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Long-term patterns in fish phenology in the western Dutch Wadden Sea in relation to climate change

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ABSTRACT

Long-term patterns in fish phenology in the western Dutch Wadden Sea were studied using a 53 year (1960-2013) high resolution time series of daily kom-fyke catches in spring and autumn. Trends in first appearance, last occurrence and peak abundance were analysed for the most common species in relation to mode of life (pelagic, demersal, benthopelagic) and biogeographic guild (northern or southern distribution). Climate change in the western Wadden Sea involved an increase in water temperature from 1980 onwards. The main pattern in first day of occurrence, peak occurrence and last day of occurrence was similar: a positive trend over time and a correlation with spring and summer water temperature. This is counterintuitive; with increasing temperature, an advanced immigration of fish species would be expected. An explanation might be that water temperatures have increased offshore as well and hence fish remain longer there, delaying their immigration to the Wadden Sea. The main trend towards later date of peak occurrence and last day of occurrence was in line with our expectations: a forward shift in immigration into the Wadden Sea implies also that peak abundance is delayed. As a consequence of the increased water temperature, autumn water temperature remains favourable longer than before. For most of the species present, the Wadden Sea is not near the edge of their distributional range. The most striking phenological shifts occurred in those individual species for which the Wadden Sea is near the southern or northern edge of their distribution.

Keywords: long term changes; phenology; fish fauna; Wadden Sea; temperature

1. Introduction

The temperate Wadden Sea area is characterized by strong seasonal patterns and annual variability in environmental conditions, especially water temperature and salinity (van Aken, 2008a,b). Cooling and warming is more rapid in the shallow Wadden Sea than the deeper adjacent North Sea and, therefore, a seasonal shift in the temperature gradient between the North Sea and the Wadden Sea occurs. The Wadden Sea has relatively low water temperatures from October to April, and high values from April to October compared with the North Sea (van Aken, 2008b). These gradients are thought to trigger and affect seasonal fish immigration in spring and emigration in autumn (see for instance Zijlstra, 1972). Offshore, in the North Sea, water temperatures have increased due to climate change and distributions of North Sea fishes have responded and shifted (Perry et al., 2005). Also, a clear warming of about 1.5 °C has occurred in the western Wadden Sea in the last 25 years (van Aken, 2008b). Environmental conditions such as water temperature and salinity directly influences fish performance by affecting metabolism e.g. Fry, 1947, 1971; Neil et al., 1994). Fish species are characterized by species-specific temperature and salinity preferences and tolerances (Freitas et al., 2010), it is possible that a combination of these factors has affected occurrence and seasonal migration patterns as has been found for other trophic levels (Edwards & Richardson, 2004) and in other areas and studies (a.o. Murawski, 1993; Rose, 2005; Pörtner & Knust, 2007; Dulvy et al., 2008; Rijnsdorp et al., 2009; Last et al., 2011). This may lead to a mismatch between presence and abundance of species and timing of long term monitoring programmes which occur in fixed time frames in the spring and autumn season.

For the phenology in the fish community in the Dutch Wadden Sea, quantitative information is available from a fyke series starting in 1960. The NIOZ fyke net series consists of daily fyke net catches of pelagic and demersal species in the subtidal western Dutch Wadden Sea in spring and autumn (van der Veer et al., 2015).

The suitability of a sampling device for the assessment of long-term trends in fish and epibenthic invertebrates relies on the assumption of a constant sampling fraction and an unchanged methodology over time. In addition, seasonal patterns of migrations and hence timing of sampling should remain optimal with respect of the seasonal abundance and distribution of the fish fauna. The former requirements appear to be fulfilled (see van der Meer et al., 1995; Tulp et al., 2008; van der Veer et al., 2015). Whether the latter is also valid is the subject of this study.

Phenology of Scyphomedusae in the western Dutch Wadden Sea has previously been studied based on catches in the NIOZ kom-fyke (van Walraven et al., 2015). It showed that the kom-fyke could be used to study phenology, if the periods of arrival or departure of species have been sampled throughout the whole time series. Several species of scyphomedusae showed earlier appearances, related to increased seawater temperature in winter. The aim of this study is to evaluate if fish phenology has shown a similar shift. The hypothesis is that the increase in water temperature by a few degrees Celsius over the past decades (van Aken, 2008b) has especially affected the presence of southern species by advancing the first day of appearance and delaying the last day of occurrence. For most northern species, the temperate zone is within the distributional range (van der Veer et al., 2015) and hence we do not expect a strong response of these species to the observed temperature change. The findings are discussed in the light of the ongoing long term fish monitoring programmes in the Wadden Sea and the extent in which observed trends in fish abundance might be biased by shifts in fish phenology.

2. Material and methods

2.1. Sampling

Since 1960, a kom-fyke trap has been operated at the entrance of the Marsdiep basin in the western Dutch Wadden Sea (Fig. 1). The kom-fyke consists of a 200 m long and 2 m high leader which starts above the high-water mark and ends in two chambers in the subtidal region with a mesh-size of 10 x 10 mm. For more details on the kom-fyke specifications see van der Veer et al. (1992). The fyke is normally deployed in March-April and removed again in October to prevent damage from possible ice floes. From 1971 onwards no fishing took place during part of the summer because of fouling of the net and clogging by macroalgae and scyphomedusae.

Normally the kom-fyke was emptied every morning, except when bad weather prevented this. Pre-1973 when catches were small, the nets were sometimes emptied every other morning. In total, 6481 daily catches were analysed for the period 1960 − 2013, whereby the following criteria were applied:

- The fishing duration was less than 48 h (this led to the exclusion of 329 records);
- The fishing duration was longer than 12 h (exclusion of 1 record);
- There was no damage of the gear upon retrieval (loose mesh panels or tears) and/or it was not clogged with debris (exclusion of 53 records). For a more detailed description of

the method and fishing gear used, see van der Veer et al. (1992) and van der Meer et al. (1995).

All catches were sorted immediately and identified to species level. For each species, fish 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 (see van der Veer et al., 2015). All information was stored in a database.

Species were characterized based on mode of life (pelagic, demersal, benthopelagic) after the classification in Fishbase (www.fishbase.org) and their biogeographic guild (northern and southern species) after Daan (2006) in line with a previous analysis (van der Veer et al. 2015). The environmental parameters considered were also in line with the previous analysis (van der Veer et al. 2015) and included water temperature and salinity obtained from long-term monitoring programme at the NIOZ sampling jetty, located < 1 km east of the kom-fyke (van Aken 2008a,b).

2.2. Trends in phenology

The trend analysis was based on species caught in at least 20 of the total of 53 years (core species). For each species, the first day of appearance and the last day of occurrence in each year was determined. If this corresponded with the first and/or the last day of fishing, that year was excluded from further analysis. For each species in each year, the day on which the highest number of individuals was caught was assumed to be the day of peak occurrence. In total 46 fish species were included in the analysis (Table 2).

To investigate whether observed phenological shifts were shared among species, common trends in the first day of appearance, last day of occurrence and day of peak occurrence were analysed for species present for >20 years by min/max auto-correlation factor analysis (MAFA) (Solow, 1994). 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. The first MAFA axis 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. Canonical correlations (cross-correlations between MAFA axes and environmental variables) allow identification of significant correlations. The canonical correlations of the individual species and the MAFA axes illustrate the relationships between individual species and the first two axes. MAFA was previously applied for trends in fish biomass (see van der Veer et al., 2015). MAFA was run with the software package Brodgar (http://www.brodgar.com).

Because of the criterion of at least 20 observations, first day of appearance, last day of occurrence and peak occurrence could be analysed for respectively 39, 39 and 44 species (Appendix 1; Table 2).

Trends in first day of occurrence were analysed for 13 pelagic, 7 bentho-pelagic and 19 demersal species. Trends in date of peak occurrence were analysed for 13 pelagic, 7 bentho-pelagic, 24 demersal. Trends in last day of occurrence could be analysed for 13 pelagic, 6 bentho-pelagic and 20 demersal species (Table 2).

3. Results

3.1. Environmental conditions

The environmental variables showed different temporal patterns (Fig. 2). Both sea water temperature and salinity varied considerably over the years. Winter, spring and summer temperature showed an increase in time, but salinity did not show a clear trend (Table 1). Except for a significant positive correlation between winter and spring temperature no other correlations were found between seasonal temperature and salinity observations (Table 1).

3.2. Trends in fish phenology

For date of first occurrence the scores of the first MAFA axis showed fluctuating values but an overall increase over time, especially during the last decades (Fig. 3). The second axis showed stronger fluctuations over time without a clear trend until 2005 after which a decrease set in. For date of peak occurrence, the first MAFA axis showed a continuous increase with a maximum around 2005 followed by a slight decrease (Figure 3). The second axis also reflected an increase, however with a maximum around 1980 followed by a decrease until the mid-1990s and a constant trend until 2013. For date of last occurrence, the MAFA scores of the first axis showed no trend until the 1990s when it increased to a maximum around the year 2000, followed by a steady decline until 2013 (Fig. 3). The scores of the second axis reflected a drop until the 1970s, followed by an increase but with some fluctuations until 2013.

A comparison of the average days of first- peak- and last occurrence per species for the first half (1960 – 1986) and second half (1987 – 2013) showed that timing of first- peak- and last occurrence differed between species (Fig. 4). Some species were relatively abundant and often caught at both the first day of fishing and the last day of fishing in both periods (pelagic: *Clupea harengus;* demersal: *Ciliata mustela, Eutrigla gurnardus, Myoxocephalus scorpius, Platichthys flesus, Pleuronectes platessa, Taurulus bubalis, Zoarces viviparus*). For the remaining species, shifts in phenology were observed when comparing the average days of first- peak- and last occurrence in the first 26 years of the time series with those in the last 27 years (Fig. 4). A first comparison of these phenological shifts between northern, temperate and southern species did not reveal clear differences. 10 out of 20 northern species were arriving more than 10 days later in the last 27 years, and 13 out of 20 northern species were leaving more than 10 days earlier. For the southern species and temperate species assemblages, consisting of 18 and 3 species respectively, shifts in either direction were observed in day of first- peak- and last occurrence with no clear common pattern (Fig. 5).

3.3. Correlation of MAFA with environmental factors

The canonical correlations illustrated the relationships between the environmental conditions and the first two MAFA axes. For all three response variables, there was a positive correlation between year and the first MAFA axis, indicating an increasing trend over time (Table 3). Apart from a positive correlation between spring, summer and autumn temperature and year, no other correlations were found.

3.4. Trends in individual species

At the species level, shifts were very clear in eelpout *Zoarces viviparus* and seabass *Dicentrarchus labrax*, which are species for which respectively the southern or northern edge of their distribution is at the same latitude as the Wadden Sea. Eelpout and seabass showed respectively the strongest decrease and increase in catch numbers with temperature increase (Fig. 6).

For trends in first occurrence (39 species investigated), four out of 15 northern (N: *Salmo trutta, Trisopterus minutus, Pollachius virens, Cyclopterus lumpus*) and one out of three temperate (NS: *Arnoglossus laterna*) species showed a significant positive correlation with the first MAFA axis (Table 4). Furthermore, two out of 19 southern species (S) (*Scophthalmus rhombus* and *Chelon labrosus*) were negatively correlated with the second MAFA axis.

Ten out of 44 species investigated showed trends in peak occurrence that were significantly correlated with one of the two MAFA axes (Table 4). Of the 20 northern species analysed 5 were positively correlated and one was negatively correlated with the first MAFA axis. Of the 19 southern species two correlated positively to the first axis, one negatively. One out of three temperate species and one northern species correlated negatively with the second axis.

Trends in last occurrence (39 species investigated) in two out of 19 southern (*Chelidonichthys lucerna and S. rhombus*), one out of three temperate (*Anguilla anguilla*) and one out of 16 northern (*Scomber scombrus*) species were significant and in one southern (*Atherina presbyter*) species negatively correlated with the fist MAFA axis. Two northern (*Belone belone, S. maximus*) species were correlated with MAFA axis 2: One species showed a significant correlation with both trends (*S. scombrus).* The number of observations per group was too low to distinguish between pelagic, benthopelagic and demersal species. Detailed plots of seasonal abundance and phenology of all species studied are included in Appendix 1.

5. Discussion

5.1. Shifts in phenology

In this study, we searched for common patterns in the trends in first appearance, last occurrence and peak occurrence by means of min/max auto-correlation factor analysis (MAFA) (Solow, 1994) and related them to environmental conditions and to the mode of living and/or biogeographic guild of individual species. The MAFA anaysis resulted in a strong similar signal for both first day of occurrence, peak occurrence and last day of occurrence and a canonical correlation with temperature conditions. The trends in environmental conditions clearly showed an increase in seasonal mean water temperature in the western Wadden Sea over the last decades in the order of 2 degrees C, in the winter, spring and summer. Although the trends in temperature for winter, spring and summer were slightly different (as reflected in a low correlation between them), the overall trend was similar, showing an increase over time, as illustrated by the strong positive correlation with time (year). The main pattern in fish occurrence (first MAFA axis) showed a positive trend over time in first day of occurrence, peak occurrence and last day of occurrence as reflected by the strong positive correlation with time (year). These trends were significantly correlated with spring and summer temperature. The second MAFA trend was not significantly correlated with environmental conditions, so it is unclear what it could represent.

The main trend in first day of occurrence is counterintuitive to expectations: with increasing temperature, an earlier immigration of fish species would be expected. However, also offshore in the North Sea, water temperatures have increased and distributions of North Sea fish species have responded and shifted (Perry et al., 2005). An explanation for the delayed arrival of many fish species might be that due to the increased water temperatures in the coastal zone, fish delay their immigration to the Wadden Sea. Immigration might still be triggered by the moment the temperature becomes more favourable inside the Wadden Sea. The main trend in date of peak occurrence and last occurrence is in line with expectations: a delay in immigration implies also a delay in peak abundance and warmer water temperatures mean that conditions remain favourable for a longer period until later in autumn.

The observed shifts in fish phenology are based on an analysis of common trends in 39-44 fish species. However, only for a small number of species first date, peak date or last date of occurrence showed a significant correlation with the main trend, indicating that other (a)biotic factors and species interactions are acting which are not included in the present analysis. The hypothesis that the increase in water temperature by two degrees Celsius over the past decades (van Aken, 2008b) has especially affected the presence of southern species by advancing the first day of appearance and delaying the last day of occurrence is only confirmed for the last day of occurrence. For several abundant northern species, the temperate zone is within the distributional range (van der Veer et al., 2015). Their response to changing temperature could not be analysed because they were present almost year-round.

Except for the advanced arrival and disappearance of respectively half and more than half of the northern species, no common trends between northern, southern and temperate species were observed. To understand observed changes in phenology, species-specific knowledge is required on physiological requirements of fish visiting the Wadden Sea. Next to physiology also altered predator-prey relations may have affected the occurrence of fish inside the Wadden Sea.

5.2. Limitations of the present study

Although the expectations of a potential impact of climate change on fish phenology are based on physiological mechanisms and principles, predictions of the impact of climate change remain mainly restricted to qualitative hypotheses, supported by various observations of recent shifts in fish population that were attributed to global change, especially warming (Rijnsdorp et al., 2009). Each fish species has a species-specific and sometimes even stage specific temperature tolerance range (Willmer et al., 2000; van der Veer et al., 2009; Freitas et al., 2010). The present study lacks these underlying species-specific quantitative mechanisms.

The first qualitative physiological framework was established with Fry's physiological classification of the environment (Fry 1947, 1971) of controlling, masking, limiting, lethal and directive factors acting on metabolism and ultimately affecting fish performance (Neill et al., 1994). Recently, dynamic energy budgets have become available that can deal with fluctuating environmental conditions (Kooijman 1993, 2000, van der Veer et al., 2009). At this stage, the limiting factor complicating any analyses of climate change is the lack of basic physiological data collected during controlled, multifactorial experiments quantifying rates of growth and metabolism (i.e. at different temperatures and feeding rates; cf. Peck et al., 2003) for most species and stages.

In this study shifts in the phenology of species were related to differences in mode of living (pelagic versus benthopelagic and demersal species) and biogeographic guild (northern cold water adapted versus southern warm water adapted species) and investigated for common trends. The current analyses is limited to a subset of all species frequenting the Wadden Sea. Transient species or species that were already present at at the start -or still at the end- of the fishing period were excluded.

5.3. Long term monitoring and climate change

Long-term monitoring of the fish community in the western Wadden Sea from 1960 to present by means of the NIOZ fyke net series indicated large biomass differences over time as well as shifts in biogeographic guild: an increase in terms of biomass of the relative contribution of southern species from the 1980s onwards parallel with increased water temperature and in line with the expectations (van der Veer et al., 2015). The present study indicates an impact of climate change (increased water temperature) on fish phenology. Under the present conditions, the operation periods of the NIOZ fyke in spring (April – June) and in autumn (September - October) are too short to incorporate many abundant core species in the present analysis of shifts in phenology. A more detailed analysis of changes in fish community of the western Wadden Sea in the future requires an extension of the NIOZ fyke sampling period not only in spring and autumn but also covering the complete summer period.

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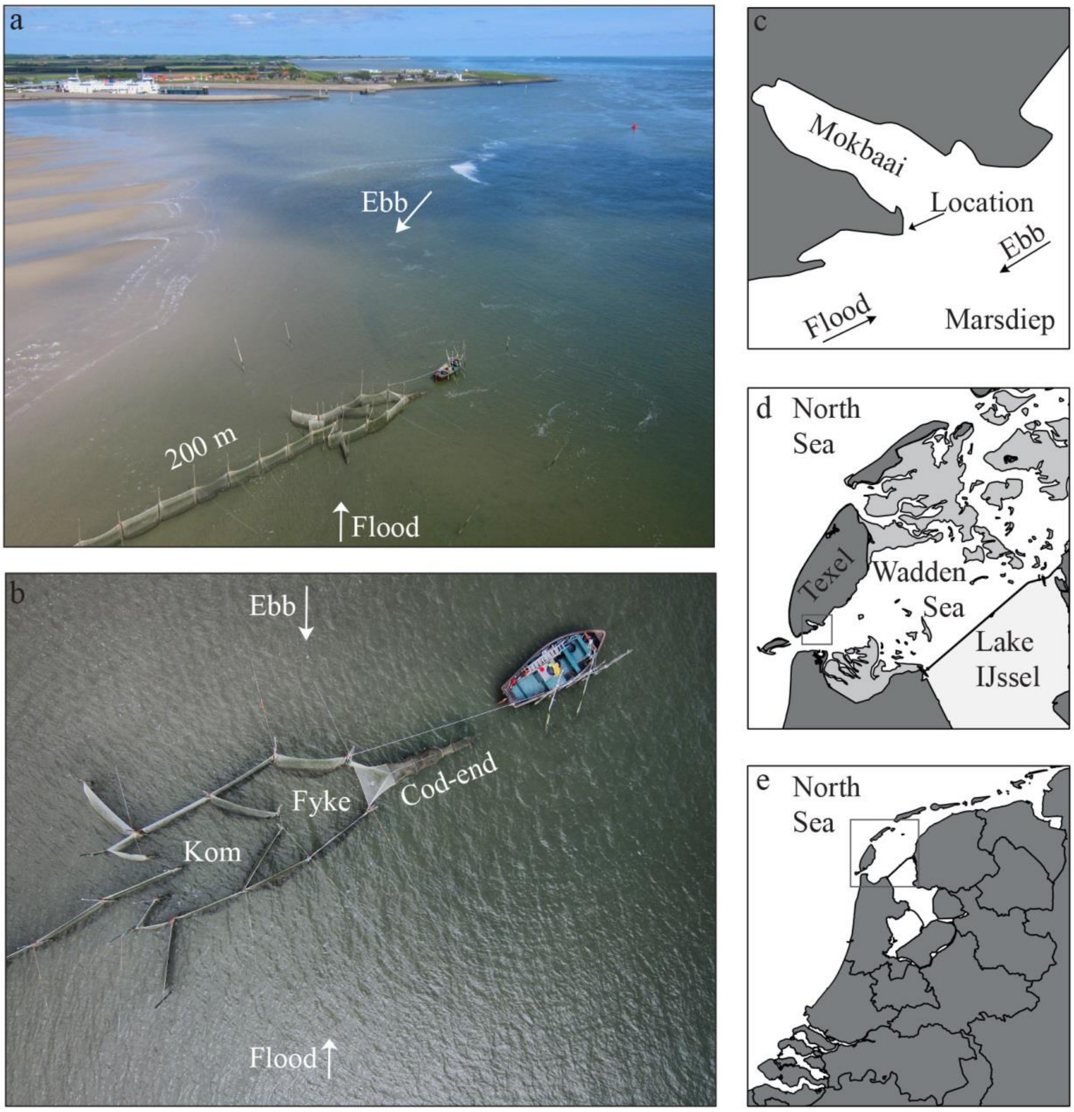


Figure 1 The NIOZ kom-fyke in the western Dutch Wadden Sea. Dark grey areas are land, light grey areas are intertidal flats. (a): aerial photograph showing the location of the kom-fyke; (b): aerial photograph showing the design of the kom-fyke. (c): location of the kom-fyke (arrow); (d): location of the study area in the western Wadden Sea; (e): location of the study area in the Netherlands. Land is dark grey, intertidal areas are light grey. The kom-fyke system is situated at the end of a 200 m long leader. Directions of tides are indicated.

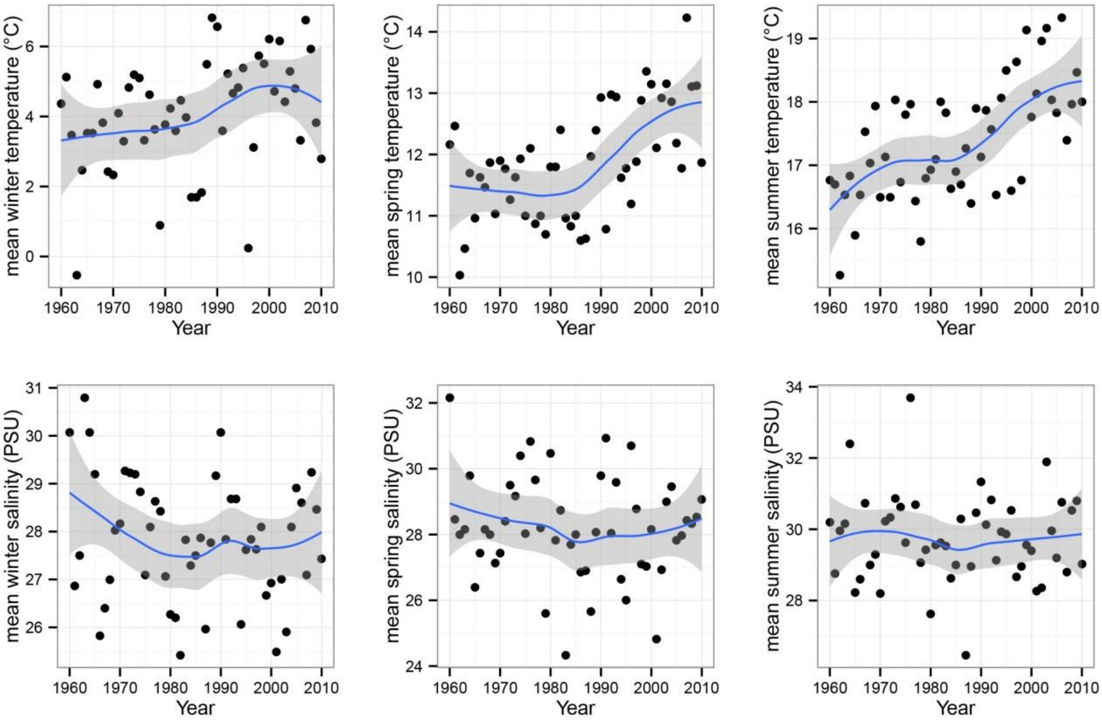


Figure 2 Trends in environmental conditions in the western Dutch Wadden Sea between 1960 and 2011. Seasonal means are for the following months: winter: January - March, spring: April - June, summer: July - September. For references see text. The solid line through the data is a LOESS smoother (LOESS span of 0.5). The shaded area is the 95% confidence interval of the smoother.

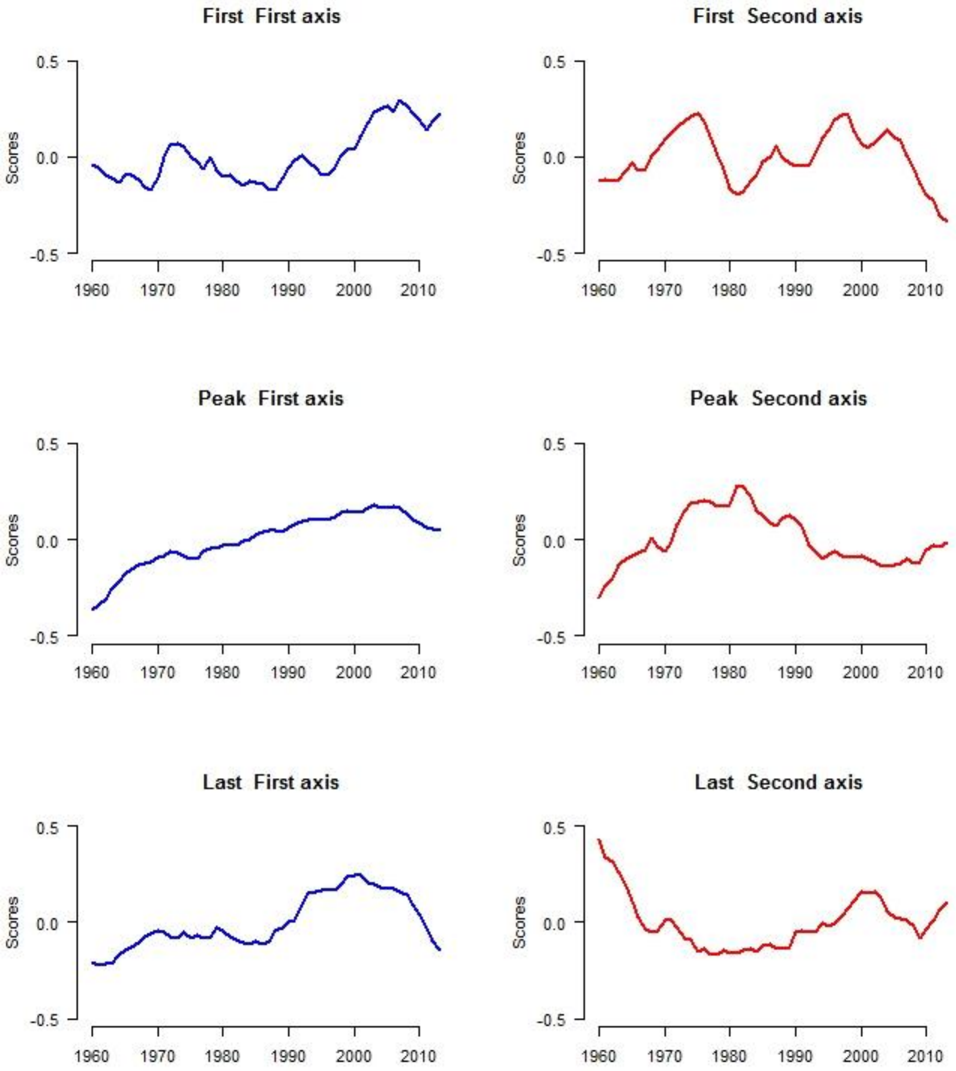


Figure 3 First (left; blue) and second (right; red) axis of min/max auto-correlation factor analysis (MAFA) of trends in day of first appearance, peak abundance and day of last occurrence of the fish fauna in the western Wadden Sea, based on species from Table 2. For more information see text.

Figure 4. Average first, peak and last occurrence of species in the kom-fyke for the first and second half of the time series (1960 – 1986 and 1987 – 2013). Changes are illustrated by colours; red = advanced, blue = delayed. N = northern, S = southern and NS = temperate. Dashed vertical lines show the average day of the start and end of the sampling period.

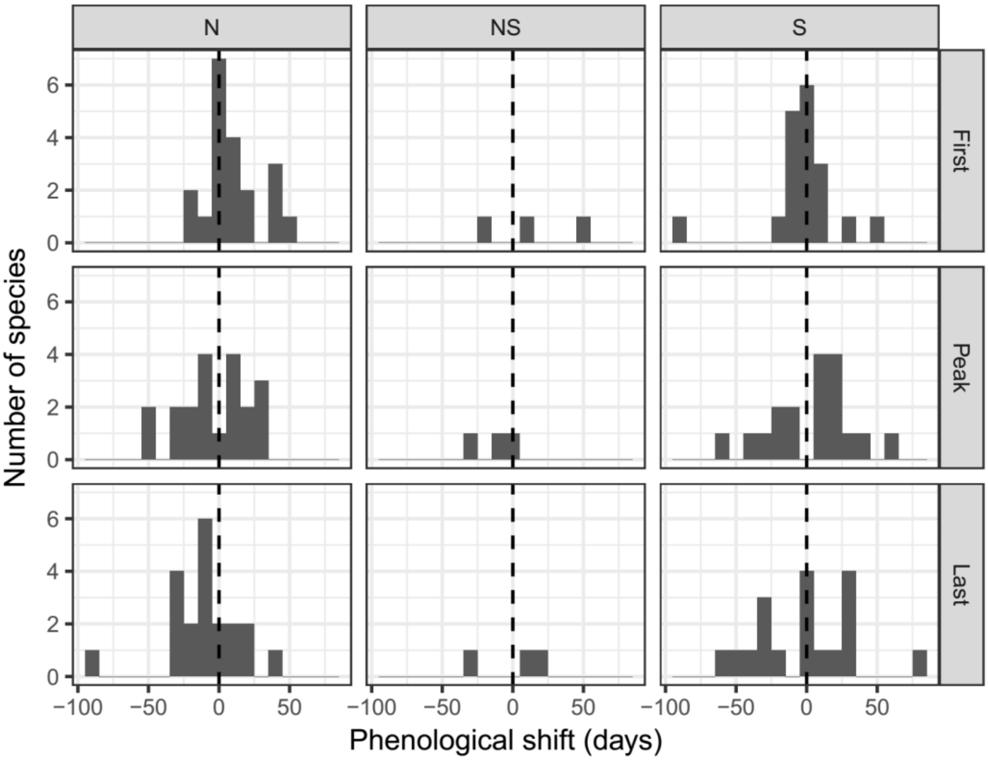


Figure 5. Shift in timing of moments of first, peak and last occurrence of species in the kom-fyke visualised as difference in Julian day of the three different moments between the first and second half of the time series (1960 – 1986 and 1987 – 2013). N = northern, S = southern and NS = temperate species. Negative values mean that the moment occurs earlier in the second half, positive values mean that the moment occurs later.

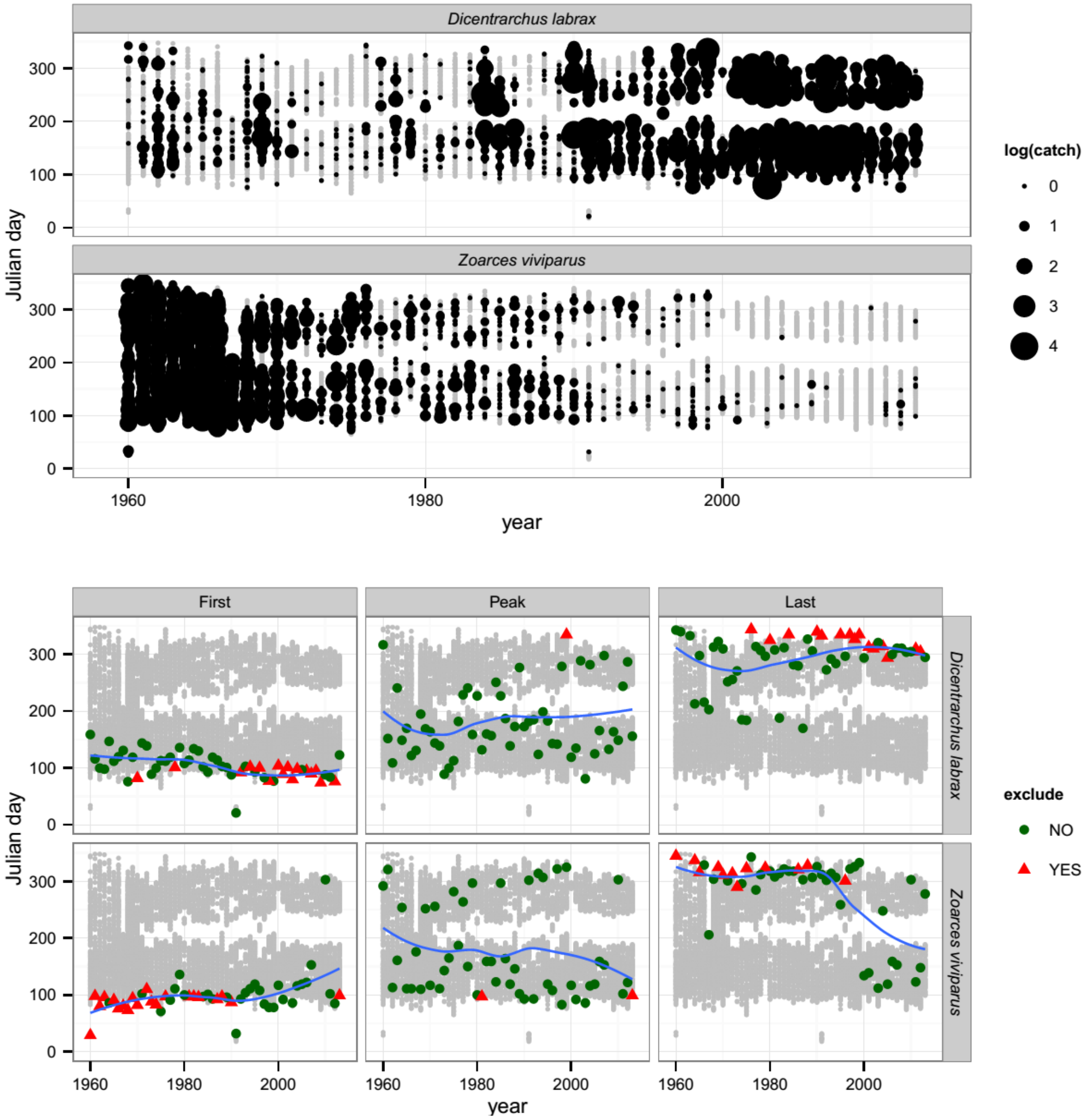


Figure 6 Daily catch (n) of the eelpout *Zoarces viviparus* and the seabass *Dicentrarchus* labrax in the NIOZ fyke (bold) (top panel), together with trends (green dots) in day of first, last and peak appearance (bottom panel). Fishing period is indicated in grey. Red triangles refer to first, peak or last day of occurrence corresponding with first or last day of fishing and these data were excluded from further analysis. The solid line through the data is a LOESS smoother (LOESS span of 0.5)

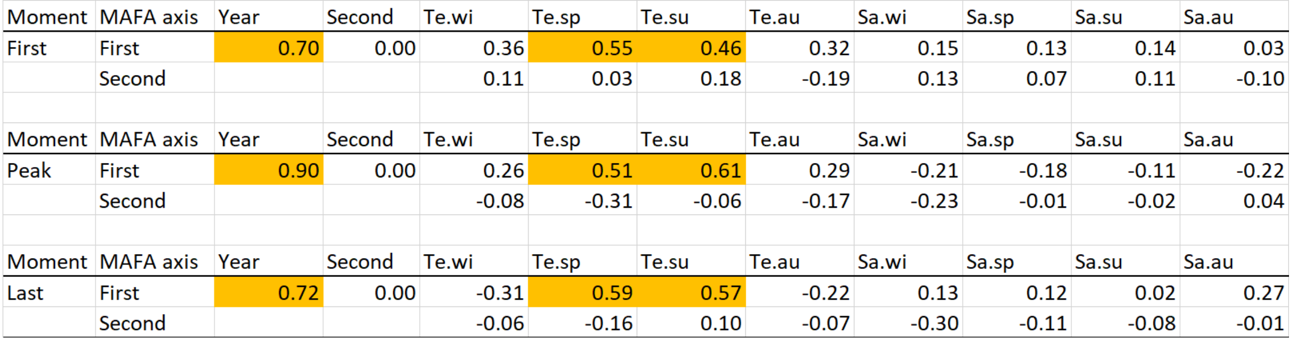
Table 1 Pearson correlation coefficients between the various environmental factors and seasons in the western Dutch Wadden Sea. Significant relationships are indicated in orange ($p < 0.01$). Te: water temperature; Sa: salinity; wi: winter; sp: spring; su: summer; au: autumn. For more information see text

	Te.wi	Te.sp	Te.su	Te.au	Sa.wi	Sa.sp	Sa.su	Sa.au
Year	0.27	0.56	0.60	0.39	-0.12	-0.14	-0.04	-0.22
Te.wi		0.62	0.19	0.07	0.10	-0.06	0.11	-0.17
Te.sp			0.31	0.13	0.05	0.08	0.06	-0.22
Te.su				0.37	-0.15	-0.08	0.33	-0.03
Te.au					-0.07	-0.23	-0.01	0.10
Sa.wi						0.24	0.34	0.24
Sa.sp							0.33	0.19
Sa.su								0.23

Table 2 Fish species included in the MAFA analysis of first appearance, peak abundance and last occurrence, together with type of species and biogeographic guild. Numbers refer to number of years included, empty cell means not included. For more info see text.

Species	Type	Biogeographic guild	First appearance	Last occurrence	Peak abundance
Agonus cataphractus	dem	N	28	40	37
Belone belone	pel	N	53	51	54
Ciliata mustela	dem	N			45
Clupea harengus	pel	N			52
Cyclopterus lumpus	benthopel	N	45	44	51
Gadus morhua	benthopel	N	27	34	49
Hyperoplus lanceolatu	dem	N	47	45	47
Limanda limanda	dem	N	28	23	46
Liparis liparis liparis	dem	N	27	20	26
Myoxocephalus scorpi	dem	N			48
Pholis gunnellus	dem	N	33	35	34
Platichthys flesus	dem	N			52
Pleuronectes platessa	dem	N			51
Pollachius pollachius	benthopel	N	49	32	53
Pollachius virens	dem	N	34	39	43
Salmo trutta trutta	pel	N	36	35	52
Scomber scombrus	pel	N	52	51	52
Scophthalmus maximu	dem	N	45	49	51
Taurulus bubalis	dem	N		21	
Trisopterus minutus	benthopel	N	38	31	38
Zoarces viviparus	dem	N	30	37	49
Ammodytes tobianus	dem	NS	35	39	38
Anguilla anguilla	dem	NS	39	30	54
Gasterosteus aculeatu	benthopel	NS	24	43	38
Alosa fallax	pel	S	27	23	54
Arnoglossus laterna	dem	S	20	21	20
Atherina presbyter	pel	S	47	51	52
Callionymus lyra	dem	S	33	34	33
Chelidonichthys lucern	dem	S	52	52	52
Chelon labrosus	dem	S	34	40	54
Dicentrarchus labrax	dem	S	38	38	53
Echiichthys vipera	dem	S	26	22	26
Engraulis encrasicolus	pel	S	41	41	41
Eutrigla gurnardus	dem	S			
Liza aurata	pel	S	30	27	31
Liza ramada	pel	S	23	22	24
Merlangius merlangus	benthopel	S	43		47
Pomatoschistus minut	dem	S	39	30	41
Sardina pilchardus	pel	S	48	47	48
Scophthalmus rhombu	dem	S	43	45	51
Solea solea	dem	S	44	41	52
Sprattus sprattus	pel	S	38	28	49
Syngnathus acus	dem	S	48	51	52
Trachurus trachurus	pel	S	53	50	54
Trisopterus luscus	benthopel	S	52	42	51
Osmerus eperlanus	pel		30	31	48
No of species included			39	39	44

Table 3 Pearson correlation coefficients between the first (First) and second (Second) MAFA axis of trends in first appearance (First), peak abundance (Peak) and last occurrence Last) of the fish fauna in the western Dutch Wadden Sea with various environmental factor and seasons in the western Dutch Wadden Sea. Te: water temperature; Sa: salinity; wi: winter; sp: spring; su: summer; au: autumn. Significant relationships are indicated in orange ($p < 0.01$). For more information see text.



Moment	MAFA axis	Year	Second	Te.wi	Te.sp	Te.su	Te.au	Sa.wi	Sa.sp	Sa.su	Sa.au
First	First	0.70	0.00	0.36	0.55	0.46	0.32	0.15	0.13	0.14	0.03
	Second			0.11	0.03	0.18	-0.19	0.13	0.07	0.11	-0.10
Moment	MAFA axis	Year	Second	Te.wi	Te.sp	Te.su	Te.au	Sa.wi	Sa.sp	Sa.su	Sa.au
Peak	First	0.90	0.00	0.26	0.51	0.61	0.29	-0.21	-0.18	-0.11	-0.22
	Second			-0.08	-0.31	-0.06	-0.17	-0.23	-0.01	-0.02	0.04
Moment	MAFA axis	Year	Second	Te.wi	Te.sp	Te.su	Te.au	Sa.wi	Sa.sp	Sa.su	Sa.au
Last	First	0.72	0.00	-0.31	0.59	0.57	-0.22	0.13	0.12	0.02	0.27
	Second			-0.06	-0.16	0.10	-0.07	-0.30	-0.11	-0.08	-0.01

Table 4 Overview of fish species in the western Dutch Wadden Sea with a significant Pearson correlation between trends in first appearance (First), peak abundance (Peak) and last occurrence Last) and the first (First) and second (Second) MAFA axis. Significant relationships are indicated in orange ($p < 0.01$). For more information see text.

	Species	**type**	**Biogeogr. fuild**	**First MAFA**	**Second MAFA**
First	*Salmo trutta trutta*	pel	N	0.34	-0.22
	Trisopterus minutus	benthopel	N	0.37	0.11
	Pollachius virens	dem	N	0.41	-0.06
	Chelon labrosus	dem	S	0.10	-0.37
	Cyclopterus lumpus	benthopel	N	0.40	0.17
	Scophthalmus rhombus	dem	S	-0.20	-0.35
	Arnoglossus laterna	dem	NS	0.52	-0.22
Peak	*Salmo trutta trutta*	pel	N	0.34	-0.22
	Trisopterus minutus	benthopel	N	0.37	0.11
	Merlangius merlangus	benthopel	S	0.30	-0.11
	Pollachius pollachius	benthopel	N	0.30	-0.20
	Pollachius virens	dem	N	0.41	-0.06
	Chelon labrosus	dem	S	0.10	-0.37
	Pomatoschistus minutus	dem	S	-0.31	-0.27
	Cyclopterus lumpus	benthopel	N	0.40	0.17
	Scophthalmus maximus	dem	N	-0.20	-0.35
	Scophthalmus rhombus	dem	S	0.52	-0.22
Last	*Anguilla anguilla*	dem	NS	0.38	0.04
	Belone belone	pel	N	0.21	0.38
	Syngnathus acus	dem	NS	0.33	0.30
	Atherina presbyter	pel	S	-0.42	0.00
	Scomber scombrus	pel	N	0.48	0.45
	Chelidonichthys lucerna	dem	S	0.32	0.13
	Scophthalmus maximus	dem	N	-0.24	0.54
	Scophthalmus rhombus	dem	S	0.34	-0.18