea. Ophelia 26, 55–64.

Bolle, L.J., Rijnsdorp, A.D., van der Veer, H.W., 2001. Recruitment variability in dab (*Limanda limanda*) in the southeastern North Sea. Journal of Sea Research 45, 255–270.

Brasseur, S.M.J.M., Tulp, I., Reijnders, P.J.H., Smit, C.J., Dijkman, E.M., Cremer, J., Kotterman, M.J.J., Meesters, H.W.G., 2004. Voedselecologie van de gewone en grijze zeehond in de nederlandse kustwateren. Alterra.

Bromley, P.J., Watson, T., Hislop, J.R.G., 1997. Diel feeding patterns and the development of food webs in pelagic 0-group cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), whiting (*Merlangius merlangus* L.), saithe (*Pollachius virens* L.), and Norway pout (*Trisopterus esmarkii* Nilsson) in the northern North Sea. Ices Journal of Marine Science 54, 846–853.

Cadee, G.C., Hegeman, J., 2002. Phytoplankton in the Marsdiep at the end of the 20th century; 30 years monitoring biomass, primary production, and Phaeocystis blooms. Journal of Sea Research 48, 97–110.

Camphuysen, C.J., 2005. The Return of the Harbour Porpoise (*Phocoena phocoena*) in Dutch Coastal Waters. Lutra, p. 48.

Catchpole, T.L., Revill, A.S., Innes, J., Pascoe, S., 2008. Evaluating the efficacy of technical measures: a case study of selection device legislation in the UK *Crangon crangon* (brown shrimp) fishery. Ices Journal of Marine Science 65, 267–275.

Colijn, F., Hesse, K.J., Ladwig, N., Tillmann, U., 2002. Effects of the large-scale uncontrolled fertilisation process along the continental coastal North Sea. Hydrobiologia 484, 133–148.

Daan, N., 1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Netherlands Journal of Sea Research 6, 479–517.

Daan, N., Gislason, H., Pope, J.G., Rice, J.C., 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? Ices Journal of Marine Science 62, 177–188.

Doeksen, A., 2006. Ecological perspectives of the north Sea C. Crangon fishery. An Inventory of its Effects on the Marine Ecosystem, Natural Resources Management. Wageningen university, Wageningen.

Elliott, M., Dewailly, F., 1995. The structure and components of European estuarine fish assemblages. Netherlands Journal of aquatic ecology 29, 397–417.

Ens, B.J., Smaal, A.C., de Vlas, J., 2004. The Effect of Shellfish Fishery on the Ecosystems of the Dutch Wadden Sea and Oosterschelde. Alterra/RIVO/RIKZ, Wageningen.

Fonds, M., Saksena, V.P., 1978. The influence of temperature on the daily food intake of young soles. In: Dankers, N., Wolff, W.J., Wolff, J.J.Z. (Eds.), Fishes and Fisheries of the Wadden Sea. Balkema Press,, Rotterdam, pp. 132–138.

Freitas, V., Campos, J., Fonds, M., Van der Veer, H.W., 2007. Potential impact of temperature change on epibenthic predator–bivalve prey interactions in temperate estuaries. Journal of Thermal Biology 32, 328–340.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9, 228–241.

Harvey, A.C., 1989. Forecasting, Structural Time Series Models and the Kalman Filter. Cambridge University Press, Cambridge.

Hiddink, J.G., 2003. Effects of suction-dredging for cockles on non-target fauna in the Wadden Sea. Journal of Sea Research 50, 315–323.

Jennings, S., Cotter, A.J.R., 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. I. Introduction. Fisheries Research 40, 103–106.

Kraan, C., Piersma, T., Dekinga, A., Koolhaas, A., van der Meer, J., 2007. Dredging for edible cockles (*Cerastoderma edule*) on intertidal flats: short-term consequences of fisher patch-choice decisions for target and non-target benthic fauna. Ices Journal of Marine Science 64, 1735–1742.

Kuipers, B.R., van Noort, G.J., 2008. Towards a natural Wadden Sea? Journal of Sea Research. doi:10.1016/j.seares.2008.04.002.

Leopold, M.F., van Damme, C.J.G., van der Veer, H.W., 1998. Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea. Journal of Sea Research 40, 93–107.

Philippart, C.J.M., Van Aken, H., Beukema, J.J., Bos, O.G., Cadee, G.C., Dekker, R., 2003. Climate-related changes in recruitment of the bivalve *Macoma balthica*. Limnology and Oceanography 48, 2171–2185.

Philippart, C.J.M., Beukema, J.J., Cadeé, G.C., Dekker, R., Goedhart, P.W., van Iperen, J.M., Leopold, M.F., Herman, P.M.J., 2007. Impacts of nutrient reduction on coastal communities. Ecosystems 10.1007/s10021-006-9006-7.

Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R., Essink, K., 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. Journal of Applied Ecology 38, 976–990.

Pihl, L., Cattrijsse, A., Codling, I., Mathieson, S., McLusky, D.S., Roberts, C., 2002. Habitat use by fishes in estuaries and other brackish areas. In: Elliott, M., Hemingway, K.L. (Eds.), Fishes in Estuaries. Blackwell Science, Oxford, pp. 10–53.

Polet, H., 2003. Evaluation of Bycatch in the Belgian Brown Shrimp (*Crangon crangon* L.) Fishery and of Technical Means to Reduce Discarding. University of Gent, Gent.

Portner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315, 95–97.

Rijnsdorp, A.D., van Leeuwen, P.I., 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. Ices Journal of Marine Science 53, 1199–1213.

Rijnsdorp, A.D., Poos, J.J., Quirijns, F.J., Hille Ris Lambers, R., De Wilde, J.W., Den Heijer, W.M., 2008. The arms race between fishers. Journal of Sea Research. doi:10.1016/j.seares.2008.1003.1003.

Roessig, J.M., Woodley, C.M., Cech, J.J., Hansen, L.J., 2004. Effects of global climate change on marine and estuarine fishes and fisheries. Reviews in Fish Biology and Fisheries 14, 251–275.

Rose, G.A., 2005. On distributional responses of North Atlantic fish to climate change. Ices Journal of Marine Science 62, 1360–1374.

Soldaat, L., Visser, H., van Roomen, M., Van Strien, A., 2007. Smoothing and trend detection in waterbird monitoring data using structural time-series analysis and the Kalman filter. Journal of Ornithology 148, 351–357.

Teal, L.R., De Leeuw, J.J., Rijnsdorp, A.D., 2008. Effects of climate change on growth of 0-group sole and plaice. Marine Ecology Progress Series 357. doi:10.3354/meps07367.

van Aken, H.M., 2003. 140 years of daily observations in a tidal inlet (Marsdiep). ICES Marine Science Symposia 219, 359–361.

van Beek, F.A., Rijnsdorp, A.D., de Clerck, R., 1989. Monitoring juvenile stocks of flatfish in the Wadden Sea and the coastal areas of the southeastern North Sea. Helgolandes Meeresuntersuchungen 43, 461–477.

van der Veer, H.W., Bergman, M.J.N., 1987. Predation by crustaceans on a newly settled 0-group Plaice *Pleuronectes platessa* population in the western Wadden Sea. Marine Ecology Progress Series 35, 203–215.

van Gils, J.A., Piersma, T., Dekinga, A., Spaans, B., Kraan, C., 2006. Shellfish dredging pushes a flexible avian top predator out of a marine protected area. Plos Biology 4, 2399–2404.

van Keeken, O.A., van Hoppe, M., Grift, R.E., Rijnsdorp, A.D., 2007. Changes in the spatial distribution of North Sea plaice (*Pleuronectes platessa*) and implications for fisheries management. Journal of Sea Research 57, 187–197.

van Marlen, B., Redant, F., Polet, H., Radcliffe, C., Revill, A.S., Kristensen, P.S., Hansen, K.E., 1998. Research into Crangon Fisheries Unerring Effect (RESCUE)-EU study 94/044, RIVO Report.

Van Raaphorst, W., De Jonge, V.N., 2004. Reconstruction of the total N and P inputs from the IJsselmeer into the Western Wadden Sea between 1935–1998. Journal of Sea Research 51, 109–131.

Verver, S., van Willigen, J.A., Bult, T.P., 2005. Verkennende beschrijving van de kleinschalige Nederlandse kustvisserij, RIVO report.

Visser, H., 2004. Estimation and detection of flexible trends. Atmospheric Environment 38, 4135–4145.

Yang, J., 1982. The dominant fish fauna in the North Sea and its determination. Journal of Fish Biology 20, 635–643.

Zijlstra, J.J., 1976. Vissen, Waddenzee. natuurgebied van Nederland. Duitsland en Denemarken. Landelijke vereniging tot behoud van de waddenzee en vereniging tot behoud van Natuurmnumenten in nederland, pp. 133–141.

Zuur, A.F., Fryer, R.J., Jolliffe, I.T., Dekker, R., Beukema, J.J., 2003. Estimating common trends in multivariate time series using dynamic factor analysis. Environmetrics 14, 665–685.

Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. Analysing Ecological Data. Springer, New York.