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This is a postprint of:

Veer, H.W. van der, Dapper, R., Henderson, P.A., Jung, A.S., Philippart, C.J.M., Witte, J.IJ. & Zuur, A.F. (2015). Changes over 50 years in fish fauna of a temperate coastal sea: Degradation of trophic structure and nursery function. *Estuarine, Coastal and Shelf Science*, 155, 156-166

Published version: [dx.doi.org/10.1016/j.ecss.2014.12.041](https://doi.org/10.1016/j.ecss.2014.12.041)

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Changes over 50 years in fish fauna of a temperate coastal sea: degradation of trophic structure and nursery function

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ABSTRACT

The ongoing daily sampling programme of the fish fauna in the Dutch Wadden Sea using fixed gear was analysed for the years 1960-2011. Spring sampling caught immigrating fish from the coastal zone and autumn samples reflected emigration of young-of-the-year. In total 82 fish species were caught with no clear trend in biodiversity. In both spring and autumn total daily catch fluctuated and peaked in the late 1970s. From 1980 to the present catches of both pelagic and demersal species showed a 10-fold decrease in total biomass. Mean individual biomass decreased in spring between 1980 and the present from about 200 to 20 g wet weight. No trend was found in autumn mean individual biomass which fluctuated around 20 g wet weight. The trophic structure remained constant for both the demersal and benthopelagic fish fauna from 1980 to 2011, whilst the trophic position of pelagic fish in spring fell from about 3.9 to 3.1. Min/max auto-correlation factor analysis showed similar trends in spring and autumn species biomass time series:

the first axis represented a decrease from the 1960s followed by stabilization from the mid-1990s. The second trend showed an increase with a maximum around 1980 followed by a steady decrease in spring and a decrease and stabilization from 2000 in autumn. It is argued that the most likely explanatory variables are a combination of external factors: increased water temperature, habitat destruction in the coastal zone (sand dredging and beach nourishment, fishing) and increased predation by top predators for the first trend, and large-scale hydrodynamic circulation for the second trend. We conclude that both the trophic structure of the coastal zone fauna and the nursery function of the Wadden Sea have been reduced since the 1980s. Our findings corroborate that ecological change in coastal ecosystems has not only occurred in the past but still continues.

KEY WORDS: fish fauna, long-term changes, coastal area, Wadden Sea, climate change, habitat destruction, top predators, NAO index

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1. Introduction

Coastal ecosystems have been under pervasive human disturbance for centuries (Jackson et al., 2001) with historical evidence worldwide for major structural and functional change due to overfishing. The current challenges relate not only to overfishing, but the combined effects of it with climate change (e.g., warming, acidification, deoxygenation), habitat destruction and pollution (Bijma et al., 2013; European Marine Board, 2013).

Present findings on long-term changes in fish communities are primarily based upon information from commercial catches, landings and stock assessments. Most ecological research addressing full communities is of shorter duration and cannot give a long historical perspective. Furthermore, most observations are from the open sea while cumulative impacts of human behaviour are considered most severe in shallow coastal waters. To examine long-term changes in coastal fish communities and identify their possible causes, we analyse a 50 year consistent time series of fish fauna in the Dutch part of the international Wadden Sea, the largest coastal ecosystem bordering the North Sea.

The Wadden Sea is a typical example of a coastal ecosystem under long-term anthropogenic pressure. Key changes in the Dutch part include the decline of the harbour seal (Reijnders and Lanckester, 1990); disappearance of the bottlenose dolphin (Reijnders and Wolff, 1983); loss of the commercial spring herring fishery; pollution events (Essink and Wolff, 1983); embankments; eutrophication (De Jonge et al., 1996; Philippart et al., 2007) and species introductions (Wolff, 1992; Van Walraven et al., 2013).

Daily monitoring of the fish fauna using fyke nets in the western part of the Dutch Wadden Sea started in 1960 and has continued without change in methodology ever since (Van der Meer et al., 1995). The main advantage of this passive sampling device is that it samples both pelagic and benthic components of mobile fauna. It has been demonstrated that fyke catches are representative of a much larger area and that they represent an, on-average, constant sampling fraction of the fauna for all the abundant and most of the rare species (Van der Meer et al., 1995). Non-commercial fyke catches such as these supply the best available data of changes in the marine ecosystem as sampling methods have not been influenced by economics, management, fishing technology and targeting patterns as normally occurs (Branch et al., 2010).

Previous papers on these fyke catches dealt with fish recruitment (Philippart et al. 1996), long-term variability in the abundance of the brown shrimp *Crangon crangon* (Campos et al. 2010), bass *Dicentrarchus labrax* (Cardoso et al. 2014) and gelatinous zooplankton (Van Walraven et al. 2014). In this paper, long-term trends in the coastal fish community are analysed by addressing the following questions: [1] what are the long-term patterns in the fish community; [2] are these long-term trends associated with environmental factors; and [3] is there an impact of climate change visible?

2. Material and methods

2.1 Sampling

A passive fish trap near the entrance of the Dutch Wadden Sea (Fig. 1) was used. This 'kom-fyke' (Nédélec, 1982) has a leader of 200 m running from above the high water mark into the subtidal where two chambers collect the fish and other specimens. The stretched mesh-size of the leader and the chambers was 20 mm. In the area, the semidiurnal lunar tide is dominating and tidal range varies between 1 and 2 m depending on weather conditions and lunar phase. Tidal currents normally do not exceed 1 m sec^{-1} , except for periods with strong wind stress. Fishing started in 1960 and has continued ever since where the kom-fyke was emptied every morning irrespective of tidal phase, except when prevented by bad weather. In most years, the kom-fyke was removed just before winter because of potential damage by ice floes and in summer because of fouling of the net and potential clogging by macroalgae and jellyfish.

Catches were sorted immediately, and all individuals were identified up to species level. For each species, numbers were counted and sometimes, when

numbers were large, only wet mass was determined. Prior to data analysis, wet masses were transformed into counts, using a fixed ratio per month, i.e. a fixed mean individual mass based on the actual measurements from 1970 onwards. All information was stored in a database.

A suite of environmental parameters were collected which were considered to potentially influence fish communities (Table 1). Large-scale hydrodynamic circulation was indexed by the North Atlantic Oscillation (NAO) during winter (Dec-March). Fish performance during winter (Dec-Feb) and summer (July-Aug) was indexed by water temperature, salinity and visibility (Secchi disk readings), obtained from long-term monitoring programmes at the NIOZ sampling jetty, located < 1 km east of the kom-fyke. Primary productivity was indexed by mean summer values (May-Sept) of concentrations of chlorophyll-a ($\mu\text{g l}^{-1}$), total-N and total-P (mg l^{-1} ; sum of dissolved inorganic, dissolved organic, and particulate compounds) in the Marsdiep basin. As nutrient concentrations only covered part of the sampling period, loadings of total-N and total-P discharged from Lake IJssel (the main freshwater source of the Marsdiep) were also included. Habitat destruction was captured by the amount of sand dredging, the amount of beach nourishment and the intensity of shrimp fisheries in the coastal zone of the North Sea and cockle fisheries in the intertidal of the Wadden Sea. To index predation pressure by top predators, abundance estimates of cormorants in the western Wadden Sea, and numbers of harbour and gray seals in the Dutch Wadden Sea and coastal zone were multiplied by their respective daily food requirements [cormorants: $575 \text{ g wet mass d}^{-1}$ (Leopold et al., 1998); harbour seal: $2.5 \text{ kg wet mass d}^{-1}$, gray seal: $3 \text{ kg wet mass d}^{-1}$ (IMARES, Brasseur pers. comm.)] and summed.

2.2. Data analysis

For each species, the length-weight relationship was determined, based on individuals collected between 1990 and 2002 (Leopold et al., 2001). For some rare species, length-weight relationships were taken from Fishbase (www.fishbase.org). For all catches, total wet biomass was estimated. First, for each species, the size-frequency distribution of the catch was converted to wet mass using the length-weight relationship. Then the total biomass of the catch was estimated by summing the individual masses (direct estimate). For the period from 1960 to 1980, no size frequency distributions were available and, therefore, total biomass of the catch could only be calculated indirectly by taking the average monthly individual mass for each species from the period 1980–2010. For comparison, this indirect estimate was also applied for the period 1980–2010. Finally, the average daily biomass of the catch was calculated for both spring (April, May, June) and autumn (September, October).

Species were characterized based on number of years found as core (≥ 20 y) or transient species (< 20 y), by mode of life (pelagic, demersal, benthopelagic) and to trophic level (the position of a species in the food chain) using Fishbase (www.fishbase.org). In addition, the biogeographic guild (northern and southern species) was determined based on Daan (2006). For each sampling date, the trophic level of the fish fauna was estimated by taking the trophic level of the various species caught and calculating the mass-weighted average trophic level. All information is presented in Appendix A.

2.3. Statistical analysis

Statistical treatments used R (R Development Core Team, 2011). Preliminary data exploration was carried out following the protocol described in Zuur et al. (2010). Multi-panel scatterplots using the `xyplot` function from the `lattice` package

(Sarkar, 2008) were applied to identify the type of relationship between environmental variables and the presence of collinearity.

Common trends in the biomass time series of the various species were extracted by min/max auto-correlation factor analysis (MAFA) (Solow, 1994), all species present for >10 years were included. This analysis is a type of principal component analysis where the axes represent a measure of autocorrelation and indicate the association between the values of the principal component at Z_t and Z_{t+k} , where k is a time lag of 1, 2 etc. The first MAFA axis has the highest autocorrelation with a time lag of 1 year and therefore represents the main trend in the data and the loadings determine the relationship of individual species time series to particular MAFA axes. Subsequently, the second MAFA axis has the second highest autocorrelation with a time lag of 1 year. Cross-correlations between MAFA axes and environmental variables, also known as canonical correlations, allow identification of significant correlations between trends in species biomass and explanatory variables. The software package Brodgar (<http://www.brodgar.com>) was used to carry out MAFA (see also Erzini et al., 2005).

3. Results

3.1. Environmental variables

The environmental variables showed different temporal patterns (Fig. 2). The NAO index showed large variability with maximum values at the beginning of the 1990s. Both local winter and summer temperature increased over the years in contrast to salinity. Secchi disc measurements were missing until mid-1970s, and showed an irregular pattern without trend. Summer chlorophyll-a concentration was available from the 1970s and peaked in the late 1980s, followed by a steady

decrease. Total-N and total-P loadings increased until the beginning of the 1980s followed by a decrease. Nutrient concentrations only covered part of the period, but were in line with the loadings. In the coastal zone, sand mining and beach nourishment increased steadily from the 1980s and also shrimp fisheries increased over time, but with large inter-annual variability. In the Dutch Wadden Sea cockle fisheries increased until around 2000 and then decreased partly because mechanical dredging was banned in 2004. Since 1990, predation pressure by top predators increased strongly as the result of the increased abundance of cormorants, harbour seals and gray seals.

Environmental variables displayed collinearity (Table 2). Summer temperature was correlated with a number of variables that also increased over time. Strong collinearity was also found between sand mining, beach nourishment, shrimp fisheries and top predators. Furthermore, summer chlorophyll was correlated with total-N and total-P loadings.

3.2. Fish fauna

In total 82 fish species were identified (Appendix A). Both in spring and autumn, the total number of core species showed no consistent trend; the number increased at an average rate of approximately 1 species every 3 years between 1960 and ca. 1987, and subsequently declined (Fig. 3). Over time, the total number of transient species increased. Between 1965 and the mid-1980s, cold water-adapted species were most abundant; their subsequent decline was not fully compensated by warm water species, resulting in a recent small decline in species number. Spring catches were, on average, dominated by demersal species (40). In addition 16 pelagic and 9 benthopelagic species were found. Most of the rare species were

demersal species. Most of the pelagic species were caught frequently; only 4 pelagic species were rarely caught.

Between 1980 and 2011, the estimated and the reconstructed mean daily total biomass were significantly correlated for both spring (Pearson correlation $r=0.98$; $n=33$; $p<0.01$) and autumn ($r=0.90$; $n=33$; $p<0.01$) values.

Large interannual variability in total biomass occurred between 1960 – 1970, followed by a period of steady increase with peak values of about 90 kg d^{-1} in spring and 40 kg d^{-1} in autumn, and finally a steady decrease to catches of around $5 - 10 \text{ kg d}^{-1}$ at present (Fig. 4). Pelagic and demersal species biomass fluctuated (Fig. 4), the largest decrease was in the demersal group in spring. Demersal species remained the dominant spring group, in autumn pelagic species became the dominant from the 1980s onwards.

In general, mean daily numbers caught were much lower in spring than in autumn (Fig. 5). In contrast, mean individual wet mass was larger in spring than in autumn (Fig. 5). Mean individual wet mass showed a decrease over time, especially in spring from around $100 - 150 \text{ g}$ in the 1980s-1990s to less than 50 g in more recent years. The decrease in autumn was less clear and mean individual mass even increased in recent years.

The average trophic level showed a significant decrease in spring of about 0.5 units from 1980 to 2011 (Pearson correlation $r=-0.48$; $n=33$; $p<0.01$). This decrease was mainly caused by the pelagic species (Fig. 6), which showed a significant decrease over time in spring (Pearson $r=-0.71$) and autumn ($r=-0.47$). Neither the demersal nor the benthopelagic species showed a trend in trophic level.

3.3. Trend analysis

Catches of individual fish species displayed different types of pattern (Appendix B) ranging from a continuous decrease (*Zoarces viviparus*) via maximum catches around the 1970s-1980s (*Belone belone*, *Gadus morhua*, *Atherina presbyter*, *Cyclopterus lumpus*, *Scophthalmus maximus*, *Pleuronectes platessa*, *Platichthys flesus*) to a steady increase (*Dicentrarchus labrax*). For many species, trends in catches differed for spring and autumn. Some species showed consistently higher catches in spring (*Alosa fallax*, *Salmo trutta*, *B. belone*, *Chelon labrosus*) or in autumn (*Clupea harengus*, *Osmerus eperlanus*, *Anguilla anguilla*, *Melangius merlangus*, *Pollachius pollachius*, *Scomber scombrus*), or showed different patterns between spring and autumn catches (*G. morhua*, *Liza ramada*).

The MAFA was performed on species that were present for at least 10 years. To reduce the influence of the most abundant species on the outcome, data were also square root transformed, but results were the same (Fig. 7). The scores of the first MAFA axis showed a continuous change over time. In spring, the decreasing trend seemed to stabilize in the mid-1990s, in contrast to autumn where the trend continued. The second axis showed for both spring and autumn an increasing trend from 1960 to a maximum around 1980 followed by a steady decrease.

The canonical correlations illustrate the relationships between species and the first two axes. Spring and autumn showed a slightly different pattern for axis 1 and a more similar pattern for spring axis 2 (Fig. 8). For the first axis significant relationships were present for 18 species in spring and for 21 in autumn, whilst for the second axis this accounted for 17 (spring) and 10 (autumn) species. For the first axis, *Anguilla anguilla*, *Belone belone*, *Trachurus trachurus*, *Zoarces viviparus*, *Myoxocephalus scorpius*, *Scophthalmus rhombus* and *Limanda limanda* had a strong declining trend and showed a significant correlation ($r > 0.50$) in either spring or autumn. *Dicentrarchus labrax* was the only species with a strong increasing trend. For the second axis, four species showed a significant correlation ($r > 0.50$) and only

during spring: *B. belone*, *Callionymus lyra*, *Chelon labrosus* and *Pleuronectes platessa*. For some groups, the spring and autumn patterns were similar. Clupeids, Gadoids, Mulids showed a strong positive correlation with the second axis, while for flatfishes the first axis was more important.

The correlations between the two MAFA axes and the explanatory variables are presented in Table 3. Highly significant correlations with the first MAFA axis existed with summer temperature, sand mining, beach nourishment, top predators and to a lesser extend with shrimp fisheries. The second MAFA axis showed highly significant correlations with the NAO winter index in spring and autumn and with parameters linked to the productivity of the area.

4. Discussion

Capture by fixed gears requires the active movement of the organism. The kom-fyke is located near a large tidal inlet of the Wadden Sea and it is expected that spring catches will contain fish that were migrating from the North Sea into the Wadden Sea whilst autumn catches will comprise fish on their way to migrate to the North Sea including the locally produced young-of-the-year (Fonds, 1983). Therefore, spring catches are considered to reflect the fauna of the coastal zone of the North Sea and autumn catches the productivity of the Wadden Sea nursery. The geographical origin of the fish species caught in the kom-fyke suggests that the observed long-term trends in fish communities may reflect a more general pattern occurring not only locally within the Wadden Sea.

4.1. Trends in environmental conditions

Climatic variability over western Europe determines the fluctuations in temperature and fresh water input (reflected in salinity) in the Wadden Sea: seasonal variation in sea surface temperature only lags a few days behind the coastal surface air temperature (Van Aken, 2008b) and the precipitation over western Europe, and the connected changes in the Rhine discharge, are mainly responsible for the inter-annual variations in the salinity (Van Aken, 2008a). This climate variability can be captured with the NAO index that shows a significant correlation with winter, spring and mean annual temperature (Van Aken, 2008b): a positive NAO index means mild and wet winters and a negative one cold, dry weather (Jones et al., 1997).

Temperature and salinity are the main forcing functions affecting fish performance. Salinity is reflecting river runoff which is found to be correlated with riverine nutrient loads, affecting chlorophyll-a and primary production (Philippart et al., 2007), and possibly riverine sediment loads and hence visibility. The length of the time series determines the perceived pattern. In the last 25 years, a clear warming of about 1.5°C has occurred in the western Wadden Sea (Van Aken, 2008b). However, over a centennial period, a cooling of about 1.5°C is observed in first 30 years and a warming in the last 25 years. An explicit greenhouse effect is not required as a forcing factor to explain recent warming because coincident variations in wind statistics and cloudiness can explain the increase (Van Aken, 2010).

Measurements of the nutrients and chlorophyll started only just before the peak in nutrient loads and concentrations in this area (Cadée and Hegeman, 2002; Philippart et al., 2007) and hence overall decreasing trends are observed. These truncated time series limit our ability to identify candidate explanatory variables for the trends in the fish fauna using correlation analyses.

Anthropogenic habitat destruction, sand mining and beach nourishment in the coastal zone, have affected the area especially since the 1980s, while fisheries were

impacting over even longer time scales. Top predators have increased recently and hence these factors showed collinearity. The correlation of these variables with productivity might be causally misleading because of the short length of the time series.

In this study we are forced to accept different baselines; 19th century for temperature, salinity and NAO winter index; 1980s for nutrients, chlorophyll, Secchi disc; 1960s for habitat destruction and top predators.

4.2. Long-term trends in the fish community

In the 1980s and 1990s the fish fauna of the Dutch Wadden Sea comprised 97 species, varying from very abundant to extremely rare (Witte and Zijlstra, 1983). In the present study, 82 species were caught over the period 1960 to 2011, indicating that these catches are a good representation of the species composition described by Witte and Zijlstra (1983). The absence of a trend in the number of species caught suggests that with respect to species richness the function of the area is unchanged.

Species composition is slowly shifting from core to transient species indicating that rare species occur more often. From the mid-1980s especially cold water-adapted forms have declined and warm water species have increased, however losses have not been fully compensated. Shifts in species or abundance due to changes in sea water temperature have also been observed in the Bristol Channel (Henderson et al., 2011) and in the eastern North Atlantic (Ter Hofstede et al., 2010). The change in the eastern North Atlantic has been linked to the decline of cod and plaice and the increase of sprat, anchovy and horse mackerel (Rijnsdorp et al., 2009). In this study, bass *Dicentrarchus labrax* in particular has increased

explosively in biomass contemporaneously with the decline in eelpout *Zoarces viviparus*.

The decrease in catch biomass from the mid-1970s was much stronger in spring than in autumn. There are indications that these trends are large-scale ones and reflect those of fish communities in the entire the Dutch Wadden Sea: beam trawl surveys showed an increase in the Wadden Sea from the 1970s to 1985 followed by a steep decrease until the mid-1990s and a temporary period of increase until 2002 (Tulp et al., 2008), a trend corresponding roughly with that of demersal fish in the kom-fyke. In these trawl surveys, the most important change has been the disappearance of I- and II-group flatfish, especially plaice *Pleuronectes platessa*, (Van der Veer et al., 2011), which were abundant in earlier times (Kuipers, 1977; De Vlas, 1979). Time series of North Sea plaice do not show decreasing trends of recruitment over the last decades (Anonymous, 2006) implying a change in the distribution of the older juvenile stages.

Seasonal variation in numbers and mean individual biomass illustrates the nursery function of the Wadden Sea: in spring low numbers of juvenile and adult fish enter the area and in autumn much higher numbers of mainly small juveniles leave. The large fluctuations in numbers of juveniles illustrate the inter-annual variability in year-class strength of the young-of-the-year of the various nursery species (especially Clupeidae and flatfish species). A slight, but clear, negative trend in both numbers and individual biomass in autumn, implies that the overall nursery function of the area has been reduced. The main changes seem to have occurred in the coastal zone as this is reflected in the spring catches. This negative pattern in both pelagic and demersal catches was not clearly observed in the long-term beam trawl survey (Tulp et al., 2008). The trends in trophic level illustrate that the composition of the pelagic fauna has been particularly affected: both in the coastal zone (spring) and the Wadden Sea (autumn): the trophic level of the pelagic fish fauna (typical

species herring *Clupea harengus* and garfish *Belone belone*) has decreased strongly in the spring, reflecting the situation amongst the coastal zone fauna. This study shows similar common trends in both spring and autumn suggesting a strong link between the coastal zone and the Wadden Sea. This implies that in both areas underlying mechanisms might be similar, which is supported by the fact that Gadoids, Clupeids and flatfish species showed similar patterns in spring and autumn. However, in terms of biomass the absolute impact seems less in the Wadden Sea than in the coastal zone of the North Sea.

4.3. Correlations between environmental factors and the fish community

In the perspective of the radical changes in coastal ecosystems including the Wadden Sea over the last 2000 years (Lotze, 2005), the present study only reflects a short moment in a history of constantly shifting baselines (Jackson et al., 2001; Pinnegar and Engelhard, 2008; Lotze and Worm, 2009). Furthermore, correlations between environmental factors and the fish community may not point to underlying relationships and potentially miss causal factors: there is collinearity among the environmental factors; the time series are relatively short; certain events such as eutrophication have only occurred once and the fish community consists of a variety of species with different life cycles and preferences.

The most important trend in the fish community as depicted by the fyke catches is the decreasing biomass from 1960 to 2000 and the stabilization hereafter. We consider the correlation with summer temperature spurious as warming by 1.5°C only started 25 years ago (Van Aken, 2010). The correlation with nutrient concentration in summer (total-N and total-P) may hint at eutrophication as an explanation in support of Boddeke and Hagel (1991). However, for the fish fauna this correlation does not imply causality as this time series is relatively short (31 years)

and only started when eutrophication was almost at its maximum. The reconstructed pattern of eutrophication since the 1930s (Van Raaphorst and De Jonge, 2004) agrees with the relatively low total fish biomass during spring in the 1960s and relatively high values in the 1980s (Fig. 4). The impact of eutrophication on productivity should act either via increased recruitment (numbers) or growth (individual biomass) or a combination of both. Neither seems to be the case: there has not been an increase in numbers nor in individual fish mass in the kom-fyke catches. Also growth patterns of 0-group plaice in the intertidal of the Wadden Sea did not show any pattern from 1975 to 2007 (Van der Veer et al., 2010).

The strong correlations of fish biomass with habitat destruction and top predators are more likely to reflect causality. Bottom-trawling fishing activities destroy the surface layer of the sediment whereas sand extraction and beach nourishment physically removes and covers the habitat consisting of sediment and the associated benthic communities. Attempts to identify the impact of beach nourishment on marine life have so far focused on benthos and birds (Baptist and Leopold, 2009; Lewis et al., 2012). Sand extraction in the coastal zone at a depth from about 20 m has increased from a few million m³ per annum at the beginning of the 1980s to 35 million m³ at present whilst a further increase is expected (Anonymous, 2013a), and this links in with sand nourishment. Along most of the Dutch coastline sand nourishment takes place regularly at intervals of a few years. Recovery of the benthic community takes a number of years (Van der Veer et al., 1985; Newell et al., 1998; Van Dalfsen & Essink, 2001) and often the community structure differs from the original due to a shift in sediment type (Desprez, 2000; Wilber and Clarke, 2001). Finally, a link with the abundance and hence consumption of top predators seems likely: cormorants and seals have increased considerably since the 1990s (e.g., Brasseur et al., 2014) and this also holds true for the harbour porpoise (Camphuysen, 2004).

The second most important trend in the fish community is an increasing trend in species abundance from 1960 to a maximum around 1980 followed by a steady decrease. This second MAFA axis showed a significant correlation with the NAO winter index and also with chlorophyll-a in summer. Following Alheit and Bakun (2010), the NAO winter index predicts synchronicity in a region comprising the North Sea, the Baltic Sea, the northwestern Mediterranean and north and central European lakes. Even shifts in species composition in Narragansett Bay (east coast of the US) could be correlated with the winter NAO index (Collie et al., 2008). Therefore, this correlation might reflect the large-scale influence of weather conditions in northern Europe acting via the food chain on the fish fauna; the strong significant correlation between NAO winter index and subsequent summer chlorophyll-a in the Wadden Sea supports this view.

The fact that roughly similar types of patterns were found in related species, i.e. the Clupeids, Gadoids, Mulids and flatfishes, suggests general underlying mechanisms. However, the present study is not suited to unravel them. An exception might be the strongly decreasing trend in eelpout *Zoarces viviparus* and increasing trend of bass *Dicentrarchus labrax*. It is very likely that they reflect a northwards shift in distribution as a response of climate change (increased water temperature) (eelpout: Pörtner and Knust, 2007; bass: Henderson and Corps, 1997).

Given that the Dutch Wadden Sea is open to migration and many fish species range over large areas, the change in trophic structure of the fish assemblage of the western Wadden Sea may reflect a more general pattern occurring in other coastal areas. On the other hand, coastal waters and open North Sea regions might differ in their response as shown by McQuatters-Gollop and Vermaat (2011). The present results are based on correlations only. The next step in the identification of underlying relationships should not only focus on climate change, habitat destruction, top predators and impact of large-scale hydrodynamic circulation but

also on regime shifts (Beaugrand, 2004; Weijerman et al., 2005; Möllmann and Diekmann, 2012) and factors indicated as responsible for these shifts such as temperature increase, gradual warming, temperature-induced modified predator-prey relationships and high fishing pressure (Beaugrand, 2004; Freitas et al., 2007; Kenny et al., 2009; Kirby et al., 2009).

This study confirms the alarming observations for offshore fisheries of Jackson et al. (2001); ecological changes occurred in the past and continue at a rapid rate in coastal ecosystems, they are damaging the ecological health of these coastal areas.

Acknowledgements

Thanks are due to all those who assisted over the years, especially to the late Henk Beumkes, Willem Jongejan, Ewout Adriaans, Sieme Gieles and Marco Kortenhoeven.

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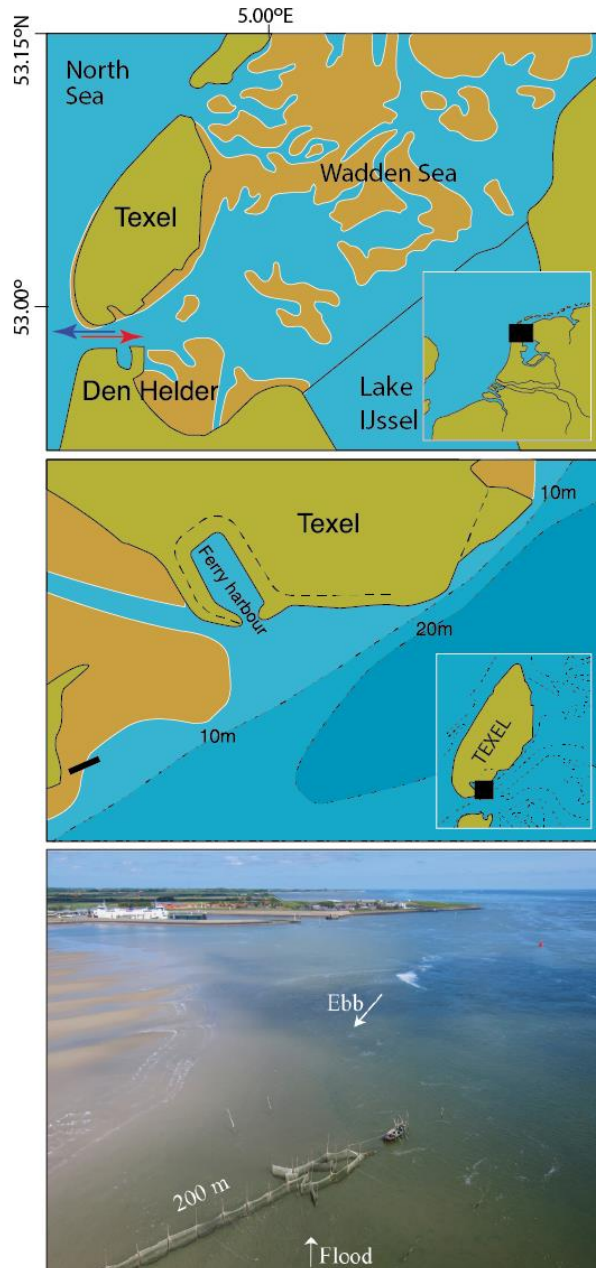


Figure 1 The sampling location near the island of Texel. Upper panel: western Dutch Wadden Sea; red arrow indicates inwards migration in spring and blue arrow outward migration in autumn. Middle panel: fyke net position (black bar); Orange: intertidal areas. Lower panel: Aerial photograph taken from a southwestern angle (courtesy of Lodewijk van Walraven)

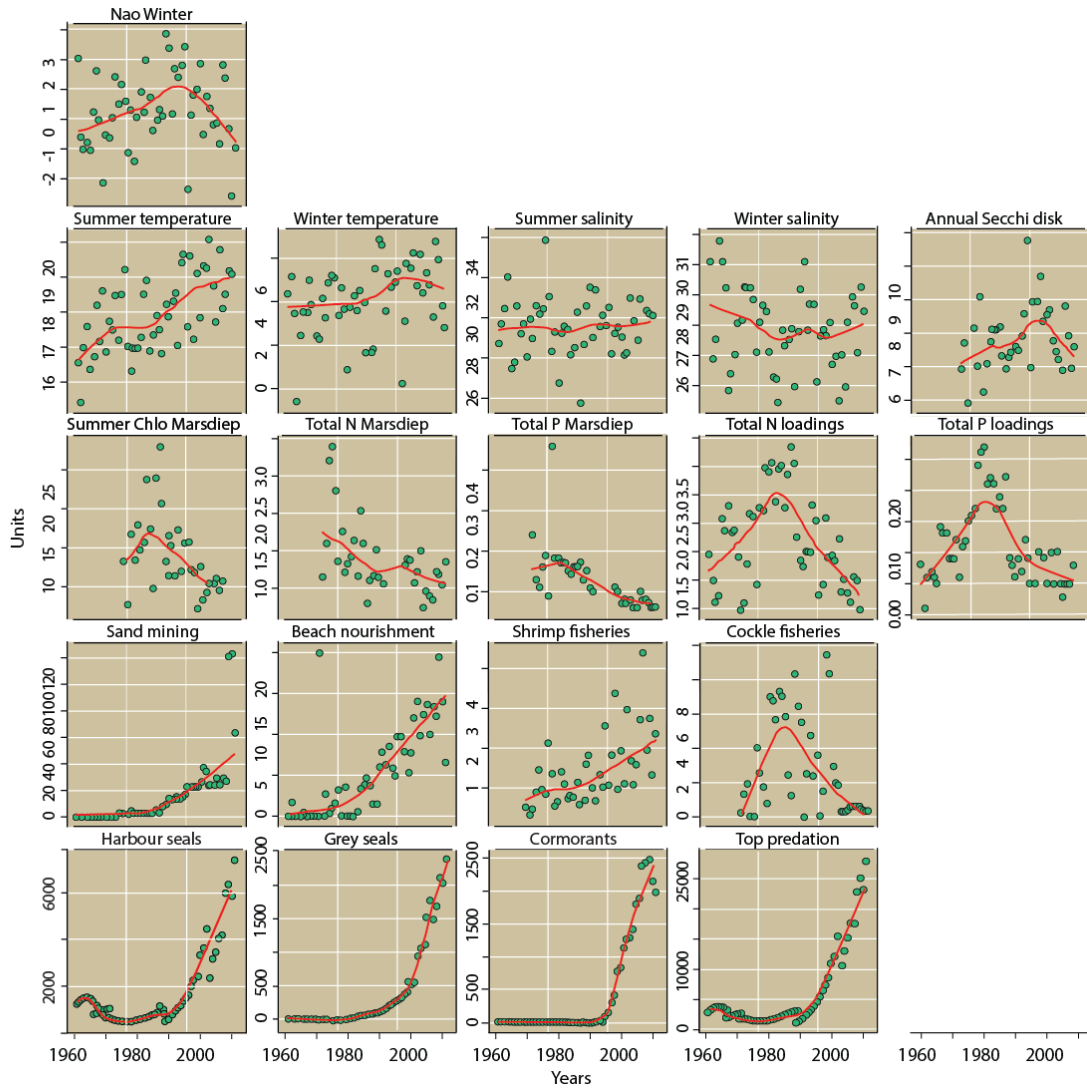


Figure 2. Time series of environmental variables in the western Dutch Wadden Sea for the period 1960 – 2011. For units and references see Table 1. A LOESS smoother with a span of 0.5 was fitted to aid visual interpretation.

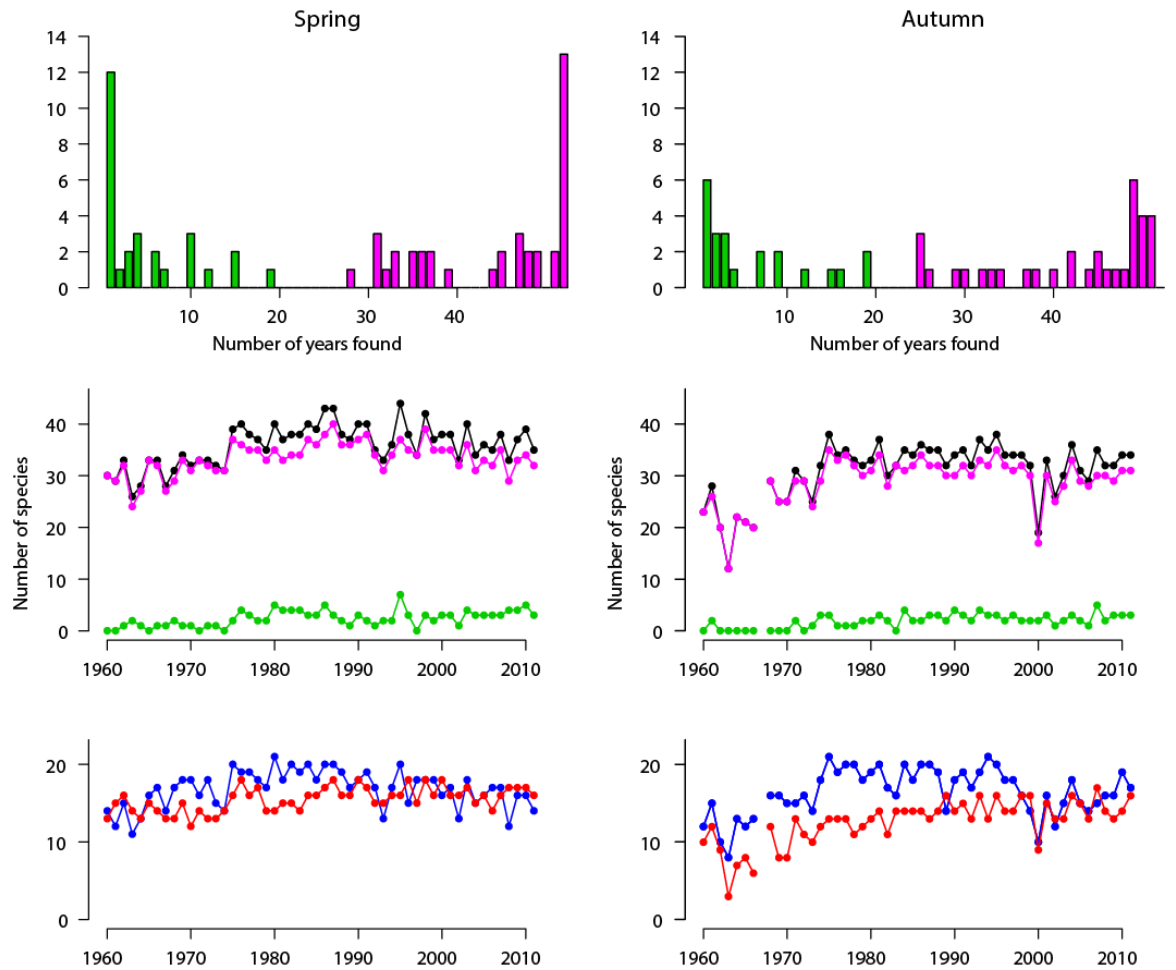


Figure 3 Characterization fish species in spring (left column) and autumn (right column).

Top panel: Number of species per number of years found, colors depict core (pink) and transient (green) species;

Middle panel: Trends in total (black), core (pink) and transient (green) species over time;

Lower panel: Trends fish fauna in warm-water adapted (red) and cold-water adapted (blue) species over time.

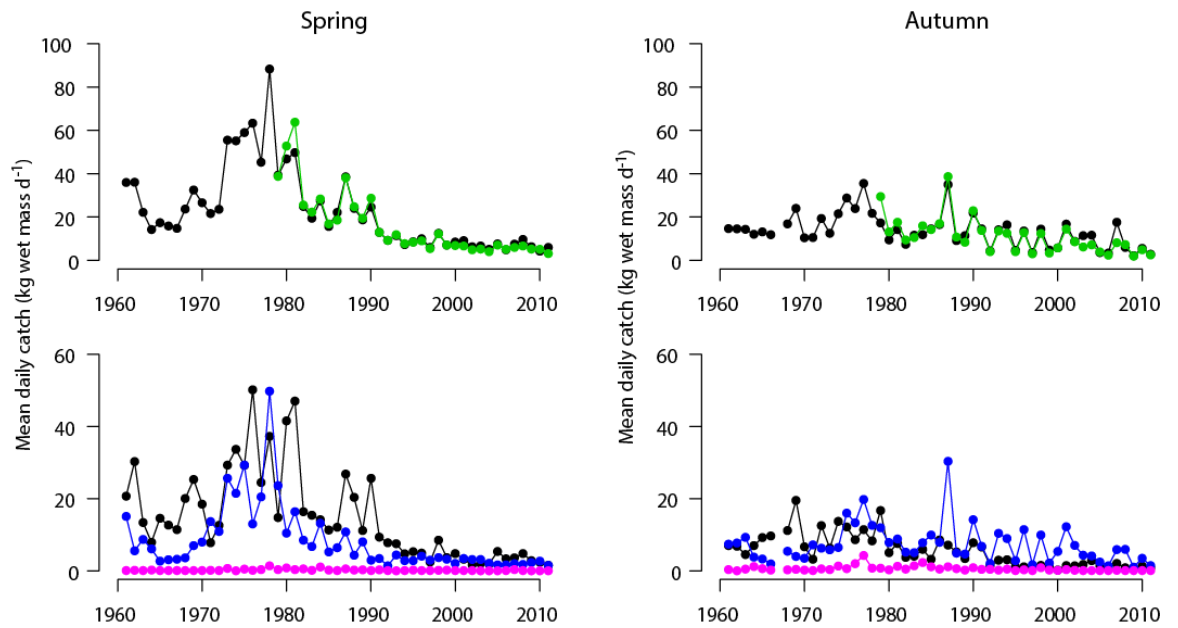


Figure 4 Trends in total daily catch (kg d^{-1}) in wet mass in spring (left column) and autumn (right column).

Top panel: Total daily catch based on direct measurements of fish size (green line) and based on reconstructed size, i.e. fixed ratio (black line);

Bottom panel: Daily catch of demersal (black line), pelagic (blue line) and benthopelagic (pink line) fish species.

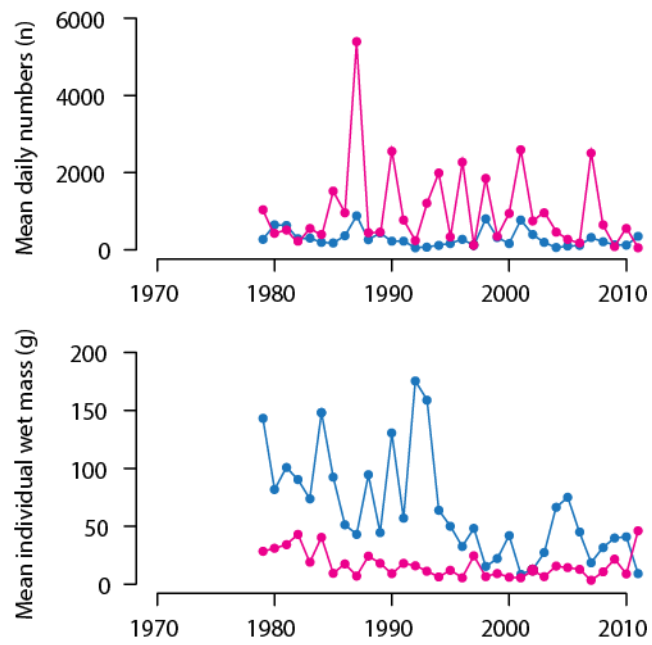


Figure 5 Trends in mean daily numbers (n) (top) and individual fish biomass (g wet mass) (bottom) in spring (blue) and autumn (red).

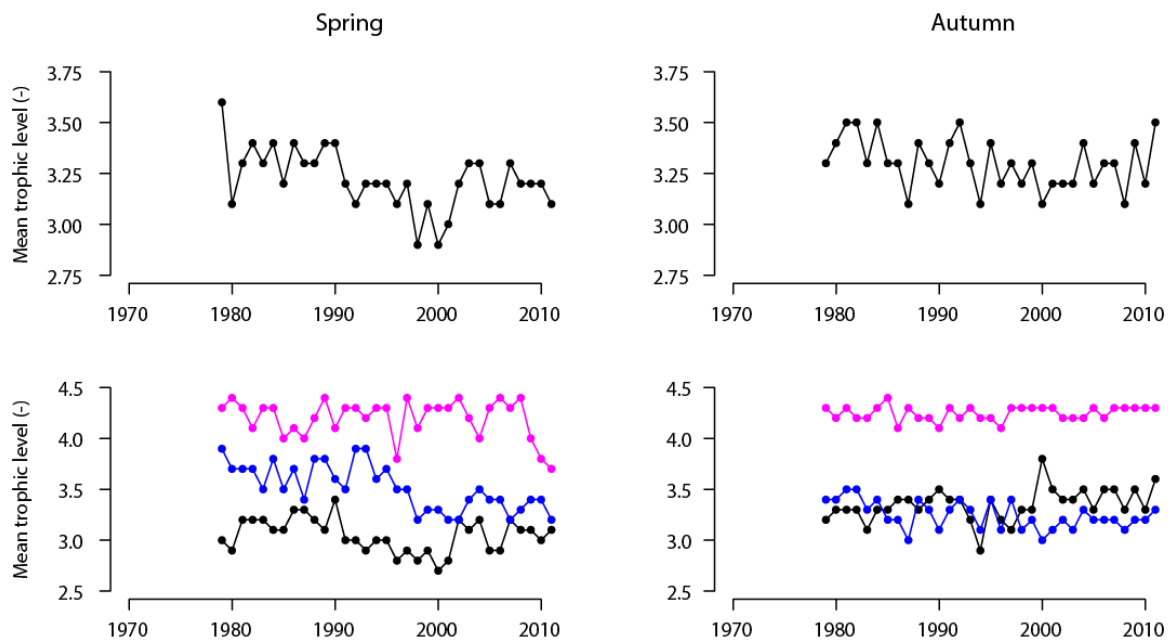


Figure 6 Trends in trophic level (-) in spring (left panel) and autumn (right panel).
Top panel: all species; Lower panel: demersal (black), pelagic (blue) and benthopelagic species (pink).

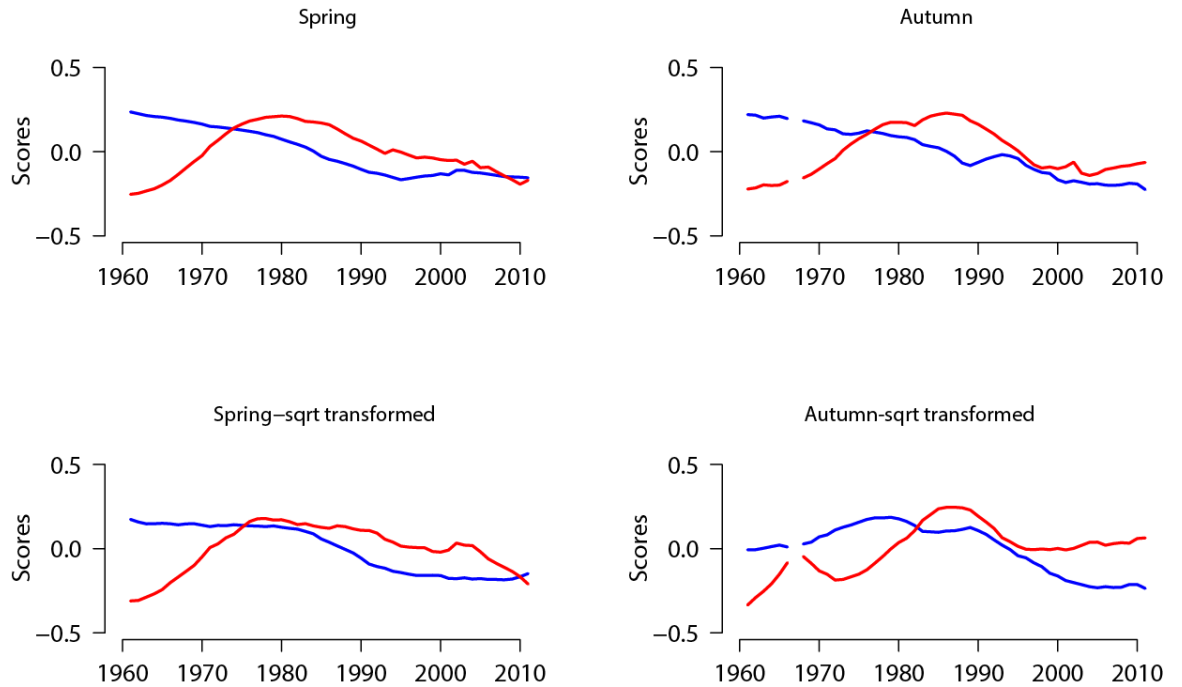


Figure 7 First (red) and second (blue) axis of min/max auto-correlation factor analysis (MAFA) of total biomass of 34 common fish species (caught in at least 10 years during the study period; see Appendix B) for spring (left panels) and autumn (right panels). Top panel: non-transformed data; lower panel: square root transformed data.

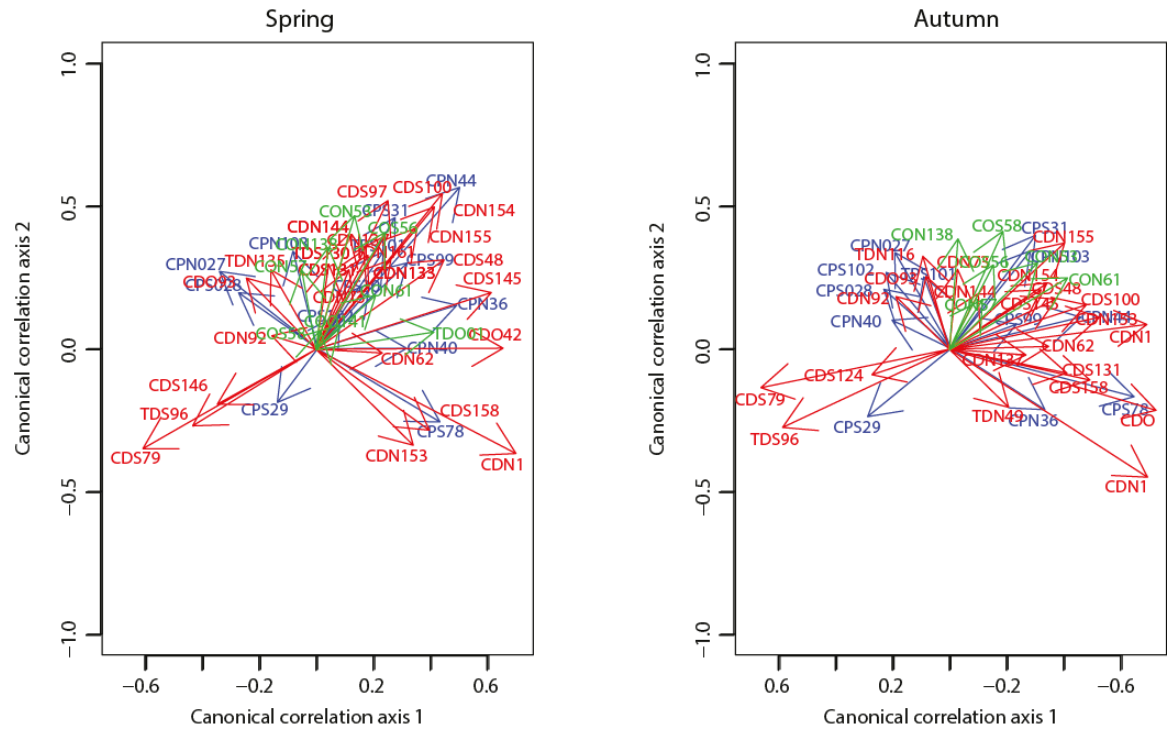


Figure 8 Canonical correlations between first and second MAFA axis and trends of the total biomass of 34 common (caught in at least 10 yrs during the study period; see Appendix B) fish species in spring (left panel) and autumn (right panel). Demersal species (red), pelagic species (blue) and benthopelagic species (green). For coding see Appendix A (Significance level $p < 0.01$ and $n = 51$: $r > 0.28$).

Table 1. Environmental variables used with references

	Environmental parameter	Area	Time series	Unit	References
Hydrodynamic circulation	NAO Dec-March	Coastal zone Wadden Sea	1960-2011	-	Jones et al. (1997) (http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm)
Fish performance	Water temperature	western Wadden Sea	1960-2011	°C	Van Aken (2003, 2010) (www.nioz.nl)
	Salinity	western Wadden Sea	1960-2011	0/00	Van Aken (2003) (www.nioz.nl)
	Secchi disc	western Wadden Sea	1974-2010	m	Philippart et al. (2013)
Productivity	Chlorophyll	western Wadden Sea	1976-2007	µg l ⁻¹	(http://live.waterbase.nl/waterbase)
	Total-N and total-P	western Wadden Sea	1972-2010	mg l ⁻¹	(http://live.waterbase.nl/waterbase)
	Total-N and total-P loadings	western Wadden Sea	1960-2004 1977-2009	mol s ⁻¹ kg s ⁻¹	Van Raaphorst & de Jonge (2004) Van Beusekom et al. (2009)
Habitat destruction	Sand mining	Coastal zone	1960-2011	10 ⁶ m ³ a ⁻¹	Anonymous (2013a)
	Beach nourishment	Coastal zone	1960-2011	10 ⁶ m ³ a ⁻¹	Rijkswaterstaat Zee en Delta Stolk, pers. comm.
	Shrimp fisheries	Coastal zone Wadden Sea	1970-2011	10 ³ km ²	Landings: Anonymous (2013b) Densities: IMARES DFS survey; Tulp pers. comm.
	Intertidal cockle fisheries	Wadden Sea	1971-2011	10 ⁶ kg a ⁻¹	Landings: IMARES; Troost pers. comm.
Top predators	Cormorants	western Wadden Sea	1980-2011	Ind.	Sovon Vogelonderzoek Nederland/Netwerk Ecologische Monitoring.
	Harbour and gray seals	Dutch Wadden Sea	1960-2011	Ind.	http://www.compendiumvoordeleefomgeving.nl/indicatoren/nl1231-Gewone-en-grijze-zeehond-in-Waddenzee-en-Deltagebied.html?i=19-135

Table 2. Pearson correlation coefficients between the various environmental factors. Significant relationships are indicated in bold ($p < 0.01$). For more information see Table 1.

		Winter temp	Winter salinity	Summer temp	Summer salinity	Secchi disc	Summer chlorophyll a	Loading total-N	Loading total-P	Sand mining	Beach nourishment	Shrimp fisheries	Cockle fisheries	Top predators
Hydrodynamic circulation	NAO index	0.26	-0.11	0.17	0.06	0.31	0.07	0.16	0.00	-0.23	-0.11	0.19	0.19	-0.18
Fish performance	Winter temperature		-0.07	0.26	0.27	-0.14	-0.46	-0.28	-0.32	0.22	0.26	0.15	-0.15	0.22
	Winter salinity			-0.21	0.06	-0.13	-0.16	-0.30	-0.37	0.06	-0.01	-0.00	-0.39	-0.03
	Summer temperature				0.35	0.18	-0.34	-0.28	-0.21	0.45	0.47	0.26	-0.27	0.46
	Summer salinity					-0.40	-0.35	-0.41	-0.20	0.07	0.05	0.06	-0.13	0.03
	Secchi disc						-0.16	0.05	-0.20	0.00	0.11	0.30	0.19	0.06
Productivity	Summer chlorophyll a							0.63	0.53	-0.55	-0.49	-0.40	0.16	-0.50
	Total N loadings								0.81	-0.38	-0.50	-0.26	0.51	-0.48
	Total P loadings									-0.32	-0.43	-0.40	0.49	-0.45
Habitat destruction	Sand mining										0.67	0.41	-0.31	0.83
	Beach nourishment											0.42	-0.48	0.69
	Shrimp fisheries												-0.10	0.58
	Cockle fisheries													-0.40
Predation	Top predators													

Table 3 Pearson correlation coefficients between the various environmental factors and the first and second axis of the min/max auto-correlation factor analysis (MAFA) for spring and autumn. Significant relationships are indicated in bold ($p < 0.01$).

		Spring		Autumn	
		First axis	Second axis	First axis	Second axis
Hydrodynamic circulation	NAO winter index	0.34	0.72	0.45	0.75
Fish performance	Winter temperature	-0.31	-0.06	-0.33	-0.05
	Winter salinity	0.18	-0.20	0.24	-0.19
	Summer temperature	-0.58	-0.03	-0.62	-0.04
	Summer salinity	0.01	-0.04	0.02	-0.04
	Secchi disc	-0.37	-0.22	-0.21	-0.24
Productivity	Summer chlorophyll a	0.26	0.49	0.41	0.61
	Total N loadings	0.10	0.61	0.21	0.68
	Total P loadings	0.18	0.76	0.25	0.74
Habitat destruction	Sand mining	-0.58	-0.38	-0.67	-0.22
	Beach nourishment	-0.67	-0.29	-0.74	-0.25
	Shrimp fisheries	-0.49	-0.52	-0.59	-0.44
	Cockle fisheries	0.04	0.40	0.19	0.45
Predation	Top predators	-0.57	-0.53	-0.75	-0.41

Appendix A Fish species caught in the kom-fyke during the period 1960 - 2011, together with length - weight relationship (L_{cm}-g wW), biogeographic guild, mode of living, and trophic status (level +/- s.d). Length-weight relationships according to: 1: Leopold et al.(2001); 2: NIOZ (unpubl.) 3:Fishbase (www.fishbase.com).Information about biogeographic guild after Daan (2006) and Fishbase, mode of living and trophic status accord Fishbase. Trophic level 1-2: Plants and herbivores; 2-3: omnivores, herbivores and detritivores; 3-4: mid level carnivores; 4-5: high level carnivores;> 5: top predators. For more information see text.

Latin name	W=a ¹ L ^b		W=a ¹ L ^b		Ref	Biogeographic guild	Mode of living	Trophic level	s.e.
	a	b	a	b					
<i>Petromyzon marinus</i>			0.0008	3.1956	2	NS	dem	4.37	0.85
<i>Lampetra fluviatilis</i>			0.0019	3.0000	2	S	dem	4.37	0.76
<i>Spilargis acanthias</i>			0.0058	2.8900	3	NS	benthopel	4.30	0.67
<i>Scyliorhinus canicula</i>			0.0031	3.0290	2	S	dem	3.69	0.55
<i>Dasyatis pastinaca</i>			0.0154	3.2126	3	S	dem	4.05	0.63
<i>Clupea harengus</i>	0.1800	3.1100			1	N	pel	3.09	0.17
<i>Sprattus sprattus</i>	0.1800	3.5000			1	S	pel	3.00	0.20
<i>Sardina pilchardus</i>	0.2200	3.0000			1	S	pel	2.80	0.23
<i>Engraulis encrasicolus</i>	0.1800	3.0000			1	S	pel	2.92	0.27
<i>Alosa fallax</i>	0.1900	3.0500			1	S	pel	3.62	0.62
<i>Salmo trutta</i>	0.2100	3.0500			1	N	pel	3.34	0.50
<i>Salmo gairdneri</i>			0.0118	3.0060	2	N	benthopel	4.40	0.39
<i>Argentina sphyraena</i>	0.1600	3.4600			1	N	bathy dem	3.62	0.52
<i>Argentina silus</i>	0.1700	3.2700			1	N	bathy dem	3.31	0.28
<i>Osmerus eperlanus</i>	0.1700	3.4000			1	N	pel	3.06	0.23
<i>Anguilla anguilla</i>	0.1100	3.2100			1	NS	dem	3.53	0.57
<i>Conger conger</i>			0.0005	3.2250	2	S	dem	3.68	0.67
<i>Belone belone</i>	0.0900	3.2800			1	N	pel	4.21	0.74
<i>Syngnatus rostellatus</i>	0.0700	3.9900			1	NS	dem	3.70	0.40
<i>Syngnatus acus</i>	0.0700	3.3300			1	S	dem	3.40	0.55
<i>Entelurus aequoreus</i>	0.0600	2.7300			1	N	dem	3.50	0.44
<i>Gadus morhua</i>	0.1900	3.2600			1	N	benthopel	4.42	0.76
<i>Melanogrammus aeglefinus</i>	0.1900	3.1900			1	N	dem	3.58	0.51
<i>Trisopterus luscus</i>	0.2100	3.2300			1	S	benthopel	3.73	0.62
<i>Trisopterus minutus</i>	0.2100	3.1000			1	N	benthopel	3.83	0.53
<i>Melanogobius merlangus</i>	0.1900	3.0900			1	S	benthopel	4.37	0.77
<i>Micromesistius poutassou</i>	0.1900	2.8400			1	NS	pel	4.00	0.68
<i>Trisopterus esmarkii</i>	0.1800	3.1500			1	N	benthopel	3.24	0.41
<i>Pollachius pollachius</i>	0.1800	3.3100			1	N	benthopel	4.15	0.72
<i>Pollachius virens</i>	0.1900	3.2700			1	N	dem	4.50	0.80
<i>Raniceps ranius</i>	0.2400	3.0000			1	N	dem	3.77	0.56
<i>Merluccius merluccius</i>	0.1700	3.1700			1	S	dem	4.28	0.73
<i>Rhinonemus cimbrius</i>	0.1600	3.1400			1	N	dem	3.53	0.22
<i>Ciliata mustela</i>	0.2000	3.1000			1	N	dem	3.93	0.67
<i>Zeus faber</i>	0.2600	3.0000			1	NS	benthopel	4.50	0.80
<i>Trachurus trachurus</i>	0.2100	2.9700			1	S	dem	3.60	0.58
<i>Dicentrarchus labrax</i>	0.2100	3.0000			1	S	dem	3.80	0.61
<i>Mullus surmuletus</i>	0.2100	3.3400			1	S	dem	3.40	0.51
<i>Spondylosoma cantharus</i>			0.0036	3.3133	3	S	benthopel	3.29	0.43
<i>Labrus bergylla</i>			0.0119	3.1151	3	N	benthopel	3.39	0.44
<i>Crenilabrus melops</i>			0.0065	3.1500	3	NS	benthopel	3.20	
<i>Hyporhamphus lanceolatus</i>	0.1400	2.9300			1	N	dem	4.15	0.70
<i>Ammodytes tobianus</i>	0.1300	3.4600			1	NS	dem	3.16	0.32
<i>Echichtys vipera</i>	0.2300	3.0000			1	S	dem	4.41	0.78
<i>Callionymus lyra</i>	0.1900	2.9600			1	S	dem	3.27	0.38
<i>Atherina presbyter</i>	0.1800	3.2700			1	S	pel	3.67	0.43
<i>Chelon labrosus</i>	0.2000	3.0400			1	S	dem	2.42	0.22
<i>Liza ramada</i>	0.2100	3.0000			1	S	pel	2.05	0.03
<i>Liza aurata</i>	0.2100	3.0000			1	S	pel	3.01	0.34
<i>Scomber scombrus</i>	0.2200	2.8500			1	N	pel	3.28	0.53
<i>Pholis gunnellus</i>	0.1400	3.5500			1	N	dem	3.52	0.45
<i>Zoarces viviparus</i>	0.1600	3.3400			1	N	dem	3.50	0.49
<i>Gobius niger</i>	0.2400	3.0000			1	S	dem	3.20	0.44
<i>Pomatoschistus minutus</i>	0.2100	2.8300			1	S	dem	3.20	0.44
<i>Pomatoschistus pictus</i>	0.2000	3.0000			1	S	dem	3.12	0.33
<i>Crystallgobius linearis</i>	0.1700	3.0000			1	NS	dem	3.40	0.45
<i>Aphia minuta</i>	0.1900	4.1700			1	S	dem	3.10	0.28
<i>Eurigila gurnardus</i>	0.2000	2.9700			1	S	dem	3.57	0.57
<i>Trigla lucerna</i>	0.2200	3.0000			1	S	dem	3.92	0.67
<i>Myoxocephalus scorpius</i>	0.2300	3.1900			1	N	dem	3.89	0.40
<i>Taurulus bubalis</i>	0.2300	3.3300			1	N	dem	3.60	0.52
<i>Agonus cataphractus</i>	0.2000	2.9000			1	N	dem	3.43	0.47
<i>Cyclopterus lumpus</i>	0.3400	3.1100			1	N	benthopel	3.89	0.09
<i>Liparis liparis</i>	0.2500	3.0900			1	N	dem	3.59	0.58
<i>Gasterosteus aculeatus</i>	0.2000	3.2100			1	NS	benthopel	3.51	0.49
<i>Pungitius pungitius</i>	0.2100	2.8600			1	N	benthopel	3.30	0.20
<i>Scophthalmus maximus</i>	0.2500	3.1800			1	N	dem	3.90	0.62
<i>Scophthalmus rhombus</i>	0.2400	3.0000			1	S	dem	3.79	0.56
<i>Arnoglossus laterna</i>	0.2000	3.1400			1	S	dem	3.59	0.54
<i>Lepidotrombus whiffiagonus</i>	0.2400	3.0000			1	N	bathy dem	4.21	0.73
<i>Phrynorhombus norvegicus</i>	0.2000	3.5000			1	N	benthopel	3.98	0.60
<i>Hippoglossus hippoglossus</i>	0.1700	3.3100			1	N	dem	4.60	0.78
<i>Limanda limanda</i>	0.2200	3.0000			1	N	dem	3.29	0.38
<i>Pleuronectes platessa</i>	0.2200	3.0200			1	N	dem	3.26	0.39
<i>Platichthys flesus</i>	0.2200	3.0000			1	N	dem	3.50	0.50
<i>Microstomus kitt</i>	0.2000	3.2700			1	N	dem	3.25	0.44
<i>Solea solea</i>	0.2000	3.0500			1	S	dem	3.25	0.43
<i>Buglossidium luteum</i>	0.2100	3.1700			1	S	dem	3.39	0.43
<i>Lophius piscatorius</i>	0.2900	2.7900			1	N	bathy dem	4.45	0.76
<i>Pomatoschistus microps</i>	0.2200	3.2700			1	NS	dem	3.30	0.43
<i>Pomatoschistus lozanoi</i>	0.1900	2.7800			1	NS	dem	3.10	0.34
<i>Callionymus reticulatus</i>	0.1900	3.0000			1	NS	dem	3.30	0.39