PROGRAMMA NAAR EEN RIJKE WADDENZEE

Wadden Sea Fish Haven

development agenda for fish in the Wadden Sea

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Pictures front page: Marianne Wildenberg and Herman Wanningen

2015 – Paddy Walker - PRW

1. Introduction

The shallow coastal waters of the Wadden Sea and its tributary estuaries and rivers provide indispensable ecological functions for fish, such as reproduction and feeding, but also serve as an acclimatisation area and transit route for long-distance diadromous fish. The Wadden Sea ecosystem is also connected with and influenced by the North Sea. Marine juveniles and marine seasonal species form an important constituent of the Wadden Sea fish fauna, which has a total of approximately 150 species of fish, including 13 freshwater species.

The Wadden Sea is protected in international policy agreements such as the Habitats Directive Natura 2000, the Water Framework Directive and the Marine Strategy Framework Directive. However, there are few direct management measures for fish species other than the diadromous fish such as Twaite shad, river lamprey and sea lamprey, also sturgeon, houting and salmon. In order to ensure the development of a healthy fish community, the three Wadden Sea countries - Denmark, Germany and the Netherlands – have developed a series of targets for fish which will be implemented through the Wadden Sea Plan. The targets have yet to be implemented.

There are signs that the fish community in the Wadden Sea has changed radically in the past decennia. Young fish, but also large predatory fish, seem to have declined in numbers, the nursery area function appears to be changed due to the decrease of the relevant species and a decline in the average fish length (Tulp *et al*., 2010). However, despite the annual surveys, we do not have a complete overview of the fish community. The abundance and distribution of pelagic fish and the use of salt marshes by fish are just two gaps in our knowledge.

The lack of coherency in policy is also a bottleneck to lasting improvement in fish communities and implementation of management and measurable targets. There is a real need to coordinate and harmonise the policy objectives as apply to fish in the Wadden Sea and North Sea coastal area, both nationally and in a trilateral perspective.

A new strategy is needed in order to implement policy, develop a research agenda en to strengthen and harmonise current monitoring programmes, both in the Netherlands as well as in the Trilateral Wadden Sea and to close the policy cycle.

This strategy should address the following:

1. Provide an overview of current policy objectives
2. Collate knowledge on the abundance of species
3. Overview of driving forces
4. Develop a programme of measures
5. Develop a science agenda
6. Investigate how fishermen’s knowledge can be used in the management and monitoring of fish and fisheries

The Dutch nature conservation programme Towards a Rich Wadden Sea (PRW) commissioned IMARES and NOIZ to analyse the survey data on fish populations in the Wadden Sea. Barbara Rodenburg from the fishermen's Society for Static Gear made an analysis of the way in which fishermen's knowledge could be used in management and monitoring.

2. Policy Background

2.1 Overview of policy objectives (N2000/WFD/MSFD/Trilateral) in the Dutch Wadden Sea

Fish are mentioned in the following policy frameworks for the Dutch Wadden Sea. See Annex 1 for an overview of the Netherlands, Germany (Schleswig-Holstein) and Denmark.

N2000 (Habitat type 1110A)

All information is from: “profielendocument H1110” (http://edepot.wur.nl/8100) in Dutch.

Typical species

According to the Habitat Directive a number of fish species are selected which are seen to be ‘typical species’ and which together form a good quality indicator for the completeness of the biological community of the habitat type. Species for H1110 are selected based on the following criteria:

- the species occur in the current monitoring programmes;
- the species are caught regularly so that trends in abundance and/or distribution can be measured;
- the species are not invasive (introduced by human activity after 1900);
- the species can be used as an indicator of en good abiotic status or good biological structure.

See Annex 3 for an overview of typical species according to the Habitat Directive (N2000) for Habitat type 1110A.

Further relevant passages in N2000 H1110A for fish are included in the description of characteristics for good structure and function:

- both small and large estuarine gradients from fresh to salt water have disappeared. There is a situation with an **unnatural division between fresh river water and salt sea water** at the sluice gates. Many species cannot survive the sudden change in salt concentration and the species diversity is lower than it should be as a result. Typical estuarine species which are adapted to a more gradual slat gradient are absent.
- The **fish community** should be so diverse that it consist of species from different feeding groups, life-history strategies and seasons which use the Wadden Sea for all or part of their life cycle.
- The coastal area is a highly productive system and is characterised by a fast turn-over of nutrients. This high productivity forms the basis for the **nursery area function** which the Wadden Sea provides for fish, as well as (migratory) birds and sea mammals.

Assessment:

H1110

- Decline in young fish in the period 1994-2007 (H1110A);
- The total biomass and productivity of fish has declined considerably – possibly due to the decline in nutrients or climate change (sea water temperature) (H1110A&B);
- The number of 'typical species' has not declined, except for eelpout (H1110A)

Overall assessment of H1110A in the Wadden Sea is **IMPROVE**

Water Framework Directive (WFD)

The Netherlands has designated the Wadden Sea as 'coastal water' under the WFD. Fish are not included in this area and there are no specific objectives for fish. The WFD does have objectives for salt marshes, eelgrass and mussel banks, which will be relevant for fish from the point of view of spawning, nursery and feeding areas and important for protection against predation.

A fish-index has been developed for transitional waters (estuaria discharging into the Wadden Sea) from NL and Germany. These indices are coordinated through an international intercalibration exercise. The Dutch fish-index for transitional waters has a metric for species composition. All species from the ecologically relevant guilds (CA, MJ, ER, MS) are analysed and compared to a reference value. There is also a metric for the abundance of selected species: sand eel, Twaite shad, flounder, herring, slakdolf, whiting (still to be implemented), pos (freshwater species). Moreover, for sand eel and Twaite shad there is an objective that all length classes are present : 0+, subadult en adult). Monitoring for the WFD takes place with and anchornet.

Marine Strategy Framework Directive (MSFD)

Although the MSFD only applies to the North Sea, the coordinating ministries (I&M and EZ) have agreed that relevant issues not tackled in the WFD could be addressed in the MSFD. This means that objectives and targets could be formulated for fish in coastal waters.

Trilateral

In 2010 the Netherlands, Germany and Denmark formulated a number of objectives for fish in the Wadden Sea area. The Wadden Sea Plan Fish Targets (Common Wadden Sea Secretariat, 2010):

- Viable stocks of populations and a natural reproduction of typical Wadden Sea fish species.
- Occurrence and abundance of fish species according to the natural dynamics in (a)biotic conditions.
- Favourable living conditions for endangered fish species.
- Maintenance of the diversity of natural habitats to provide substratum for spawning and nursery functions for juvenile fish.
- Maintaining and restoring the possibilities for the passage of migrating fish between the Wadden Sea and inland waters

During the most recent Trilateral Ministers Conference 4th -5th February 2014 the commitment for the implementation of these targets was described as follows: " **Acknowledge** the importance of fish for the Wadden Sea ecosystem and therefore **instruct** the WSB (Wadden Sea Board) to work on the further implementation of the trilateral fish targets of the Wadden Sea Plan." This gives all parties the necessary background to develop and implement the fish targets.

In the last Quality Status Report (Marencic *et al*., 2009; Jager *et al*., 2009) all relevant knowledge on the fish community in the Wadden Sea was brought together. The main conclusions are given in Annex 2. In Annex 3 there is an overview of the species covered in the QSR and N2000.

2.2 Nature Restoration Programme Programma Rijke Waddenzee (PRW)

In the Dutch Wadden Sea there is an ongoing restoration programme - Programma Rijke Waddenzee (PRW), which was started in 2009. The overall objective is to allow the development of a biologically rich and diverse Wadden Sea which is resilient enough to support sustainable use such as fisheries. The programme is run as a network organisation, enabling dialogue between parties and identifying issues to be tackled. There are four major themes and for three of those objectives with relevance for fish have been formulated. See below.

Theme	Objective
Food web and biodiversity	The food web is in balance, with healthy populations of fish, migratory fish and large predatory fish. Fish profit from the productive Wadden Sea for both feeding and nursery areas. Young fish find food and refuge in extensive mussel banks, and eel grass beds.
Wadden coastal areas	The recovery of stocks of migratory fish is aided by the development of estuarine areas, both small and large.
International	A Wadden Sea ecosystem that is not healthy is a threat to birds of the East-Atlantic flyway and to populations of fish and marine mammals. The life-cycle of fish and their habitat use should be more widely studied.

Specifically this means:

- Support the development of a fish community with large individuals and predatory fish;
- Enhance the nursery area function for young fish;
- Restoration of populations of migratory fish.

The objectives are highly abstract and in order to gain some understanding of the fish populations in the Wadden Sea, PRW granted a short project to the Centre for Marine Policy in 2011 to give an overview of the available knowledge to answer the following:

1. What is the current status of the fish community in the Wadden Sea?
2. What are the drivers determining this status?
3. Is it possible to formulate management measures?

The results were presented in a (Dutch) report (Kraan *et al*., 2012) and are summarised below:

Status
- There is information on commercial demersal fish species such as plaice and sole from fisheries monitoring programmes
- Little is known over pelagic and non-commercial species

Drivers
- Climate change
- Habitat availability
- Connectivity – estuaries, Wadden Sea :North Sea and across the Wadden Sea

Measures
- International cooperation is necessary

2.3 Summary

Despite the intentions described in policy directives little headway has been made in the improvement of fish stocks, or even to gain a better insight into the status of the fish community. This is primarily due to the highly abstract level of objectives in policy and the inability to translate these into management measures. The ‘ Plan Do Check Act’ (PDCA) policy cycle is in effect decoupled.

Currently there are only a few management measures being carried out specifically for fish (in the Dutch Wadden Sea). There are plans for habitat protection and closed areas for shrimp fisheries, as well as reducing by-catch. For diadromous fish there are several initiatives to improve migration such fish passages and river restoration. For example the Westerwoldse Aa. However, the lack of relevant research and abstract objectives make it difficult to formulate specific management measures. The above can be summarised in Table 1 below. With this new strategy it is hoped that it will be possible to effectively close the policy cycle.

Table 1. *An overview of the current state of the art as regards policy, research needed and current and proposed monitoring of fish in the Wadden Sea, as well as management measures. TMAP = Trilateral Monitoring & Assessment Programme of the Common Wadden Sea Secretariat; WG Fish is the TMAP Ad hoc working group on fish.*

	Netherlands	Trilateral Wadden Sea
Policy *	N2000 Water Framework directive (WFD) Marine Strategy Framework Directive (MSFD)	} **+ Fish targets**
Research	Habitat use Connectivity (estuaries, North Sea –Wadden Sea) Effects of climate change Species composition – including non-commercial and pelagic species	} **+ international cooperation**
Monitoring	To underpin policy Ecosystem approach Concerted monitoring programmes such as WaLTER (Wadden Sea Long Term Ecosystem Research)	} **+ TMAP +WG Fish**
Management	**Restoration of estuarine gradients** **Habitat protection** **By-catch mitigation, e.g. shrimp fisheries**	} **+ international cooperation**

* See also policy overview in Annex 1.

3. Insight in status and functioning of the Wadden Sea fish fauna - summary of current knowledge and research agenda[1]

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3. 1. Introduction

The Wadden Sea is an important nursery area for various commercial and non-commercial fish species (Zijlstra, 1972; Van Beek *et al*., 1989; Tulp *et al*., 2008). The area is a typical example of a coastal ecosystem under long-term anthropogenic pressure (Jackson *et al*. 2001). Currently, the area faces the combined effects of anthropogenic pressures such as fishing, climate change (e.g., warming, acidification, deoxygenation), habitat destruction and pollution (Bijma *et al*., 2013; European Marine Board, 2013).

The most recent quality status report (QSR) of the Wadden Sea (Wolff *et al*., 2010) concluded, mainly based on the Demersal Fish Survey data (DFS) (Jager *et al*., 2009), that on the one hand, the number of fish species and the species composition remained fairly stable over the last decades, on the other hand the abundance of several fish species seemed to have decreased to levels below the long-term average and that the factors (natural or anthropogenic) causing these changes are still largely unknown. Both a recent update of the DFS data (Tulp *et al*., 2015) and an analysis of the NIOZ fyke catches 1960 – 2011 (Van der Veer *et al*., 2015) confirmed this conclusion. In the QSR some changes over the last decades were highlighted, but as a main conclusion Wolff *et al*. (2010) stated that the estuarine resident species, i.e. those species spending the major part of their life cycle in the Wadden Sea, are still the least known and understood group, although of all fish species they may reflect the status and quality of the Wadden Sea ecosystem the best.

First, a brief summary will be presented about our insight in the present status of the Wadden Sea fish fauna, its changes over time and the potential underlying causes. Next, gaps in knowledge will be identified, and suggestions for a research agenda will be made. The objectives of the PRW are described in general terms in Table 1.

Table 1. *Target scenario of the programme towards a rich Wadden Sea (Anon, 2010)*

Theme	Objective
Food web and biodiversity	The food web is in balance, with healthy populations of fish, migratory fish and large predatory fish. Fish profit from the productive Wadden Sea for both feeding and nursery areas. Young fish find food and refuge in extensive mussel banks, and eel grass beds.
Wadden coastal areas	The recovery of stocks of migratory fish is aided by the development of estuarine areas, both small and large.
International	A Wadden Sea ecosystem that is not healthy is a threat to birds of the East-Atlantic flyway and to populations of fish and marine mammals. The life-cycle of fish and their habitat use should be more widely studied.

[1] IMARES and NIOZ are writing two scientific articles based on the analyses they carried out for this project. The draft manuscripts can be found in Annexes 4 and 5.

3.2. Present status

It should be kept in mind that until now, coastal systems such as the Wadden Sea are already degrading from the medieval time onwards, with acceleration during the last 150 – 300 years (Lotze *et al*. 2006). This means that any study on long term changes in the fish community only represents a short snapshot in time and does not include the past historical state. The only reference points are the situation at the start of the available time series. The loss of memory or lack of information of the historical situation means that our references also suffer from what has been called in fishery science the phenomena of "shifting baselines" (Pauly, 1995): with each generation of scientists and fishermen the reference baseline of resources and abundances change or in other words: the length of the time series determines our historical reference point.

For the Dutch Wadden Sea two long term data sets are available: the NIOZ fyke series (high resolution, daily pelagic and demersal fish in spring and autumn at a single location; 1960 – present) and the DFS survey (once a year, spatial demersal survey covering the subtidal and gullies of the Wadden Sea, 1970 - present). Results from both time series have been analysed and published, respectively by van der Veer *et al*. (2015), van Walraven *et al*. (2015) and by Tulp *et al*. (2008, 2015). The trends are shown for the Ems-Dollard, Wadden Sea and coastal area in Figure 3.1 below.

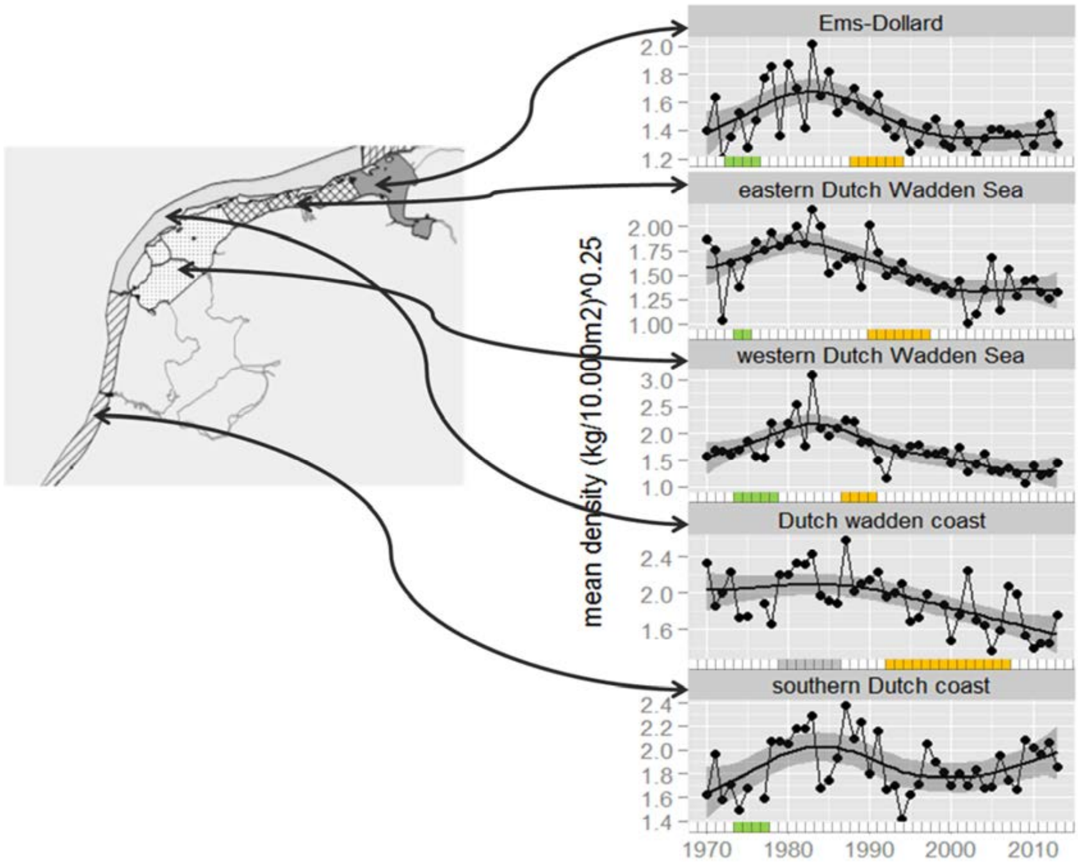

Figure 3.1 *Mean density of fish species, based on the DFS data. Green shows a period of increase in density, yellow of decrease and white shows stable densities.*

3.2.1. Species composition

Both the DFS and the NIOZ fyke indicated that species composition has been rather stable over the time period 1960 – present. However, it should be kept in mind that some fish types (rays, sharks) had already disappeared before the start of both time series (Lozan, 1994).

3.2.2. Long term trends

Both the DFS (demersal species only, pelagic species caught suboptimal) and the NIOZ fyke (demersal and pelagic species) showed a more or less similar long term increase from the start of the series to the early 1990s followed by a declining trend in total fish biomass until the early 2000s for the western Dutch Wadden Sea. See Figures 3.2 and 3.3 for the trends in marine juveniles and estuarine residents, respectively. The DFS series showed a similar trend for the eastern Wadden Sea. In Figure 3.4 the trends are shown for different fish guilds in the Dutch coast and Wadden Sea.

The NIOZ fyke series suggests that the composition of the fish fauna is still shifting to smaller individuals: mean individual biomass decreased between 1980 and the present from about 200 to 20 g wet weight. The DFS survey shows a decline in size for a limited number of species , but most species did not show this pattern.

Parallel with the decline in biomass, also the food web structure for pelagic species changed: 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 (van der Veer *et al.* 2015).

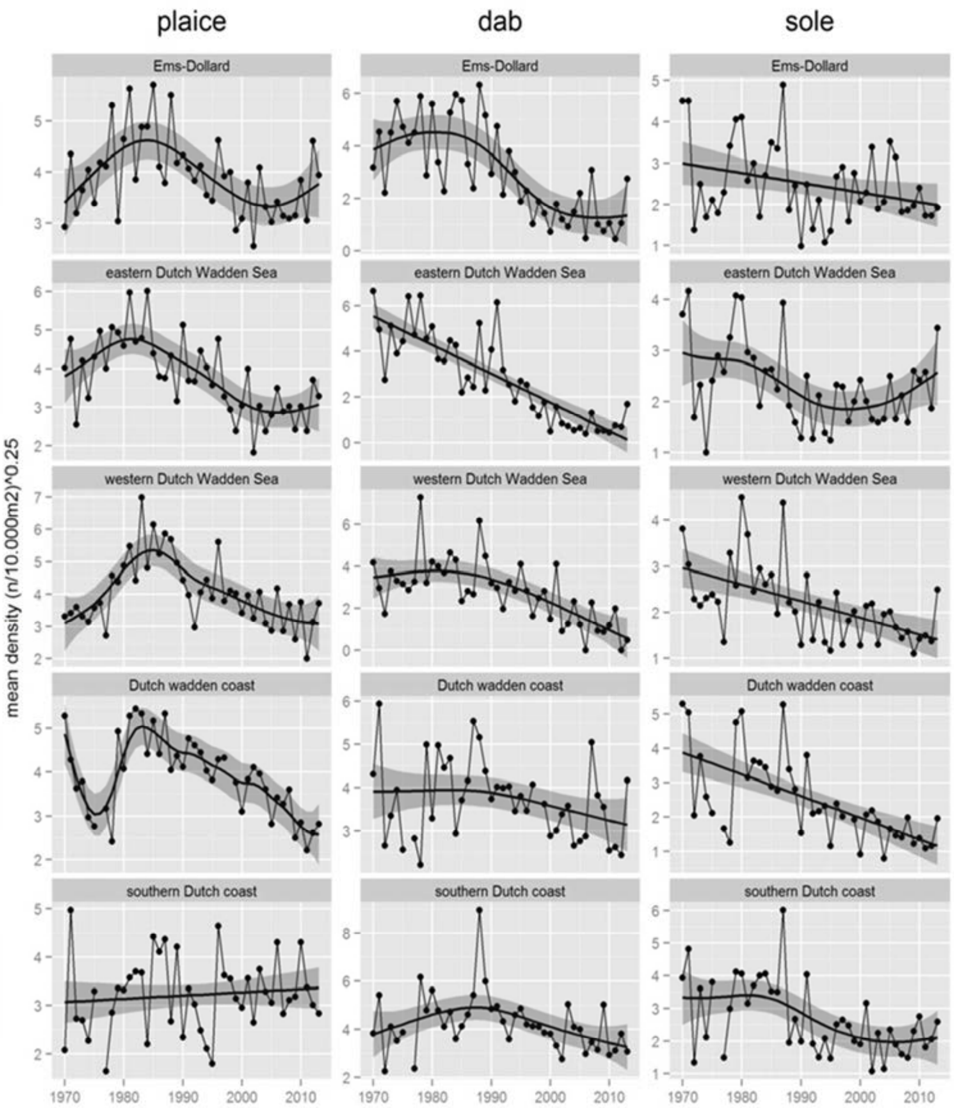

Figure 3.2 Trends in the density of marine juvenile flatfish based on the DFS and analysed using Trendspotter (Tulp *et al*., 2015 (see also Annex 4)).

3.2.3. Correlations

An attempt was made to investigate correlations between developments in the Wadden Sea fish fauna with developments in biotic and abiotic variables in two studies (Tulp et al. 2008; Van der Veer et al., 2015).

Common trends in the DFS were best described by models containing variables from all categories of environmental variables (abiotic, biotic and fisheries related variables).

For the NIOZ fyke series two main trends were identified 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.

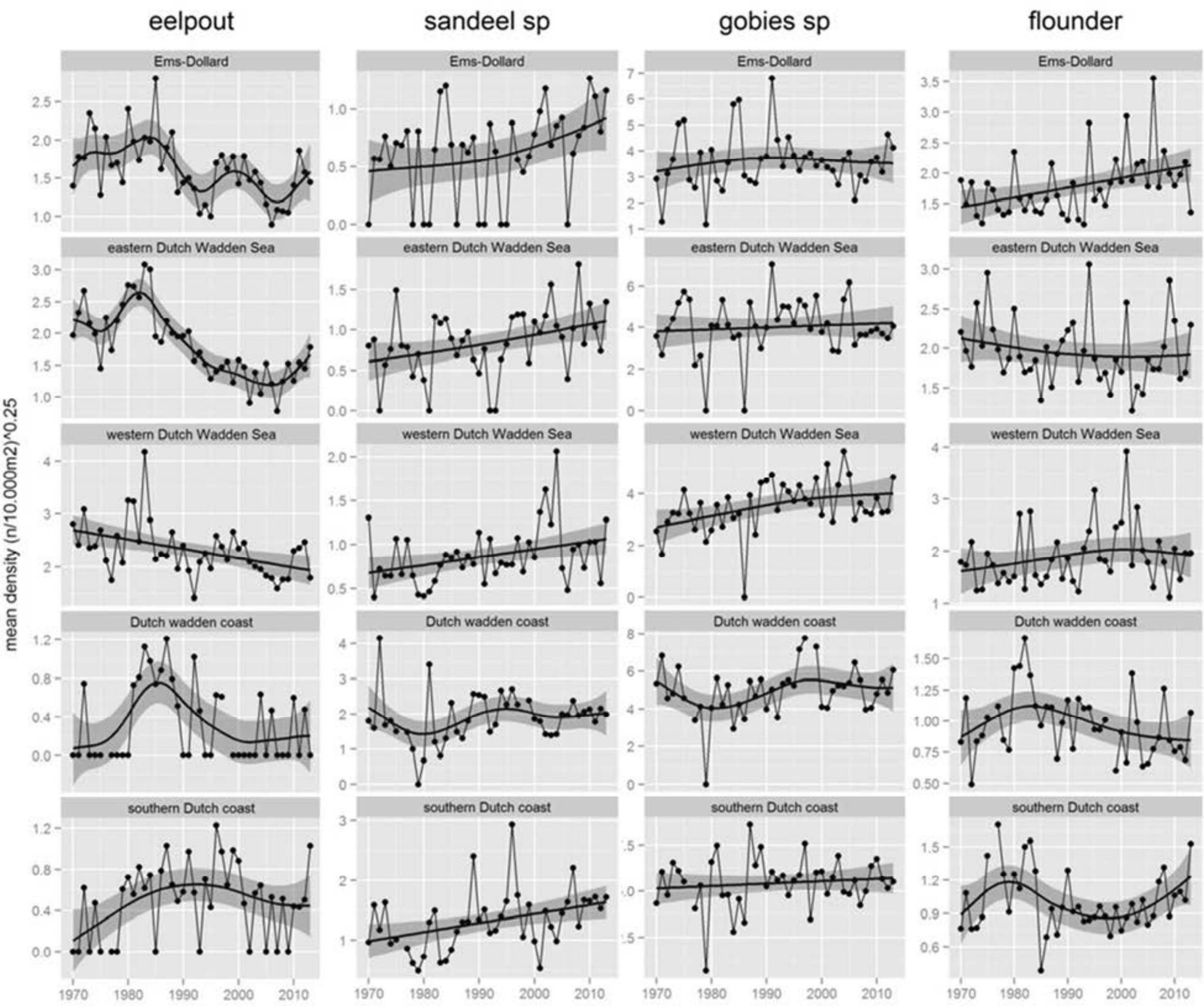

Figure 3.3. *Trends in four estuarine resident species based on the DFS and analysed using Trendspotter (Tulp et al., 2015 (see also Annex 4)).*

However these correlation studies do not provide insight into causal relationships. In order to investigate underlying mechanisms more in depth studies are needed.

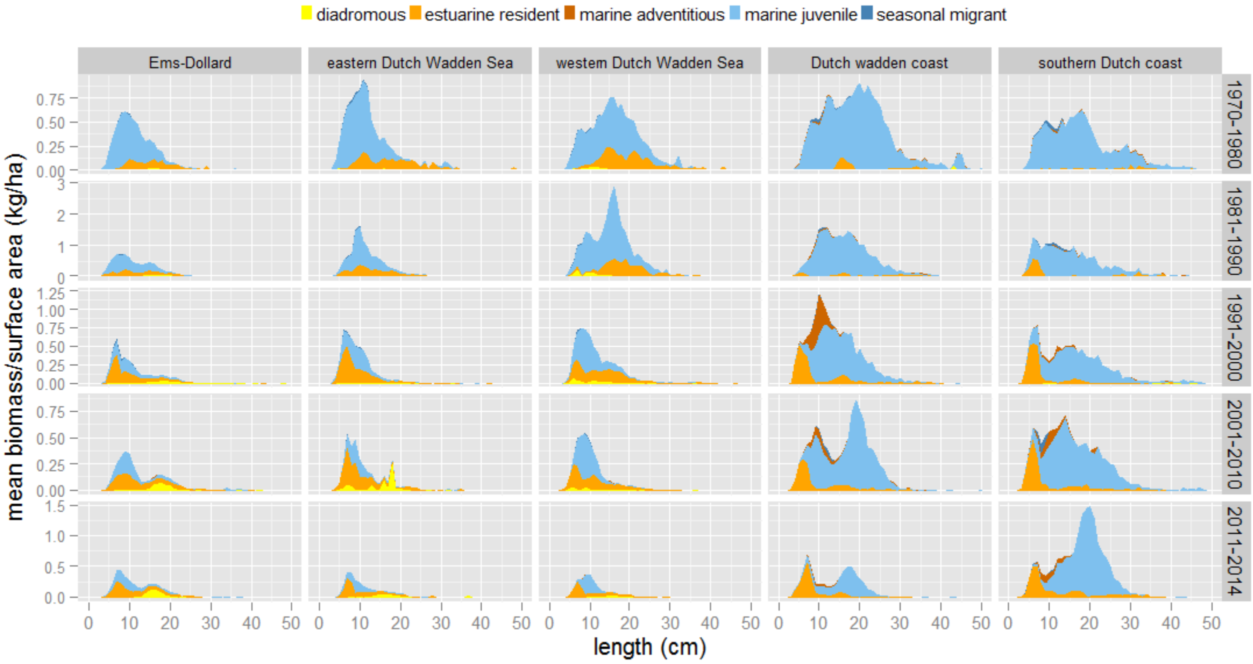

Figure 3.4. *Long-term trends in fish guilds in Dutch coastal waters and the Wadden Sea (Tulp, pers. comm.)*

3.2.4. Underlying mechanisms

Underlying mechanisms have only been studied for a small number of species. The disappearance of juvenile plaice has been shown to be related to a change in growth potential in the coastal area (Teal *et al.*, 2012). Pörtner & Knust (2007) showed that the decline in eelpout was likely caused by declining oxygen levels as a results of warmer water. A recent analysis of the fish abundance of the NIOZ fyke suggested at least a link with climate change (increased water temperature) from 1980 onwards: the relative importance of southern species in terms of biomass increased. Shifts are most striking in individual species that are near their southern (the eelpout *Zoarces viviparous*) or northern (the sea bass *Dicentrarchus labrax*) edge of the distribution in the Wadden Sea. They show respectively a strong decrease and increase in biomass with climate change. However, the analysis is hampered by the fact that for most species basic information on physiological performance is lacking.

To identify drivers for developments for certain species, a species specific approach is necessary in which knowledge on physiological and habitat requirements are crucial. The concept of a flyway in which all areas necessary for life cycle closure represented has proven very useful for waterbirds Similarly a ‘fishway’ concept should be applied to study the key processes and life stages for fish species. Combining knowledge on species physiology with lab and field experiments and model work can improve the understanding of mechanisms steering observed trends.

4. Driving forces

Ingrid Tulp & Henk van der Veer

Observed patterns

The analyses of available time series has resulted in the following observations in the Wadden Sea:

The DFS (Tulp et al., Manuscript - see Annex 4):

- Analysis restricted to trends in common species, no info on rare species and only few migratory species. For such species a passive gear with a much higher catch effort is more suitable.
- Total fish biomass shows an increase from 1970 to 1980, a peak in the mid 1980s and a strong decline especially from 1980-2000, with a stable trend since then. This pattern is similar in all tidal basins. The pattern in the coastal area deviates from that especially in the past 10 years, with a further decline in the Dutch Wadden coast and an increase along the mainland coast.
- Most dramatic declines in the Wadden Sea have occurred in marine juveniles. The timing of the declines are however not similar for all species.
- Resident species show more variable trends in the Wadden Sea: both increases and decreases occurred and trends in many cases differed between the Wadden Sea areas and the coastal zones. Over the time series both declines and increases are observed among species that can fulfil their life cycle within the Wadden Sea, with no clear overall trend.
- The fraction of fish belonging to the largest size classes decreased since the mid 1980s, not only in the Wadden Sea, but also in adjacent coastal areas.
- The fyke series (Van der Veer *et al*., 2015 (in press - see Annex 5); van Walraven *et al*., Manuscript)
- Correlates with trends in total fish biomass are water temperature, sand dredging and beach nourishment, fishing and predation, and large-scale hydrodynamic circulation
- 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.
- Of the 36 species examined the peak occurrence advanced in 17 and retarded in 19. The change in occurrence in the Wadden Sea was not so obvious in a shift of the first day of appearance but much more in an earlier date (20 of 36 species, 11 retarded, 5 unchanged) of the last observation in the season: fish are leaving the area earlier than they used to.
- Our image of the fish fauna in the Wadden Sea is limited to the past 50 years. Major changes before that time were described by (Lotze, 2005, 2007) and refs therein and include the disappearance of large groundfish and declines of migratory species, already in the end of the 19th century/beginning of the 20th century, mainly due to (over)fishing.

Causes

In order to define restoration measures for the Wadden Sea for the local fish fauna we need to consider that many species only spend part of their life within the Wadden Sea. Causes for declines can lie within, but also outside the Wadden Sea. Therefore the fishway (swimway) concept, whereby the importance of the Wadden Sea for each particular species is studied, should have a central place in restoration measures. For PRW it is sensible to concentrate on issues that can be tackled within the Wadden Sea. Therefore, there is a need to distinguish between causes within the Wadden Sea, at its borders (coastal area, connections to fresh water), or outside the Wadden Sea (North Sea and further).

The major causes for recent declines are only known for a few species. For **plaice** it is shown that the shallow Wadden Sea and coastal area have become too warm for especially the 1-group plaice to grow (Teal *et al*., 2012). The spawning stock of plaice however is at an all-time high, which means that the 1-group plaice probably have found areas more suitable to grow, likely further offshore (van Keeken et al., 2007). **Eelpout** in the German Wadden Sea declined because of decreased oxygen levels associated with warmer water temperatures (Pörtner and Knust, 2007). In addition correlative studies have shown relations between total fish biomass trends and all sorts of a(biotic) aspects (predation pressure, water quality, turbidity) and human activities (fisheries, sand extraction, beach nourishments, shell extraction).

Currently different fisheries take place in the Wadden Sea, of which the mussel seed fisheries and shrimp fisheries are the largest. Impact of those fisheries can act on fish via effect on the bottom (altered fish habitat), or bycatch (shrimp fisheries) or via food web interactions. Bycatch in shrimp fisheries is limited to fish smaller than 10cm, larger fish are hardly caught because of the use of the sieve net, which is compulsory from 1 Jan 2013 onwards. The bycatch in the shrimp fisheries on the plaice population was recently estimated to cause a reduction of 12-17% (van der Hammen *et al*., 2015). In the order of magnitude of 10.000s and 100.000s of river lamprey and twaite shad respectively (both Natura 2000 species), are bycaught annually. Similar computations of the effect of this bycatch on the total population and other non-commercial species cannot be made, because population estimates are missing.

Many species spend part of their lives in the North Sea, an area which is heavily impacted by human activities (fisheries, sand dredging, beach nourishments, pollution). For those species restoration aims set for the Wadden Sea can only succeed if management in the North Sea is involved as well.

5. Recovery measures for fish in the Wadden Sea

Recovery measures

Based on the current knowledge what concrete recovery measures can be formulated? Logically this can only be done for species/groups of species for which the causes of declines are known. A species specific approach focussing on combining knowledge on species physiology with lab and field experiments and model work is needed to improve the mechanistic understanding of observed trends. However that is still a long way to go, so based on practical thinking, we come up with the following suggestions (see next page):

***Table 5.1**. Possible restoration measures*

Improving connectivity	It is clear that the connectivity of the Wadden Sea with the fresh water has become severely hampered in the last century. Any measure that improves the connectivity should be welcomed. The fish migration river is a good example, although the expected impact on total populations is difficult to estimate beforehand.
Adapting to climate change	The warming of the water temperature is of course not limited to the Wadden Sea and not a cause that can be influenced locally. However mitigation is possible by providing deeper areas, or give special protection to gullies with cooler water to provide refuges at times of high temperatures.
Reducing fishing impact	The role of fisheries in the Wadden Sea is probably indirect, local fishermen do not catch the larger fish. The bycatch of juvenile and small fish is however considerable and although these are discarded, only part of those will survive and be able to grow up to adult size. By catching large quantities of shrimp, the Wadden Sea food web is likely changed which may indirectly affect the fish fauna. Any measure reducing the fishing effort either in in time (at periods with highest bycatch rates) or space (in areas with highest bycatch rates) is likely to alter the local fish fauna, in the sense that it creates the possibility for a more natural development locally. Recent investigations have shown that the shrimp fisheries is growth overfishing the shrimp stock. This means that by fishing less at more sensible times, the same yield can be achieved but a lower fishing effort. Such measure would also reduce bottom impact. This does not mean that reduction in fishing effort will automatically result in a measurable improvement of the fish fauna (however that is defined), only that there is better opportunity for natural processes. Fisheries in the North Sea is still quite intensive and in the beam trawl fisheries also larger (adult) fish are caught. The impact of that fisheries on the fish fauna in the Wadden Sea is poorly understood. Proposing measures for the Wadden Sea in isolation therefore does not seem sensible.
Wise sand nourishments	Sand nourishments take place yearly in different parts along the coast and every 3-5 years at the same location. Recovery time of abundance and biomass of the local benthic fauna after sand nourishments has been estimated at 1 year, full recovery of the community after 2-5 years (Borsje *et al*., 2010). This means the benthic community hardly gets the time to recover. Sand nourishments taking this into account with less frequent disturbances would be preferred (e.g. sand motor).
Restoring resilience	The Wadden Sea has always been an area characterised by a large natural dynamic processes. In such a dynamic environment species dynamics go up and down depending on variation in habitat availability, food or other circumstances. By reducing the natural dynamics, the resilience of the system to additional pressures has been greatly reduced. The restoration of the potential for natural processes (appearing and disappearing of certain habitats) will reinforce the resilience of the system.
Alertness for toxic substances	Currently the attention for potential effects of toxic chemicals in river runoff has little attention. However given the speed at which new chemicals are introduced, we should stay alert.

Species

It is not possible to give species specific restoration measures based on current knowledge. Moreover the development of fish populations is unpredictable and cannot be managed. However, some of the restoration measures will benefit specific guilds or species.

Possible restoration measure	Species to benefit – based on current knowledge
Improving connectivity	The diadromous species such as Twaite shad, smelt, river and sea lampreys, eel, sea trout, houting but also species such as flounder will benefit; species such as herring and anchovy will also benefit from improving the accessibility and size of brackish water areas
Adapting to climate change	The marine juvenile species which visit the Wadden Sea for part of their life-cycle will benefit, specifically plaice and eelpout
Reducing fishing impact	Demersal (flatfish) and pelagic (e.g. sprat, whiting) species, both resident and marine juveniles will benefit through by-catch reduction but this measure should not be seen in isolation from North Sea fisheries
Wise sand nourishments	All species will benefit through trophic interactions and habitat improvement; specific restoration of habitats in the Wadden Sea will benefit the estuarine residents such as bull rout and eelpout and also flounder
Restoring resilience	All species will benefit through trophic interactions and habitat improvement
Alertness for toxic substances	All species will be affected through trophic interactions

6. Gaps in knowledge/Research agenda

With respect to the status and functioning of the Wadden Sea fish fauna, the key issues are:

[1] Large predators and large predatory species have disappeared from the Wadden Sea already before the start (1960) of the present time series;

[2] Observed trends in biomass derived from the fyke series are correlated with patterns in habitat destruction/loss (beach nourishment, shrimp fisheries) and climate (climate change and large scale hydrodynamic circulation patterns (NAO));

[3] Insight in underlying mechanisms behind population developments is lacking for most species;

[4] Spatial scale of the various processes is unknown (tidal basin, eastern versus western Wadden Sea; Wadden Sea versus coastal zone);

[5] For most species it is not known whether population regulation takes place within the Wadden Sea or in other areas where they occur during some part of their life cycle

[4] Climate change seems to have an impact at least at single species level; this was shown for plaice and eelpout (Pörtner & Knust, 2007; Teal et al., 2012);

[5] There is a lack of insight in physiological performance of most of the species;

[6] There is a lack of knowledge in the food web structure of the Wadden Sea and in species interactions (including predator-prey relationships);

[7] There is a lack of insight in the role of the Wadden Sea in the life cycle of various species;

[8] Pelagic species and migratory species are poorly covered in the current monitoring scheme

[9] Major fish predators (terns, seals, cormorants) underwent major changes in the past decades and the relationships with developments in fish abundance are unclear.

Table 6.1 *The research agenda should include the aspects shown in the table below*

Spatial scale of processes	1. What are the main underlying mechanisms behind changes in trends and at what scale are they operating? 2. Which processes related to the fish fauna are operating at a local scale (tidal basin) or at a large scale (North Sea or other part of the fishway)? 3. What is the impact of morphological and hydrodynamic variability between tidal basins on the functioning of the ecosystem and the carrying capacity for fish? 4. What is the relationship and connectivity between coastal zone and Wadden Sea, within the Wadden Sea between tidal basins and between the Wadden Sea and the fresh water tributaries? 5. Is connectivity with fresh water areas limiting for migratory species? 6. What are the spatial and diurnal dynamics in distribution of the various species? 7. What is the spatial and seasonal dynamics in by-catch in shrimp fisheries and what is the impact on recruitment of the various by-catch species?
Food web structure	8. What is the relationship and interaction between the pelagic and demersal species? 9. How is the food web structure in the Wadden Sea, how variable is it and what is the importance of biological (prey-predator etc.) interactions. Which parts are controlled bottum up and which top down? What is the food choice of various fish species? How is the seasonal availability for (pelagic fish) as food for birds? 10. What is the (demersal and pelagic filter-feeding) carrying capacity of the area, and how variable is it in space and time? 11. What is the role of the brown shrimp *Crangon crangon* and other crustaceans as prey and predator in the system? 12. What is the impact of invasive species on the Wadden Sea ecosystem and the carrying capacity for fish, especially of those that are successful and becoming abundant (the polychaetes *Marenzelleria* cf. *wireni*, the Atlantic jackknife clam *Ensis directus*, the Pacific oyster *Crassostrea gigas,* the colonial tunicate *Didemnum vexillum* and the comb jelly *Mnemiopsis leidyi)*
Habitat	13. What are habitat preferences for various species? 14. How did different habitats (surface area mudflats, biogenic structures, eelgrass, sediment types) develop over the past decades?
Historical reconstructions	15. What has been the impact of eutrophication on the system; can it be reconstructed by means of otolith growth analysis? 16. What is the impact of North Sea fisheries on the Wadden Sea fish fauna, can it be reconstructed from achieved Wadden Sea landings during 1940 – 1945 when North Sea fisheries was banned? 17. Use case studies on species that were abundant in the past and have disappeared (i.e. dab) to provide information about underlying mechanisms?
Physiological performance of species	18. What is the physiological performance of the various fish species in the Wadden Sea. What are their physiological limits? 19. Can future changes in species composition and distribution be predicted from physiological requirements and performance of the individual species?

7. Fishermen's knowledge

7.1 Static gear fishermen

Fishermen and women spend a large part of their working life at sea. They observe and measure on a daily basis. Fishermen know where the fish are, but is it in their interest to let managers know? In order to enhance the dialogue between fishermen, scientists and managers, a number of conditions should be met.

Condition1: find common ground:

- Can we agree on:
- Conservation for nature and people?
- Fish production as management target?
- Fishery as part of the heritage?

And to find an inclusive conservation strategy that takes coastal communities into account?

Condition 2: create a safe space:

- Acknowledge the vulnerable position of fishers
- Start with (small) group of dedicated people
- Include interpreter(s) so that everyone knows what they are talking about.
- There should be no pressure to share all information
- Share the results!

The knowledge and expertise that fishermen can bring to the table is, a.o.:

- Information on changing habitats: e.g. old turf deposits have been covered with sand
- Behaviour of species: seals, fish
- Abundance of invasive species
- Changes in distribution, catches and abundance of fish species

7.2 Shrimp fishermen

On January 16th 2015 the status of fish in the Wadden Sea and the results from the IMARES/NIOZ analysis of data from the DFS and fyke survey were discussed with a number of shrimp fishermen and their representatives with Ingrid Tulp (IMARES) and Paddy Walker (PRW).

First, the fishermen first gave an overview of what they thought had happened with the fish populations, which species had changed most (either increase or decrease) and what they considered the driving factors for the changes observed. Following this, Ingrid Tulp gave a presentation in which the DFS survey data were presented. There was a high level of consensus between the results from the scientific survey data and the information and observations from the fishermen. However, the fishermen also had extra information on species such as mackerel and herring, which do not appear in the survey data, and valuable insights into changes in habitats, for example how the tidal flats have become less steep and sandier in the past years. It was a very good exchange of information and ideas.

Summarising:

Numbers of fish dropped in the past decades, following an increase in the 1980's. The main reasons that fishermen gave for the decline in fish species were:

- Decline of nutrients in the environment
- Climate – increase in water temperature
- Predation by seals and birds (cormorants)
- Changes in habitats, sedimentation and hydrology

Conclusions from discussions with shrimp fishermen.

The fishermen would like to be more involved in the management process. This could be achieved by:

- Regular (annual?) meetings between fishermen and scientists in which the survey results are discussed;
- Fishermen being involved in scientific surveys and vice versa – scientists and NGOs joining fishermen during their work.

8. Conclusions

It is clear that fish populations have declined in the Wadden Sea since the 1980's. The drivers are unclear, but increased water temperature, damage of coastal habitats (through sand nourishment, dredging and fisheries) and heightened predation by top predators probably play a role.

The largest decrease can be seen in the marine juvenile species, such as plaice and cod, that are present in the Wadden Sea during early life stages. Estuarine resident species such as gobies, show an increase or stable trend. For juvenile plaice and eel pout there is a clear relationship between rising water temperatures and decrease in density, but it is not possible to draw conclusions for other species. The size structure of the fish community changed in all areas, with generally the strongest declines in the largest size classes. Most size classes show higher densities in the mid 1980s and a decline afterwards.

This study shows that there is a lack of data on the fish community in the Wadden Sea. Not only on the drivers affecting the trends, but also on the species themselves. This is especially the case for the pelagic species such as anchovy and sandeel, as the current monitoring techniques are not suitable for these species. Insight into the entire community, and the associated food web relationships, is important.

Restoration of fish migrations routes and brackish water areas will not only benefit the diadrome (migrating) species, but also species such as herring and flounder which need brackish water areas as spawning and nursery areas.

It is important to develop insight into the role the Wadden Sea plays in the life-cycle of the various species in order to develop successful management measures. A life-cycle analysis per fish species in which the importance of the Wadden Sea to the status of the population can be quantified is recommended. This 'swimway' approach will support the development of management measures. This is especially relevant because it is likely that factors outside the Wadden Sea (North Sea, estuaries, rivers) determine the distribution and abundance of the species in the Wadden Sea itself.

Important habitats for fish have disappeared in the past decennia. The Wadden Sea is sandier and shallower than it used to be due to human activities such as sand nourishments and management of channels. An historical analysis of the development of habitats, combined with case studies of non-commercial fish species such as dab, could provide information on measures for habitat restoration.

Fishermen and women have a wealth of information and expertise on fish and how to catch them, but also insights in the ecosystem and how it has changed in the past years. Enabling an exchange of ideas and information between fishermen, scientists and managers would enhance the management process for both fisheries and fish.

In this report suggestions have been made for possible management measures and a research agenda which will be addressed at a later stage.

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Annex 1 - Policy objectives for fish in European or Trilateral policy documents. Information about Marine Strategy Framework Directive (MSFD) for both Germany SH and Denmark refers to fish in the North Sea.

In separate document – attached.

Annex 2 – Quality Status Report 2009 – Chapter 14 - Fish

In the last Quality Status Report (Marencic *et al*., 2009; Jager *et al*., 2009) all relevant knowledge on the fish community in the Wadden Sea was brought together. Main conclusions were:

Monitoring

- Monitoring programmes should extended to include:
  - spatial coverage of the demersal fish surveys to the Danish Wadden Sea.
  - sampling sites for pelagic fish as these are considered indicators of trophic integrity
  - sampling periods twice a year for fish with seasonal patterns of abundance
- The value of new national monitoring programs can be increased by trilateral 'tuning' and harmonization of methods, gear, sampling sites and sampling times.

Research

For a better understanding of the observed changes in the fish community

- More fundamental research on processes (ecosystem level, species level), anthropogenic impacts and climate change is required.
- More knowledge on the dynamics of Wadden Sea fish populations in relation to North Sea and estuarine populations is required.
- The functional relationship (*e.g.* food, shelter) between fish species and habitats (*e.g.* tidal flats, mussel beds, reed beds, salt marshes) should be investigated.
- The international accessibility of data and results from applied research projects (such as EIA studies on fish) should be enhanced.
- Funding for concomitant research on the ecology and changes in abundance of fish remains indispensable to understand trends observed in TMAP fish monitoring.

Management

- The further development and implementation of trilateral targets concerning fish is necessary to structure and focus the TMAP fish monitoring.
- Continue with the initiated development of a suitable and acceptable assessment tool, taking into account the lack of knowledge on reference conditions and cause-effects-relationships.
- Effective management of Wadden Sea fish cannot be achieved without tuning with North Sea and estuarine management.

Trilateral policy

- Involve Denmark in the trilateral (in practice bilateral) work of the TMAP fish expert group.
- Consider the most appropriate way and enable the continuation of the fruitful and stimulating cooperation on the joint analyses of fish monitoring data.

Annex 3 – Typical Wadden Sea fish species from QSR and N2000

Typical Wadden Sea fish species from QSR and N2000. Upper fourteen = priority species selected for spatial and temporal analyses by Bolle *et al*., 2009 and used in the QSR (REF). Last seven species also mentioned in N2000 species as related to the habitat designated for the Wadden Sea (H1110). Species marked with * are designated species for N2000 for the Wadden Sea. Species in **bold** type = in both QSR and N2000. Guild: CA = diadromous; ER = estuarine resident; MJ = marine juvenile; MS = marine seasonal. Sensitivity to driving forces: CC = climate change; FM = fishing mortality; HD = habitat degradation; LP = local pressures; NE = nutrient enrichment.

Species	Common name	Guild	Stratification	Benthic habitat	Sensitivity to driving forces
*Alosa fallax**	Twaite shad	CA	Pelagic		HD
Osmerus eperlanus	Smelt	CA	Pelagic		HD; FM
*Lampetra fluviatilis**	River lamprey	CA	Pelagic		-
Platichthys flesus	Flounder	ER	Demersal	Mud-sand	HD
Zoarces vivparus	Eelpout	ER	Demersal	Mud-plants	HD; LP
Ammodytes spp.	Sandeel	ER	Pelagic & buried	Sand	HD; FM
Pleuronectes platessa	Plaice	MJ	Demersal	Mud-sand	CC; NE; HD; FM
Solea vulgaris	Sole	MJ	Demersal	Mud-sand	CC; NE; HD; FM
Limanda limanda	Dab	MJ	Demersal	Sand	NE; HD; FM
Gadus morhua	Cod	MJ	Demersal		CC; HD; FM
Merlangus merlangus	Whiting	MJ	Demersal		HD; FM
Clupea harengus	Herring	MJ	Pelagic		CC; HD; FM
Sprattus sprattus	Sprat	MS	Pelagic		HD; FM
Engraulis encrasicolus	Anchovy	MS	Pelagic		CC
*Petromyzon marinus**	Sea lamprey	CA	Pelagic		-
Liparis liparis	Sea snail	ER	Demersal	Mud-hard	HD
Myoxocephalus scorpius	Bull rout	ER	Demersal	Mud-plants	HD; LP
Pholius gunnellus	Butterfish	ER	Demersal	Mud-plants	HD
Pomatoschistus minutus	Sand goby	ER	Demersal	Sand	HD
Syngnathus acus	Greater pipefish	ER	Demersal	Sand-plants	HD
Syngnathus rostellatus	Nilsson's pipefish	ER	Demersal	Sand-plants	HD

* Designated species in N2000 H1110

Annex 4 Manuscript in preparation: Tulp *et al*. in prep.

LONG-TERM FISH TRENDS IN THE DUTCH WADDEN SEA AND ADJACENT COASTAL AREAS

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ABSTRACT

The Wadden Sea is traditionally an area with an important function for (demersal) fish species: as a growing area for juveniles, as a feeding area, as passage to and from fresh water and for resident species that complete their whole life cycle there. As a follow up on a study investigating trends in demersal fish for the Wadden Sea as a whole we analysed and classified trends of 24 fish species per tidal basin and compared them to trends in the adjacent coastal areas in the North Sea. We use two long-term time series: an annual beamtrawl survey (DFS) with a high spatial but a fyke series producing data in a daily interval. The questions we asked ourselves were: (1) Do (demersal) fish trends in different parts of the Wadden Sea and adjoining coastal areas show similar or different patterns? (2) do trends in functional groups of species (guilds) differ between tidal basins inside and outside the Wadden Sea? (3) do trends in size structure differ between tidal basins and inside and outside the Wadden Sea (4) has timing changed relative to the timing of the DFS survey and if so is this a likely cause for changes observed in species trends?

Total fish biomass showed a similar pattern in all tidal basins with an increase from 1970 to 1980, a peak in the mid 1980s and a strong decline especially from 1980-2000, with a stable trend since. The pattern in the coastal area deviates from that especially in the past 10 years, with a further decline in the Dutch Wadden coast and an increase along the mainland coast. Most dramatic declines in the Wadden Sea have occurred in species belonging to the marine juvenile guild. The timing of the declines are however not similar for all species. Resident species show more variable trends in the Wadden Sea: both increases and decreases occurred and trends in many cases differed between the Wadden Sea areas and the coastal zones.

The combined use of both surveys showed that for some species the DFS is not optimally timed. For most species there was no clear signal that timing has advanced in relation to the timing of the survey in recent

years. The only exception is eelpout, for which the timing of the DFS no longer encompasses its presence in the Wadden Sea.

This analysis is limited to the more common species for which a proper trend analysis was possible, development of the rare species are not included. Based on the current analysis we formulate research needs which concentrate on a species specific approach focussing on combining knowledge on species physiology with lab and field experiments and model work to improve the mechanistic understanding of observed trends.

INTRODUCTION

Many fish species rely on shallow coastal habitat for at least one of their life stages. A suit of flatfish and other groundfish and pelagic fish species reach these areas as postlarvae and spend their juvenile phase here (marine juveniles, (Elliott *et al*., 2007; van der Veer *et al*., 2000)). Other species inhabit the area on route to either marine or fresh water spawning sites (diadromous species) or during certain times of the year (marine seasonal migrants) or occasionally (marine adventitious species) (Elliott *et al*., 2007). In addition to such temporary visitors, many species spend (almost) their entire life in the shallow waters (estuarine residents) (Elliott and Hemingway, 2002). Naturally such coastal areas support large numbers of fish (Elliott and Hemingway, 2002) that make use of the suitable habitat characterised by a high food availability and shelter from predators.

The Wadden Sea is a coastal area for which the function for various fish species has been described (Tulp *et al*., 2008; van der Veer *et al*., 2001; Van der Veer *et al*., 2015 (in press); Zijlstra, 1972). Structural monitoring of the fish fauna takes place since 1960-1970 by two major monitoring programs: a fyke program in the Western Wadden Sea and an annual beam trawl survey covering the entire Dutch Wadden Sea. The Wadden Sea connects fresh water habitat with the North Sea and provides a relatively sheltered area consisting of intertidal mudflats, gullies ranging in depth from several decimetres to 30m. The borders consist of salt marshes which are cross-cut by gullies. Both intertidal and subtidal habitats have been shown to be of great importance to both commercial and non-commercial species.

The fyke scheme run by NIOZ since 1960 has shown that many species from the western Wadden Sea are declining (Van der Veer *et al*., 2015 (in press); van der Veer *et al*., 2011). Trends in the Dutch Wadden Sea as a whole, based on a demersal fish survey (DFS) carried out by IMARES, were analysed before (Tulp *et al*., 2008). In both lower and higher levels of the ecosystem contrasting trends have been found between tidal basins within the Wadden Sea (Ens *et al*., 2009; Tulp *et al*., 2008) (P. Herman pers.comm). The tidal basins greatly differ in sediment, nutrients, salinity water visibility and stoichiometry. Therefore a basin approach in time series analysis may provide better inside in potential drivers. This notion gave rise to a re-analysis of the Wadden Sea fish data per tidal basin. Adjoining coastal areas North of islands and along the main coast are included in the comparative analysis as well to provide a reference for the patterns observed within the Wadden Sea. In course of the survey period the timing of the DFS survey in the Wadden Sea as advanced (ca 1 month in 40 years) because of practical planning reasons. The changed timing of the survey could partly explain trends in fish species: if the residence period of fish in the Wadden Sea has changed, such phenological changes in combination with a change in timing of the survey may lead to time trends that do not reflect true population changes. The fyke scheme provides day to day values for fish abundance and will be used here to test if the DFS was timed in the right period for different species.

The questions we want to answer here are:

(1) Do (demersal) fish trends in different parts of the Wadden Sea and adjoining coastal areas show similar or different patterns? (2) do trends in functional groups of species (guilds) differ between tidal basins inside and outside the Wadden Sea? (3) do trends in size structure differ between tidal basins and inside and outside the Wadden Sea (4) has timing changed relative to the timing of the DFS survey and if so is this a likely cause for changes observed in species trends?

Based on the DFS we calculate and classify trends of 24 fish species and of total fish biomass for the Western Dutch Wadden Sea, the Eastern Dutch Wadden Sea, the Ems-Dollard, the Dutch Wadden coast (coast north of the Dutch islands) and the southern Dutch coast (mainland west coast). To sketch the size structure of the community we also analyse the abundance per size class of the total fish abundance. The fyke series is then used to investigate if a changed timing may (partly) explain observed time trends.

METHODS

Sampling: DFS

The Dutch Demersal Fish Survey (DFS) covers the coastal waters (up to 25m depth) from the southern border of the Netherlands to Esbjerg, including the Wadden Sea, the outer part of the Ems-Dollard estuary, the Westerschelde and the Oosterschelde (van Beek *et al.*, 1989). This survey has been carried out in September-October since 1970. Areas are delineated according to tidal basins or other geographic features and defined in the original survey design (Boddeke *et al.*, 1972). For the purpose of this paper data from five distinct regions (groups of delineated areas) were analysed (from northeast to southwest): Ems-Dollard, Eastern Dutch Wadden Sea, Western Dutch Wadden Sea, Dutch Wadden coast and southern Dutch coast. This division is in accordance with the Trilateral Monitoring and Assessment program (Bolle *et al.*, 2009; Jager *et al.*, 2009). The estuaries all have natural borders. The number of hauls area was kept as constant as possible and are presented in Table 1. In several years not all sampling points were sampled due to adverse weather and. For each haul, the position, date, time of day and depth were recorded. Within the Wadden Sea sampling was carried out with a 3 m-beam trawl, while along the coast a 6 m beam was used. The beam trawls were rigged with one tickler chain, a bobbin rope, and a fine-meshed cod-end (20 mm). Both gears were rigged similarly, only the size of the beam differed. The reason for the choice of a different size is that a 3 m beam is more manoeuvrable in the estuaries where sampling often took place in narrow gullies. The 6 m beam is used along the coast because a 3 m beam would be too light in this less sheltered and generally deeper area. The expectation is that densities (raised to n/10000 m^2) derived from both these gears do not differ, although they have never been formally compared. For the calculations of indices as input for stock assessments the data from both 3 and 6 m beam are treated in a similar combined way (ICES, 2011). Fishing was restricted to the tidal channels and gullies deeper than 2 m because of the draught of the research vessel. The combination of low fishing speed (2-3 knots) and fine mesh size results in selection of the smaller fish species and younger year classes and other epibenthos. Sample locations were stratified by depth. The mean abundance per area was calculated for all subareas in the period 1970-2013 weighed by surface area for five depth strata (intervals of 5 m) within the subareas. Surface areas of depth strata used were taken from ICES (2011).

Sampling: fyke

Since 1960, a kom-fyke trap has been operating 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 see van der Veer et al. (1992). Fishing normally started in March - April and lasted until October. In winter the trap was removed because of possible damage by ice floes and from 1971 onwards no fishing took place during part of the summer because of fouling of the net and clogging by macroalgae and sometimes by 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 on alternate mornings. Here data for the period 1960 – 2013 were analysed, whereby catches were selected according to the following criteria:

Fishing duration less than 48 h (exclusion of 329 records) and longer than 12 h (exclusion of 1 record)

-no damage of the gear upon retrieval (loose mesh panels or tears) and/or not clogged with debris (exclusion of 53 records). In total, 6481 daily catches were available for further analysis.

All catches were sorted out immediately and identified 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 (see van der Veer et al. 2015). All information was stored in a database. 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).

Data analyses

Time series of 24 most common species occurring both in the Dutch Wadden Sea and the coastal area (Table 1) were analysed using Trendspotter, a computer program based on structural time-series analysis (Harvey, 1989) in combination with the Kalman filter (Visser, 2004). The Kalman filter algorithm operates recursively on streams of noisy input data to produce a statistically optimal estimate of the underlying system state (Kalman, 1960). The program is used to identify periods with significant increases or decreases beyond annual fluctuations, by estimating smoothed population numbers for a time series with N equidistant measurements over time. TrendSpotter also estimates the standard deviations of the smoothed population numbers. Finally, it estimates the standard deviations of the differences between consecutive time points and any time point with respect to the last. The estimation of confidence intervals is based on the deviations of time point values from the smoothed line. The output also produces autocorrelation functions. A more detailed description of the method can be found in Visser (2004) and Soldaat *et al*. (2007). This method accounts for serial correlation and provides confidence limits to test for changes in abundance. The classification of trends in the last decade was based on the 95% confidence interval of the yearly change rate method presented in Soldaat *et al*. (2007). We distinguish among strong increase, moderate increase, stable, moderate decline, steep decline and uncertain. A yearly change rate of 1.00 means no change. A strong increase is characterised by a yearly change rate of at least 1.05 (5% increase per year), while the lower confidence limit is no less than 1.05. Similarly a steep decline is characterised by a yearly change rate ≤0.95, with the upper confidence limit <0.95. A moderate increase has a lower confidence limit between 1.00 and 1.05 and a moderate decline between 0.95 and 1.00. In stable trends the confidence interval includes 1.00 and lower CL ≥0.95 and upper CL ≤ 1.05. Uncertain trends have a confidence interval containing 1.00 and the lower CL < 0.95 OR upper CL > 1.05. Apart from a classification by year an overall classification of the last decade was made. Densities were 4^{th} root transformed before analyses because of non-normality. Trend analyses were carried out based on density in numbers and for two size classes separately (small<54 mm, large≥54 mm, the cut-off point determined by the commercial size in the shrimp fisheries).

Trends are presented for five different areas: three areas within the Wadden Sea (Ems-Dollard estuary, eastern and western Dutch Wadden Sea), the North Sea coast along the Wadden Sea islands (Dutch Wadden coast), and the North Sea coast along the mainland (southern Dutch coast, **Fout! Verwijzingsbron niet gevonden.**).

Trends are grouped in ecological guilds: ca=catadromous/anadromous, mj=marine juveniles, ma=marine adventitious, er=estuarine resident, ms=marine seasonal migrant according to (Elliott and Hemingway, 2002) (Table 1). Common trends per guild are calculated by averaging the normalised trends across all individual species per guild.

RESULTS

Total fish biomass

Total fish biomass showed similar trends in four out of five areas, with an increase from 1970 to 1980 and a decrease from the late 1980's onwards (Figure 2, Table 2). Along the Dutch Wadden coast the peak in the 1980's was not observed. The decrease stopped in the Ems-Dollard, the eastern Dutch Wadden Sea and the southern Dutch coast around late 1990s, but is still ongoing in the western Dutch Wadden Sea and along the Dutch Wadden coast although the trend is classified as uncertain since 2007 (Dutch Wadden coast) and 1997 (western Dutch Wadden Sea). The species that contribute most to the total fish biomass are plaice, dab, whiting, gobies sp, flounder and sole (Figure 3).

Species trends

Species belonging to the resident guild (Figure 4, Table 3) show variable trends. Eelpout declines significantly in the Western Wadden Sea and did so in the eastern Wadden sea and Ems-Dollard, but is recovering in the latter two regions in the past five years. Hooknose declined in both west and eastern Wadden Sea. Species that are relatively stable in all three Wadden Sea areas are rock gunnel, gobies, five-bearded rockling, common seasnail, rock gunnel. Flounder shows contrasts between the Ems-Dollard (increase) and rather stable trends in western and eastern Wadden sea. Sandeel increase in throughout the Wadden Sea, although there are years with zero catches especially in the east. In comparison to the coastal areas along the islands (Wadden coast) and the mainland coast there are striking patterns that are different from those observed inside the Wadden Sea: the increase in bullrout that started earlier along the Wadden than the mainland coast, the increase of common sea snail, five-bearded rockling, hooknose (mainland coast) and pipefishes (Wadden coast). The increase in sandeels is also observed along the mainland coast.

Most dramatic changes in the Wadden Sea have occurred in the species belonging to the marine juvenile guild. Plaice, whiting, cod and bib show a dome-shaped pattern with a peak in mid 1980's with a strong decline. Current levels of plaice in the western Dutch Wadden Sea are similar to those in 1970s, but in the eastern Dutch Wadden Sea even lower. Whiting also has decreased to lower levels than those in the 1970s. Plaice is recovering in the Ems-Dollard in recent years. The pattern in dab is somewhat different: a steady decline in all areas but most predominant in the eastern Wadden Sea. Sole showed a steady decrease in the west and Ems-Dollard and a less clear trend in the east. In contrast to all decreasing marine juveniles brill is increasing in the eastern Dutch Wadden Sea. After the initial increase in the mid 1980's herring has shown a stable trend throughout. Tub gurnard was historically not an abundant species, but recently shows an increase in the Ems-Dollard and the east (although not significant yet). Smelt is only regularly caught in the west and increased there from 1970 until early 2000 and a steady trend since.

Contrasts with the coastal area are apparent for whiting: stable along the Wadden coast and along the mainland coast whiting is increasing recently. Trends for cod are more stable. Bib and tub gurnard show a pattern very similar in all areas, in and outside the Wadden Sea. The pattern for plaice is similar along the wadden coast, but the trend is more stable along the mainland coast. For dab the trends is similar but much less pronounced. Sole declined strongest along the Wadden coast.

The diadromous species eel shows a two peaked pattern throughout the Wadden Sea, with peaks around 1980 and 2000 (Figure 6, Table 5). Strongest declines were observed around mid 1980s. Current levels are close to zero. A more continuous decline (without the peaks in 2000) were observed in the coastal areas. The other diadromous species, smelt, shows positive trends in the eastern Wadden Sea and Ems-Dollard, and a decline in the western Wadden Sea, although the trend is too variable to be classified as such (Table 5). In the coastal areas the species is too rare to calculate a reliable trend. The only seasonal migrant in this study, sprat, shows no clear overall trend, although it seems to be declining throughout the Wadden Sea and more stable along the coast (Figure 6, Table 5). Common dragonet is the only marine advantageous species in this study and inside the Wadden Sea it only occurs regularly in the western Dutch Wadden Sea. The trend there is uncertain. Along the coasts densities are stable.

Timing

For some species the timing of the DFS survey is not optimal (regardless of a potential change in timing). Tub gurnard and pipefish are species that occur more regularly in spring. Some species such as common dragonet, hooknose and common seasnail are caught too irregularly in the fyke to derive any information on timing.

A change in phenology could be one of the reasons for observed trends. The DFS is survey is always carried out at the same time of year in August-September, however there has been a shift over the years resulting in a advancement of the start of the survey of ca 1 month over the whole period. If phenology has changed so that certain species leave the Wadden Sea earlier than they used to this could be an explanation for observed declines for instance. To check for this potential effect we compared the time window during which each species was caught in the fyke series to the timing of the DFS survey (Figure 7). For most species there was no clear signal that timing has advanced in relation to the timing of the survey in recent years. The only exception is eelpout, for which the timing of the DFS no longer encompasses its presence in the Wadden Sea anymore (van Walraven *et al*., Manuscript). Problematic in this analysis are species that are relatively rare and not caught well in the fyke (e.g. hooknose, common dragonet).

Guilds

Combining species per guild shows that marine juveniles have similar patterns in all three Wadden Sea areas, with a peak in the mid-1980s and a decline since (**Fout! Verwijzingsbron niet gevonden.**). In the eastern Dutch Wadden Sea and Ems-Dollard however the trend is increasing in recent years. Patterns in the coastal area are different, with an extended peak along the Wadden coast and no decline along the mainland coast. In the eastern Dutch Wadden Sea resident species show a similar pattern as the marine juveniles, but in the Ems-Dollard and western Dutch Wadden Sea there is no sign of decline. In the coastal areas resident species seem to be increasing over the past 30 years. Marine seasonal migrants, diadromous species and marine advantageous species are each represented by a small number of species, which explains why the patterns shows much more variation and amplitude.

Size

The size structure of the fish community changed in all areas, with generally the strongest declines in the largest size classes (Figure 9). Most size classes show higher densities in the mid 1980s and a decline afterwards. The abundance of the smallest size class (≤5cm) has been relatively constant in the western Dutch Wadden Sea, decreased since the mid 1980s in the Ems-Dollard but has increased since that period in the coastal areas.

DISCUSSION

Guild specific comparison of trends in the Wadden Sea and the coastal area

For many species trends in all three Wadden Sea areas were similar, for some species they differed. In general they were similar for marine juveniles (dab, plaice, sole, herring, whiting, bib). However the decline in dab started earlier and progressed longer than for plaice and sole (Table 3 Figure 5). Compared to the coast declines were stronger in the Wadden Sea apart from sole along the southern Dutch coast. Greater sandeel and brill (in the eastern Dutch Wadden Sea) are the exceptions amongst marine juvenile species, showing an increase both in the western Dutch Wadden Sea and coastal areas; the species is not abundant in the eastern Dutch Wadden Sea and Ems-Dollard. In comparison to the coastal area trends of bib, greater sandeel, herring, plaice, sole were very similar. Clear differences in trends between Wadden Sea and coast were found for whiting, cod and dab.

As resident species can complete their life cycle within the Wadden Sea, any cause for obvious trends must be sought within the Wadden Sea. Residency does not automatically mean that they spend their entire life there, migration to other areas is still possible. However, the trend analyses did not show an overall similar trend between species. Eelpout is clearly declining in all Wadden Sea areas, although this might partially be explained by the fact that this species is leaving the Wadden Sea earlier than it used to (van Walraven *et al*., Manuscript). For eelpout the Netherlands is the southern edge of its distribution (Andriashev, 1986; Pörtner and Knust, 2007). The species also largely retreated from the more offshore areas covered by more offshore surveys (Daan et al in prep). The decline is also clear in German coastal waters and has been linked to an increase of water temperatures above the thermal maximum for the species, leading to oxygen limitation (Pörtner and Knust, 2007). Of the 10 studied resident species showing clearly changing trends in the Wadden Sea were bullrout (increase unil mid 1980s, decrease until 1990s, stable thereafter), flounder (increase throughout period in the Ems-Dollard, stabel elsewhere), hooknose (declines in all Wadden Sea areas, but a recent recovery in the Ems-Dollard), rock gunnel (stable in Ems-Dollard and western Dutch Wadden Sea, decline in eastern Dutch Wadden

Sea in 1990s), and sandeel sp. (increase everywhere apart from Ems-Dollard). Resident species showing clear trends in the coast were five-bearded rockling (increase), sandeel sp.(increase), pipefish (increase), common seasnail (increase), hooknose (increase). The periods of decline recorded in any of the resident species (eelpout, bullrout, hooknose, rock gunnel) all took place inside the Wadden Sea, none in the coastal zone (Table 3).

The division of species in functional groups was based on (Elliott *et al.*, 2007), but can be debated for some species. Flounder for instance is characterised as resident, but could equally well be part of the diadromous or marine juvenile category.

Size structure

The clear shift from larger sized fish to smaller sized fish as observed further offshore (Daan *et al.*, 2005) was not so obvious in the Wadden Sea. Densities of larger sized decreased, but also those of smaller sized fish (Figure 9). This disproportionate decrease in the larger sized fish is more apparent in the two coastal areas.

Timing

Fish can respond in various ways to changing circumstances such as a change in water temperature. A shallow area as the Wadden Sea easily warms up in summer. Possibilities to find deeper areas with cooler water are limited and fish may leave the Wadden Sea if temperatures become too high. This could lead to a change in the period during which they are present. In response to warming sea water, species may arrive earlier in the year than they used to, and also leave earlier. The analysis of phenology of the fyke series showed that of 36 species examined the peak occurrence advanced in 17 and retarded in 19 (van Walraven *et al.*, Manuscript). The change in occurrence in the Wadden Sea was not so obvious in a shift of the first day of appearance but much more in an earlier date (20 of 36 species, 11 retarded, 5 unchanged) of the last observation in the season: fish are leaving the area earlier than they used to. Our analyses showed that a changed timing of fish cannot be an explanation for trends observed. Only in the case of eelpout the period of the survey is no longer timed in the period when it is present in the Wadden Sea (Figure 7). But even if the timing of the survey is still within the period of presence, the timing relative to the peak occurrence may still be altered.

Mechanistic understanding of observed trends

The description of these trends is a first step towards explaining local population fluctuations. For many of the 24 species reported here, we know very little on their habitat requirements, habitat use, seasonal migrations and physiological requirements. Underlying mechanisms have only been studied for a small number of species. The disappearance of juvenile plaice has been shown to be related to a change in growth potential in the coastal area (Teal *et al.*, 2012). Pörtner & Knust (2007) showed that the decline in eelpout was likely caused by declining oxygen levels as a result of warmer water. To identify drivers for developments for certain species, a species specific approach is necessary in which knowledge on physiological and habitat requirements are crucial. Combining knowledge on species physiology with lab and field experiments and model work can improve the understanding of mechanisms steering observed trends.

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TABLES

Table 1. List of fish species analysed with scientific and common names, and information on protection status and guilds. Species marked with * are designated species for N2000 for the Wadden Sea. Guild: ca = diadromous; er = estuarine resident; mj = marine juvenile; ms = marine seasonal.

common name	**scientific name**	**functional group**
eel	*Anguilla anguilla*	ca
herring*	*Clupea harengus*	mj
sprat	*Sprattus sprattus*	ms
smelt*	*Osmerus eperlanus*	ca
whiting	*Merlangus merlangus*	mj
cod	*Gadus morhua*	mj
bib	*Trisopterus luscus*	mj
five-bearded rockling	*Ciliata mustela*	er
pipefish sp	*Syngnathus* sp	er
tub gurnard	*Chelidonichthys lucerna*	mj
bullrout	*Myoxocephalus scorpius*	er
hooknose	*Agonus cataphractus*	er
common seasnail	*Liparis liparis*	er
eelpout*	*Zoarces vivparus*	er
rock gunnel	*Pholius gunnellus*	er
sandeel sp	*Ammodytes* sp	er
greater sandeel	*Hyperoplus lanceola*	mj
common dragonet	*Callionymus lyra*	ma
gobies sp	*Pomatoschistus* sp	er
brill	*Scophthalmus rhombus*	mj
flounder*	*Platichthys flesus*	er
plaice*	*Pleuronectes platessa*	mj
dab	*Limanda limanda*	mj
sole	*Solea vulgaris*	mj

Table 2. Results of trend analyses of total biomass. The classification (as per Soldaat *et al.* (2007)) of the trends is given: ++ strong increase, + moderate increase, -- strong decrease, -moderate increase, - moderate decrease, 0 stable , ? uncertain. Yearly change rate (the smoothed population number in the last year compared with the smoothed population number in the first year, where >1 means increase and <1 decrease of population) in the last decade with range are given in the three but last columns. The trend classification as well as the number of zeros and missing values are given in the final three columns. Empty lines indicate species-region combinations for which the catching probability was too low to estimate trends.

region	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
Ems-Dollard	?	?	?	?	+	+	+	+	?	?	?	?	?	?	?	?	?	?	-	-	-	-
Dutch wadden coast	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	?	?	?	?	?
E Dutch Wadden Sea	?	?	?	?	?	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-
W Dutch Wadden Sea	?	?	?	?	?	+	+	+	+	+	?	?	?	?	?	?	?	-	-	-	-	?
southern Dutch coast	?	?	?	?	?	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?

region	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	YCR min last decade	YCR mean last decade	YCR max last decade	trend last decade	n years with 0	n years with missing values
Ems-Dollard	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	2	?	0	0
Dutch wadden coast	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	?	?	?	?	?	0	1	1	-	0	2
E Dutch Wadden Sea	-	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	2	?	0	0
W Dutch Wadden Sea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	2	?	0	0
southern Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	3	?	0	1

Table 3. Results of trend analyses of resident species ordered alphabetically. The classification (as per Soldaat *et al.* (2007)) of the trends is given: ++ strong increase, + moderate increase,-- strong decrease, -moderate increase, - moderate decrease, 0 stable , ? uncertain. Yearly change rate (the smoothed population number in the last year compared with the smoothed population number in the first year, where >1 means increase and <1 decrease of population) in the last decade with range are given in the three but last columns. The trend classification as well as the number of zeros and missing values are given in the final three columns. Empty lines indicate species-region combinations for which the catching probability was too low to estimate trends.

species	region																																																		
bullrout	Ems-Dollard	?	+	+	+	+	++	++	++	++	+	?	?	?	?	?	?	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.2	1.1	3.4	?	1	0
	D. Wadden coast	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	?	?	?	?	?	?	?	?	?	0.9	2.2	4.4	?	13	2
	E Dutch Wadden S.	?	?	?	?	?	?	++	++	+	?	?	?	?	?	--	--	--	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	1.1	6.9	?	0	0
	W Dutch Wadden S.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.6	0.8	1.1	?	0	0
	S Dutch coast	?	?	?	?	?	?	+	+	+	+	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	+	+	+	+	+	+	1.7	3.4	6.3	++	12	1
common sea snail	Ems-Dollard	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.6	0.9	1.3	?	2	0
	D. Wadden coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	+	+	+	+	++	++	++	++	++	+	+	+	+	?	2.4	11.2	33.7	++	18	2
	E Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.4	2.6	9.1	?	2	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	0.4	1.6	?	2	0
	S Dutch coast	?	?	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	+	++	+	+	?	?	?	3.3	17.0	54.6	++	4	1
eelpout	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.4	1.5	4.2	?	0	0
	D. Wadden coast																																																24	2
	E Dutch Wadden S.	?	?	?	?	?	?	?	+	++	+	?	?	?	?	--	--	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1.0	3.3	8.0	+	0	0
	W Dutch Wadden S.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.6	0.7	0.9	--	0	0
	S Dutch coast	?	?	?	?	?	?	+	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.5	4.5	?	12	1
five-bearded rockling	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.3	1.0	2.4	?	1	0
	D. Wadden coast	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1.5	2.2	3.3	++	13	2
	E Dutch Wadden S.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.8	1.0	1.2	?	0	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.9	1.2	1.7	?	1	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.9	6.1	21.7	?	7	1
flounder	Ems-Dollard	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1.1	1.4	1.7	++	0	0
	D. Wadden coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.2	0.8	2.2	?	0	2
	E Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	0.7	1.1	1.6	?	0	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.3	0.8	1.7	?	0	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1.1	3.4	8.3	++	0	1
gobies sp	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.4	0.9	1.8	?	0	0
	D. Wadden coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.2	0.8	2.3	?	1	2
	E Dutch Wadden S.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.8	1.1	1.5	?	2	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	+	+	+	+	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.6	1.1	1.8	?	1	0
	S Dutch coast	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9	1.1	1.4	?	0	1
hooknose	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	+	+	+	+	?	?	1.6	4.7	11.2	++	0	0
	D. Wadden coast	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.7	0.9	1.2	?	0	2
	E Dutch Wadden S.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	0.7	1.0	-	0	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	0.0	0.3	1.4	?	0	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	+	+	+	+	+	?	?	?	?	1.2	3.4	7.8	++	1	1
pipefish sp	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	+	++	++	++	++	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	1.3	5.2	?	1	0
	D. Wadden coast	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1.4	2.0	2.7	++	2	2
	E Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.3	1.4	?	0	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	0.5	1.6	?	0	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.9	1.5	2.4	?	2	1
rock gunnel	Ems-Dollard	?	?	?	+	+	+	++	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.5	4.3	?	11	0
	D. Wadden coast																																																24	2
	E Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.8	13.7	?	8	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	0.7	1.1	1.7	?	0	0
	S Dutch coast																																																25	1
sandeel sp	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.9	2.6	6.1	?	10	0
	D. Wadden coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.2	1.2	4.4	?	1	2
	E Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	?	?	?	?	?	1.0	1.7	2.6	?	4	0
	W Dutch Wadden S.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1.1	1.4	1.9	++	0	0
	S Dutch coast	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1.1	1.5	1.9	++	0	1

Table 4. Results of trend analyses of marine juvenile species ordered alphabetically. The classification (as per Soldaat *et al.* (2007)) of the trends is given: ++ strong increase, + moderate increase, -- strong decrease, - moderate increase, - moderate decrease, 0 stable , ? uncertain. Yearly change rate (the smoothed population number in the last year compared with the smoothed population number in the first year, where >1 means increase and <1 decrease of population) in the last decade with range are given in the three but last columns. The trend classification as well as the number of zeros and missing values are given in the final three columns. Empty lines indicate species-region combinations for which the catching probability was too low to estimate trends.

species	region																																																	
bib	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.4	0.9	18	?	12	0
	D. Wadden coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	-	-	-	-	--	--	--	--	--	--	--	--	--	--	-	-	-	-	?	?	?	?	?	?	?	0.0	0.1	0.9	--	2	2
	E Dutch Wadden S.	?	?	?	?	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.2	7.0	?	7	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	-	-	-	-	-	-	-	--	-	-	-	-	-	-	?	?	?	?	0.0	0.0	0.7	--	2	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	-	-	-	-	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	0.0	0.1	16	?	1	1
brill	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.4	15	4.1	?	20	0
	D. Wadden coast	?	?	?	?	?	+	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	0.9	3.3	?	5	2
	E Dutch Wadden S.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	12	19	2.7	++	10	0
	W Dutch Wadden S.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.7	10	15	?	3	0
	S Dutch coast	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	12	19	2.8	++	11	1
cod	Ems-Dollard	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1	0.3	0.8	--	6	0
	D. Wadden coast	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.3	2.1	7.6	--	3	2
	E Dutch Wadden S.	--	--	?	?	++	++	++	+	?	?	--	--	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.6	13.8	?	1	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	-	-	-	?	?	?	?	?	?	?	?	?	?	0.0	0.1	11	?	5	0
	S Dutch coast	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.7	10	14	?	1	1
dab	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	--	--	--	--	--	--	--	--	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.9	14.6	?	0	0
	D. Wadden coast	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.3	0.7	12	?	0	2
	E Dutch Wadden S.	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.0	0.0	0.0	--	0	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	-	-	-	--	--	--	--	--	--	--	--	--	--	--	-	-	?	?	?	0.0	0.0	0.5	--	2	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	0.5	15	?	0	1
greater sandeel	Ems-Dollard																																																38	0
	D. Wadden coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.2	19	7.4	?	1	2
	E Dutch Wadden S.																																																25	0
	W Dutch Wadden S.	?	?	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.4	10	2.2	?	4	0
	S Dutch coast	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	+	+	+	+	+	+	+	+	+	+	16	2.1	2.7	++	7	1
herring	Ems-Dollard	++	++	++	++	++	++	++	++	++	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.2	10	3.3	?	1	0
	D. Wadden coast	?	?	?	?	?	?	++	++	++	++	?	?	?	?	--	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.5	2.9	?	0	2
	E Dutch Wadden S.	?	?	?	++	++	++	++	++	++	++	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.5	2.7	?	0	0
	W Dutch Wadden S.	?	?	?	+	+	++	++	++	++	++	++	++	++	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	0.6	17	?	0	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.4	19	?	0	1
plaice	Ems-Dollard	?	?	?	?	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.6	16	3.5	?	0	0
	D. Wadden coast	--	--	--	-	?	?	?	++	++	++	++	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	0.2	0.8	--	0	2
	E Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.3	12	3.2	?	0	0
	W Dutch Wadden S.	?	?	?	?	?	+	+	++	++	++	+	+	?	?	?	?	?	?	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	0.6	19	?	0	0
	S Dutch coast	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9	11	13	?	0	1
sole	Ems-Dollard	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	0.6	10	-	0	0
	D. Wadden coast	-	-	-	-	-	-	-	-	-	-	-	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.1	0.2	0.4	--	0	2
	E Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.8	3.1	8.5	?	0	0
	W Dutch Wadden S.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	--	--	0.2	0.4	0.6	--	0	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	12	5.2	?	0	1
tub gurnard	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	+	+	+	+	+	?	?	?	?	?	?	?	?	10	3.5	9.1	?	16	0
	D. Wadden coast	?	?	?	?	?	?	?	?	?	?	?	?	?	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	0.8	3.0	?	3	2
	E Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	16	25.5	###	++	19	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.8	14	2.3	?	11	0
	S Dutch coast	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	11	17	2.5	++	10	1
whiting	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.1	12	5.1	?	0	0
	D. Wadden coast	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.7	10	13	?	0	2
	E Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	--	--	--	--	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	14	9.0	?	0	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	-	-	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	0.1	0.5	19	?	0	0
	S Dutch coast	?	?	?	+	+	++	+	+	?	?	?	?	?	-	--	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.8	2.7	7.0	?	0	1

Table 5. Results of trend analyses of marine seasonal migrants (sprat), diadromous species (eel, smelt) and marine advantageous (common dragonet) species ordered alphabetically. The classification (as per Soldaat *et al.* (2007)) of the trends is given: ++ strong increase, + moderate increase, -- strong decrease, -moderate increase, - moderate decrease, 0 stable , ? uncertain. Yearly change rate (the smoothed population number in the last year compared with the smoothed population number in the first year, where >1 means increase and <1 decrease of population) in the last decade with range are given in the three but last columns. The trend classification as well as the number of zeros and missing values are given in the final three columns. Empty lines indicate species-region combinations for which the catching probability was too low to estimate trends.

species	region																																																	
sprat	Ems-Dollard	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.2	17	?	2	0
	D. Wadden coast	?	?	?	?	?	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.6	3.2	?	0	2
	E Dutch Wadden S.	?	++	++	++	++	++	++	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.6	7.1	?	1	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.1	15	?	3	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.3	11	2.9	?	0	1
eel	Ems-Dollard	?	?	?	?	?	?	?	++	++	++	++	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.0	11	?	14	0
	D. Wadden coast	-	-	-	-	-	-	-	-	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	?	?	?	?	?	0.0	17	0.1	--	22	2
	E Dutch Wadden S.	?	?	+	++	++	?	?	?	?	?	?	?	?	?	-	--	--	--	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.0	0.4	--	13	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	--	--	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.0	15	?	10	0
	S Dutch coast	?	?	?	?	?	?	?	?	++	++	+	?	?	?	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.6	###	?	13	1
smelt	Ems-Dollard	++	++	++	++	++	++	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.8	2.0	4.1	?	1	0
	D. Wadden coast																																																28	2
	E Dutch Wadden S.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	11	15	2.1	++	2	0
	W Dutch Wadden S.	?	+	+	++	++	++	++	++	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.3	14	?	1	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.4	3.0	113	?	21	1
common dragonet	Ems-Dollard																																																27	0
	D. Wadden coast	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.8	11	14	?	0	2
	E Dutch Wadden S.																																																32	0
	W Dutch Wadden S.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.0	0.3	13	?	9	0
	S Dutch coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0.9	12	17	?	0	1

FIGURE CAPTIONS

Figure 1. Map of the study area with the five regions used in the analyses indicated and the location of the fyke on the south tip of Texel.

Figure 2. Trends of (square 4^{th} root transformed) total fish biomass in the different regions. The line indicates the trend model, the grey area the 95% confidence intervals.

Figure 3. Trends in biomass of the 18 species contributing most to total biomass

Figure 4. Trends of (square 4^{th} root transformed) densities of 10 resident species. The line indicates the trend model, the grey area the 95% confidence intervals.

Figure 5. Trends of (square 4^{th} root transformed) densities of 10 marine juvenile species. The line indicates the trend model, the grey area the 95% confidence intervals.

Figure 6. Trends of (square 4^{th} root transformed) densities of diadromous, marine advantageous and marine seasonal migrant species. The line indicates the trend model, the grey area the 95% confidence intervals.

Figure 7. Timing of species in the continuous fyke series to the date of the DFS survey. White dots indicate that the timing of the DFS survey for each species-year combination fall within the period between first and last observation in the fyke series. Black dots indicate that DFS timing is outside this window, and grey dots indicate there is no information on first or last observation in the fyke series.

Figure 8. Mean normalised trends of fish species categorised in five guilds: ca=catadromous/anadromous, mj=marine juveniles, ma=marine advantageous, er=estuarine resident, ms=marine seasonal migrant.

Figure 9. Densities of fish of different length classes in the five areas.

Figures

Figure 1

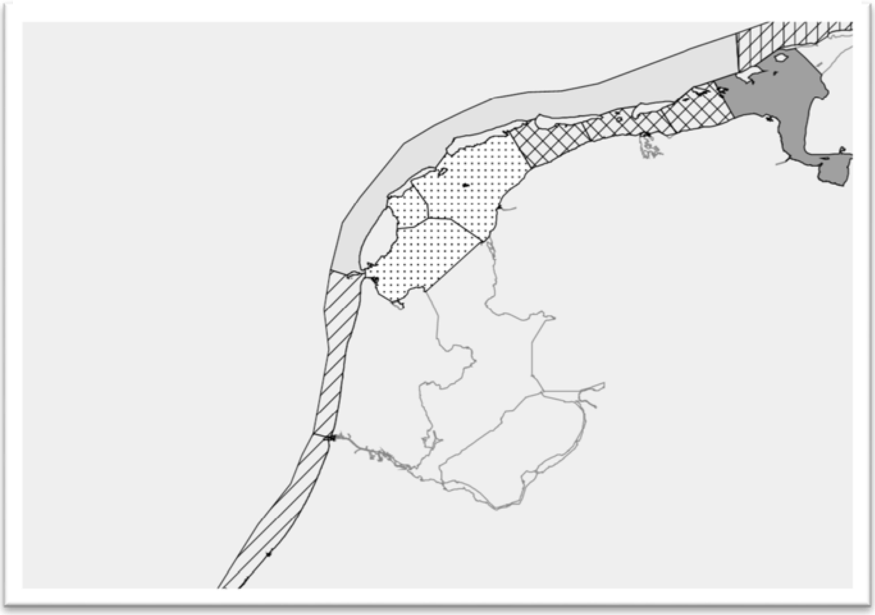
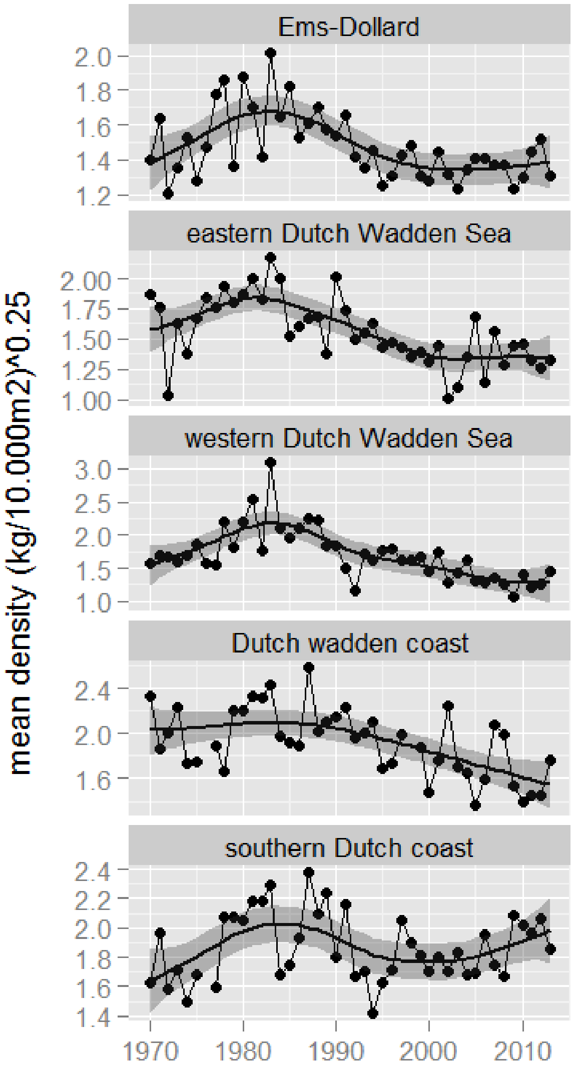


Figure 2



Ems-Dollard
eastern Dutch Wadden Sea
western Dutch Wadden Sea
Dutch wadden coast
southern Dutch coast
mean density (kg/10.000m2)^0.25
2.0
1.8
1.6
1.4
1.2
2.00
1.75
1.50
1.25
1.00
3.0
2.5
2.0
1.5
1.0
2.4
2.0
1.6
2.4
2.2
2.0
1.8
1.6
1.4
1970
1980
1990
2000
2010

Figure 3

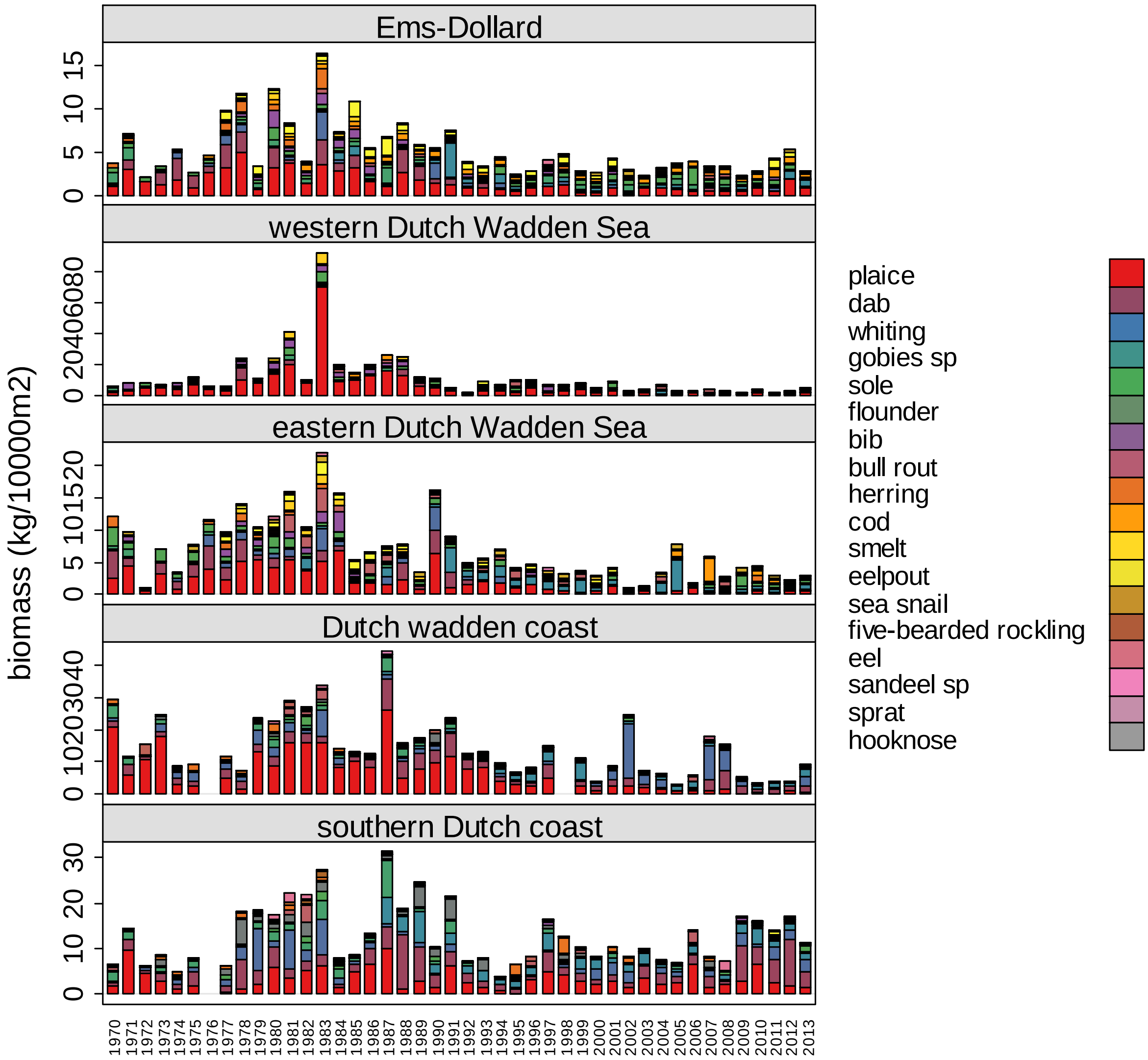
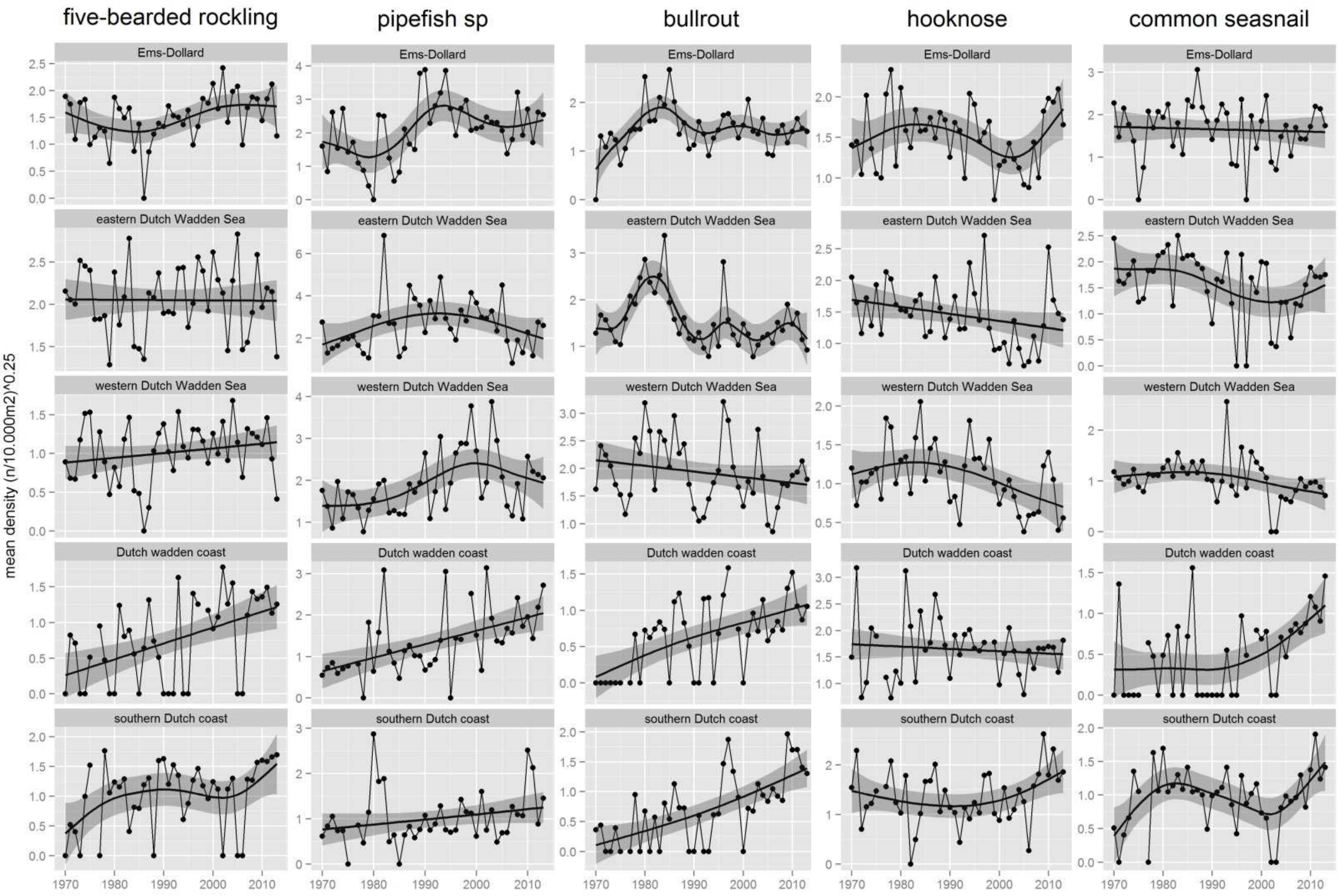

Ems-Dollard
western Dutch Wadden Sea
eastern Dutch Wadden Sea
Dutch wadden coast
southern Dutch coast
biomass (kg/10000m2)
plaice
dab
whiting
gobies sp
sole
flounder
bib
bull rout
herring
cod
smelt
eelpout
sea snail
five-bearded rockling
eel
sandeel sp
sprat
hooknose

Figure 4


five-bearded rockling
pipefish sp
bullrout
hooknose
common seasnail
Ems-Dollard
eastern Dutch Wadden Sea
western Dutch Wadden Sea
Dutch wadden coast
southern Dutch coast
mean density (n/10.000m2)^0.25
1970
1980
1990
2000
2010

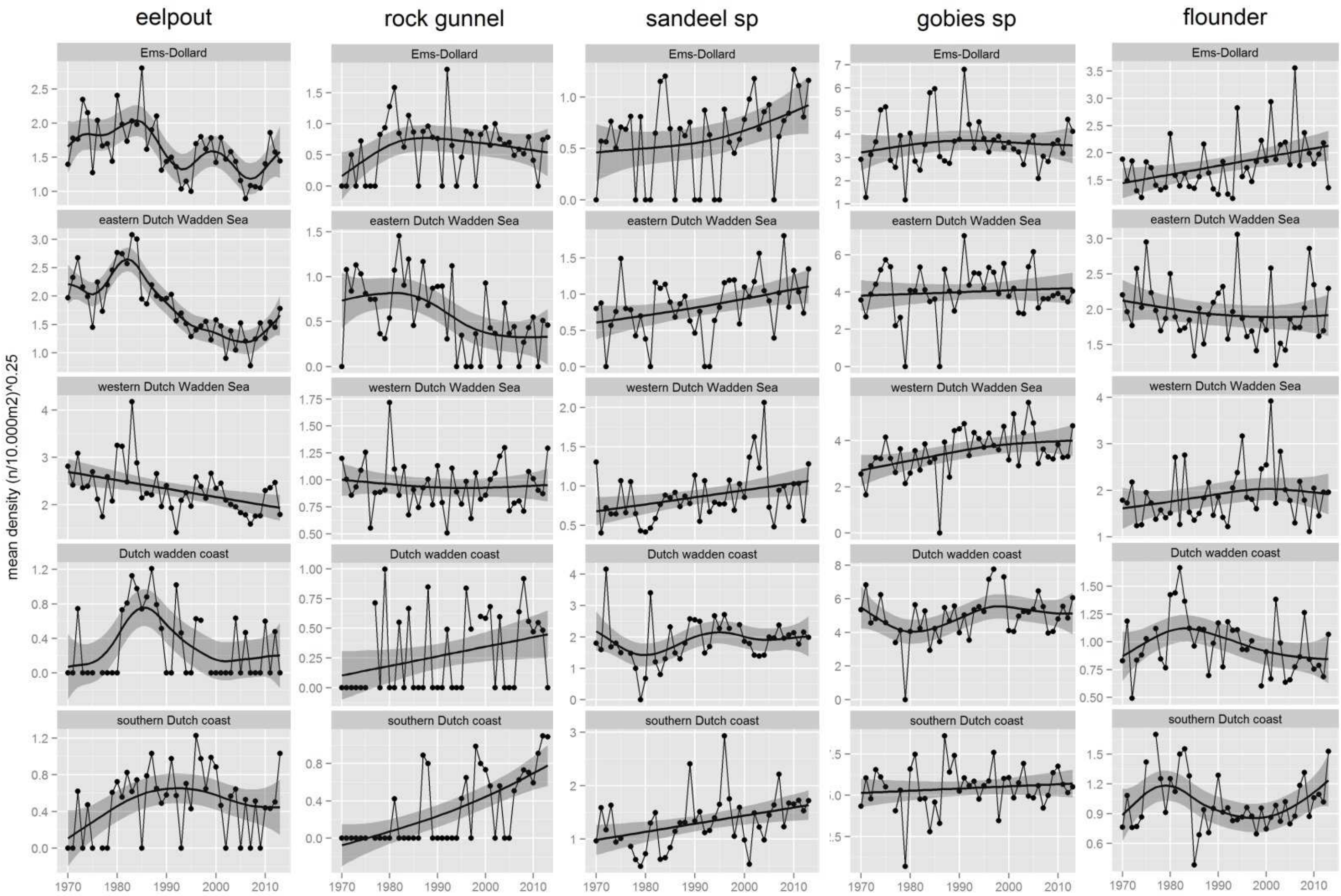
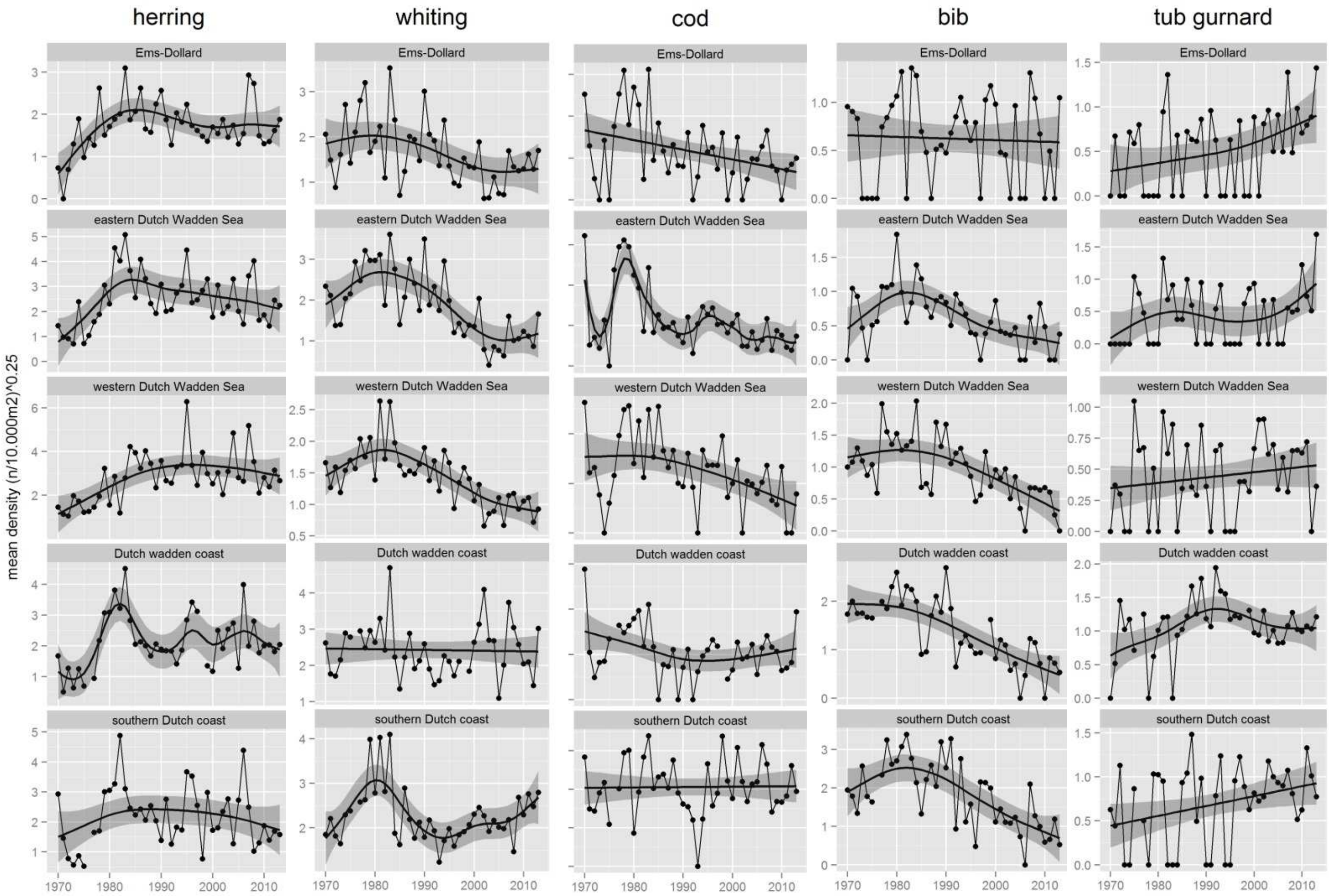

eelpout
rock gunnel
sandeel sp
gobies sp
flounder
Ems-Dollard
eastern Dutch Wadden Sea
western Dutch Wadden Sea
Dutch wadden coast
southern Dutch coast
mean density (n/10.000m2)^0.25
1970
1980
1990
2000
2010

Figure 5


herring
whiting
cod
bib
tub gurnard
Ems-Dollard
eastern Dutch Wadden Sea
western Dutch Wadden Sea
Dutch wadden coast
southern Dutch coast
mean density (n/10.000m2)^0.25
1970
1980
1990
2000
2010

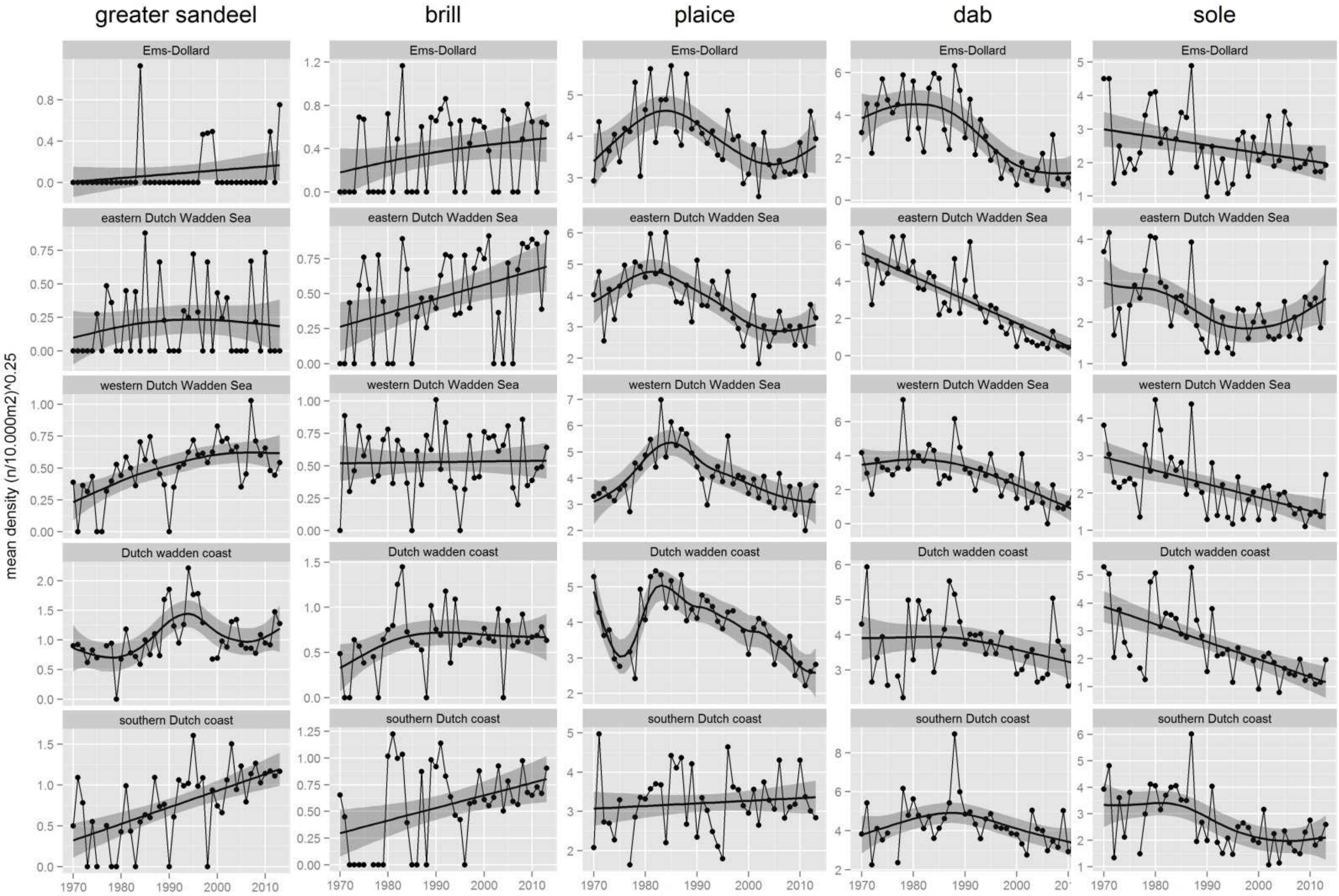

greater sandeel
brill
plaice
dab
sole
Ems-Dollard
eastern Dutch Wadden Sea
western Dutch Wadden Sea
Dutch wadden coast
southern Dutch coast
mean density (n/10.000m2)^0.25
1970
1980
1990
2000
2010

Figure 6

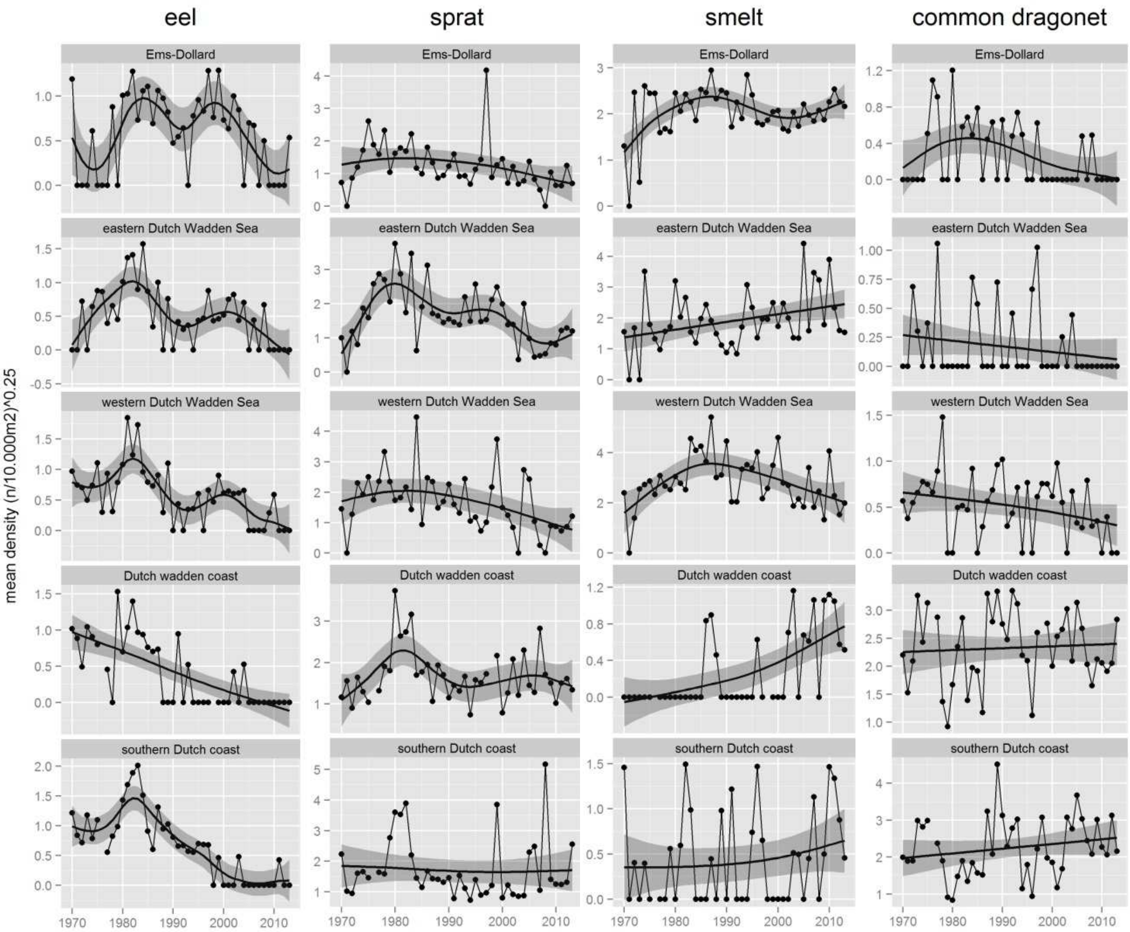

eel
sprat
smelt
common dragonet
Ems-Dollard
eastern Dutch Wadden Sea
western Dutch Wadden Sea
Dutch wadden coast
southern Dutch coast
mean density (n/10.000m2)^0.25
1970
1980
1990
2000
2010

Figure 7

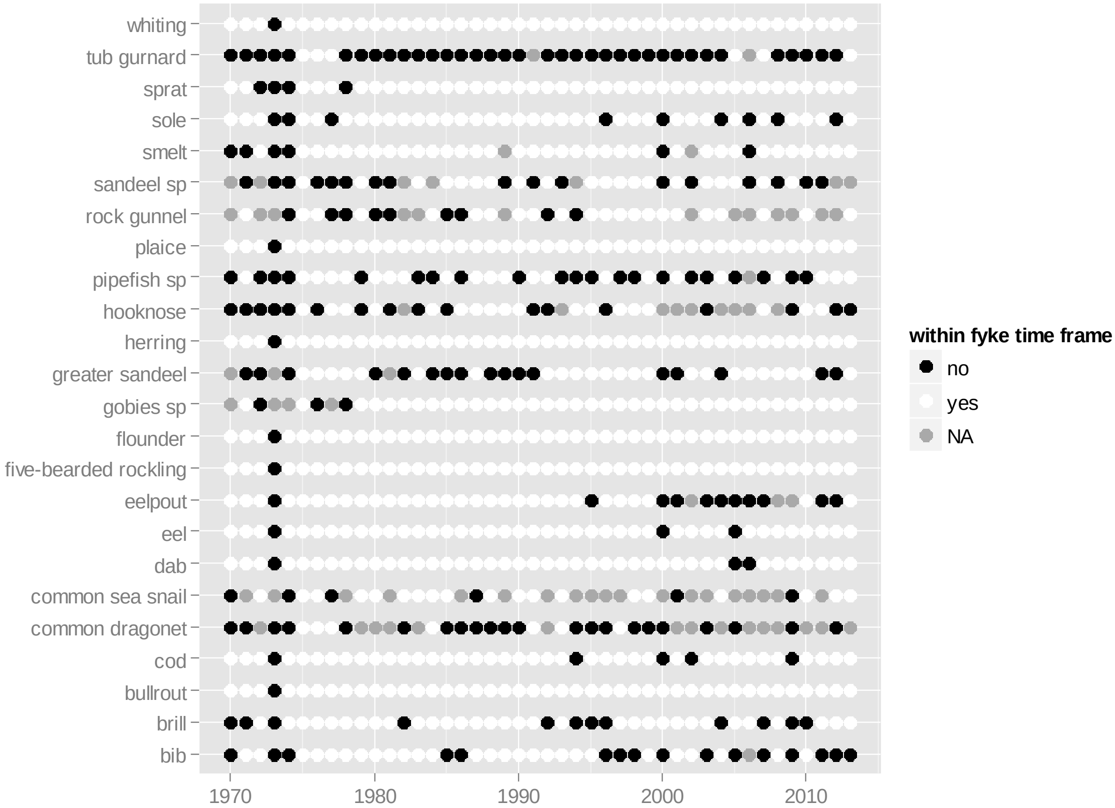
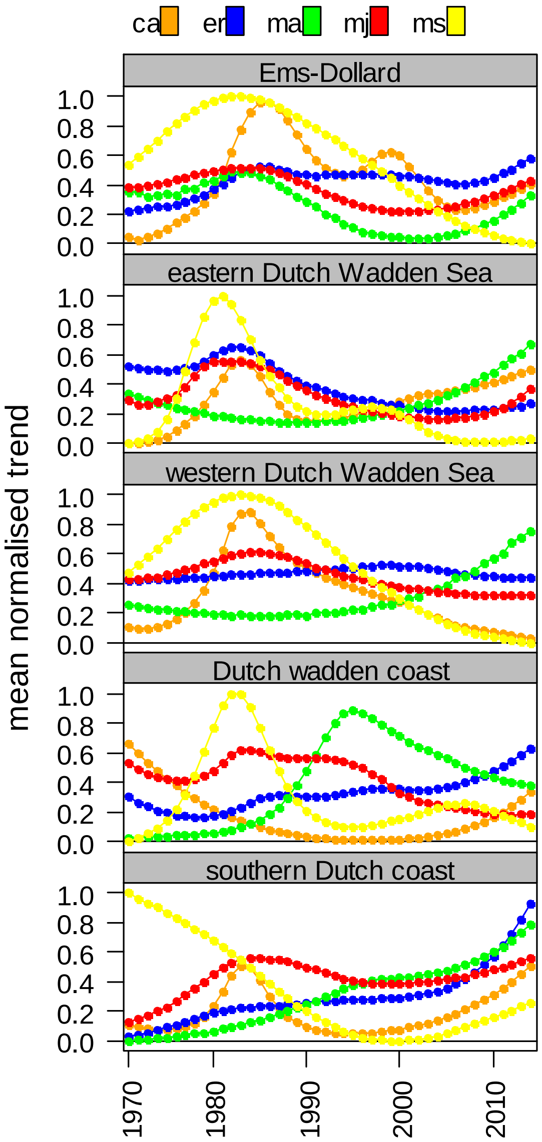
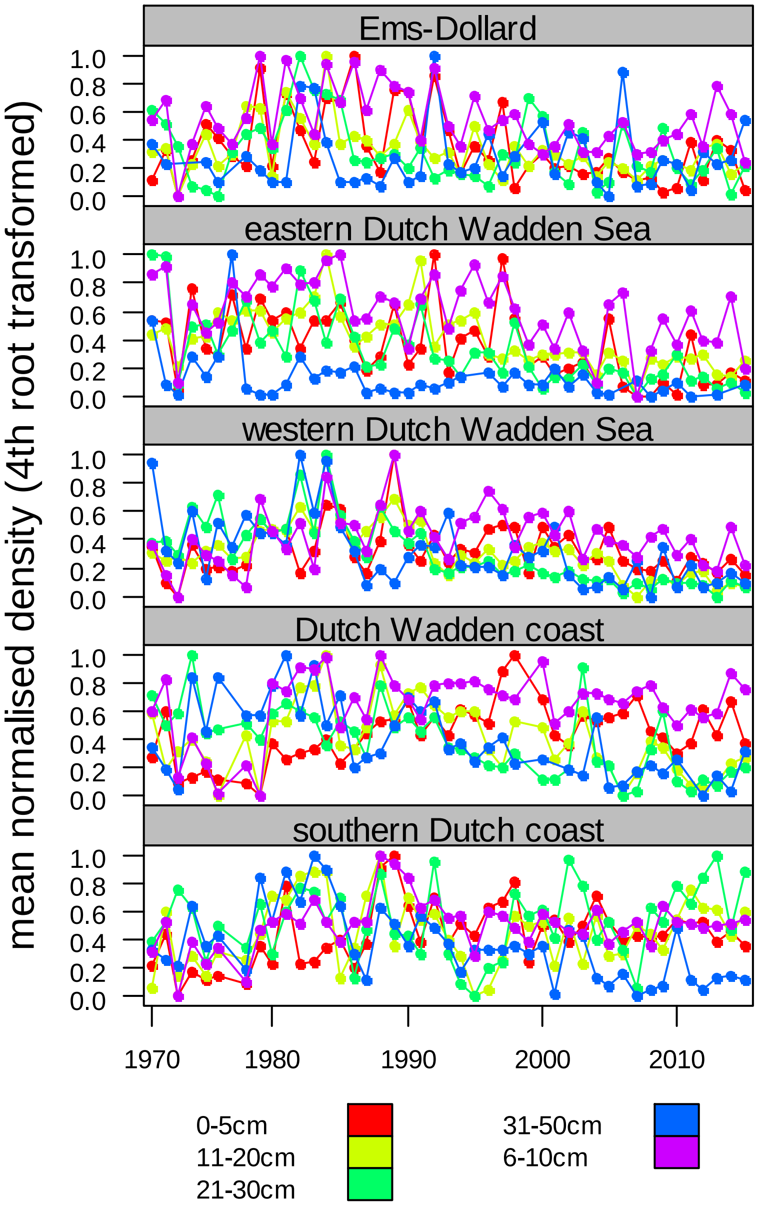

whiting
tub gurnard
sprat
sole
smelt
sandeel sp
rock gunnel
plaice
pipefish sp
hooknose
herring
greater sandeel
gobies sp
flounder
five-bearded rockling
eelpout
eel
dab
common sea snail
common dragonet
cod
bullrout
brill
bib
1970
1980
1990
2000
2010
within fyke time frame
no
yes
NA

Figure 8



ca
er
ma
mj
ms
Ems-Dollard
eastern Dutch Wadden Sea
western Dutch Wadden Sea
Dutch wadden coast
southern Dutch coast
mean normalised trend
1.0
0.8
0.6
0.4
0.2
0.0
1970
1980
1990
2000
2010

Figure 9


Ems-Dollard
eastern Dutch Wadden Sea
western Dutch Wadden Sea
Dutch Wadden coast
southern Dutch coast
mean normalised density (4th root transformed)
1.0
0.8
0.6
0.4
0.2
0.0
1970
1980
1990
2000
2010
0-5cm
11-20cm
21-30cm
31-50cm
6-10cm

Annex 5 Maunscript in preparation: Walraven *et al*.

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 in relation to climate change were studied using a 50-year (1960-2011) high resolution time series of daily kom-fyke catches in spring and autumn. Trends in the fish community were analysed for individual species in relation to species type (core or transient species) and biogeographic guild (northern or southern species) with respect to presence/absence, biomass, first appearance and last occurrence and duration. The analysis is restricted by the lack of basic information on physiological performance for most of the fish species. Climate change in the western Wadden Sea involved especially an increase in water temperature from 1980 onwards. Core species (present in most of the years, at least for 20 years) were the dominant group for both northern and southern species. Transient species were found only incidentally. Both the number of northern and southern species showed a significant trend over time: a dome-shaped curve with a decreasing for the 1990-ties onwards for the northern species and an increase in the 1980-ties followed by stabilization for the southern species. As a consequence, contribution of southern species became larger from the 1980-ties onwards. The relative importance of southern species also increased in terms of biomass. None of the southern species and only one northern species did show a negative relationship in first day of appearance over time. Shifts in last day of occurrence occurred in more species (6), however without any relationship to biogeographic guild. The fish community in the Wadden Sea appeared to be rather robust to date of first appearance and last occurrence, because for most of the species present, the Wadden Sea is not near the edge of their distributional range. A large group of relatively abundant species were often already caught at both the first day of fishing and the last day of fishing. However, nevertheless, the fish community has already shown some shifts, most striking in those individual species near their southern (the eelpout *Zoarces viviparous*) or northern (the sea bass *Dicentrarchus labrax*) edge of the distribution in the Wadden Sea, and showing the strongest respectively decrease and increase in biomass with climate change.

Keywords: long term changes; phenology; fish faunas; Wadden Sea; climate change;

1. Introduction

Coastal systems such as the Wadden Sea are already degrading from the medieval time onwards, with acceleration during the last 150 – 300 years (Lotze *et al*. 2006). This means that any study on long term changes in the fish community only represents a short snapshot in time and does not include the past historical state. The only reference points are the situation at the start of the series. The loss of memory or lack of information of the historical situation means that our references also suffer from what has been called in fishery science the phenomena of "shifting baselines" (Pauly, 1995): with each generation of scientists and fishermen the reference baseline of resources and abundances change or in other words: the length of the time series determines our historical reference point.

For the Dutch Wadden Sea, information on fish community is available from two ongoing monitoring series: the Demersal Fish Survey (DFS), a beam trawl survey in autumn each year, covering the subtidal and deeper tidal channels of the Wadden Sea and the coastal zone (Zijlstra 1972, Tulp *et al*. 2008) and the NIOZ fyke net series, daily fyke net catches in the subtidal in the western Wadden Sea in spring and autumn (Van der Veer et al., 2015), with reference points (starting dates) of respectively 1970 and 1960.

The DFS has been analysed for the period 1970 – 2006 and over this time period the demersal fish community consisting of 34 fish species showed patterns that varied widely among individual species whereby overall total fish biomass showed a dome shape pattern with an increase from 1970 to 1985 and a subsequent decline until the early 2000s. The best description was by models containing various categories of environmental variables. The NIOZ fyke net series comprise information about both the pelagic and demersal fish community. Both spring and autumn showed similar trends whereby total catch in biomass peaked in the late 1970s and also followed by a decrease from 1980 to the early 2000's present (van der Veer *et al*., 2015). As most likely explanatory variables increased water temperature, habitat destruction in the coastal zone (sand dredging and beach nourishment, fishing) and increased predation by top predators was suggested, superimposed on an effect of large-scale hydrodynamic circulation (van der Veer *et al*., 2015).

Although both the DFS and NIOZ fyke series suggest similar types of explanatory variables, the underlying mechanisms remain unclear, especially to what extend they hold true for individual species. Furthermore, the importance of species interactions (predator-prey relationships) is unknown and shifts in species phenology over time as a response to especially changes in water temperature in the area (van Aken, 2008b) might have affected the catches and hence observed patterns in biomass. In this paper, the focus is on fish phenology and the long-term patterns in fish phenology in the western Dutch Wadden Sea are analysed and discussed in relation to the observed eutrophication and climate change in the area. In a previous paper, a similar analysis has been performed for scyphomedusae catches in relation to climate change and eutrophication (van Walraven et al., 2015).

2. Conceptual framework

The conceptual framework built on a framework for the effect of climate change on fish populations (Rijnsdorp *et al*., 2009) and a previous analysis of long-term changes in the fish fauna in the western Dutch Wadden Sea (1960-2011), in which besides large-scale hydrodynamic circulation habitat destruction in the coastal zone (sand dredging and beach nourishment, fishing), increased predation by top predators, also increased water temperature were marked as potential explanatory variables (van der Veer *et al*. 2015).

Environmental water temperature and also salinity directly influences fish performance by affecting metabolism e.g. Fry, 1947, 1971). Species are characterized by species-specific temperature and salinity preference and tolerance ranges and in a temperate area as the Wadden Sea, a mixture of species with different biogeographic guild such as boreal (cold water) or Lusitanian (warm water) can be found (Yang, 1982). Based on the location of the Wadden Sea relative to the distributional range of a species, the fish fauna can be divided into core (being present in most of the years) and transient (being found irregularly based on prevailing environmental conditions) species (van der Veer *et al*. 2015).

The analysis of shifts in phenology of the fish fauna in the Wadden Sea due to climate change is based on the following observations:

[1] In estuarine areas such as the Wadden Sea the most important factors are changes in water temperature and in salinity;

[2] The temperate estuarine Wadden Sea shows a seasonal pattern in water temperature and to a lesser extent in salinity (van Aken 2008a,b);

[3] Shallow temperate estuarine areas such as the Wadden Sea are characterized by a more rapid cooling down and warming up than the coastal zone and as a consequence a seasonal shift in temperature gradient occurs with lower water temperature from October to April, and higher values from April to October (van Aken 2008b);

[4] During the last decades, an increase in water temperature by a few decrease Celcius has been observed in the western Wadden Sea (van Aken 2008b);

[5] Transient species will be more sensitive to climate change than core species;

[6] Cold and warm water species will show opposite reactions to climate change;

[7] Mobile pelagic species will be more sensitive to climate change than more sessile demersal species.

[8] Irreversible non-genetic adaptation to environmental conditions experienced during early development will affect temperature and salinity tolerance later on during juvenile and adult stage (Kinne 1962, van der Veer *et al*. 2000).

Some of these observations can be tested, which lead to the following hypotheses about impact of climate change in the Wadden Sea:

I. Trends in presence/absence of species

Number of northern cold water species will show a decreasing trend over time and number of southern species will show an increase over time. This trend will be stronger in transient species than in core species;

II. Trends in biomass

Biomass of northern cold water species will show a decreasing trend over time and biomass of southern species will show an increase over time. This trend will be stronger in transient species than in core species;

III. Trends in first appearance and last occurrence

With increasing temperature, first day of appearance of southern species will be earlier and last day of occurrence will be later in the year. No relationships with temperature are expected. For the core northern species, the temperate zone is within the distributional range and hence they will not be affected. Transient species will be more sensitive than core species.

3. Material and methods

3.1. Sampling

Since 1960, a kom-fyke trap has been operating at the entrance of the Marsdiep basin in the western Dutch Wadden Sea (Fig. **Fout! Verwijzingsbron niet gevonden.**). 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 see van der Veer *et al.* (1992). Fishing normally started in March - April and lasted until October. In winter the trap was removed because of possible damage by ice floes and from 1971 onwards no fishing took place during part of the summer because of fouling of the net and clogging by macroalgae and sometimes by 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 on alternate mornings. Here data for the period 1960 – 2013 were analysed, whereby catches were selected according to the following criteria:

-fishing duration less than 48 h (exclusion of 329 records)

-fishing duration longer than 12 h (exclusion of 1 record)

-no damage of the gear upon retrieval (loose mesh panels or tears) and/or no clogged with debris (exclusion of 53 records). In total, 6481 daily catches were available for further analysis.

All catches were sorted out immediately and identified 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 (see van der Veer *et al*. 2015). All information was stored in a database. 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).

Since for most species information on their physiological performance is lacking, species were characterized in line with a previous analysis (van der Veer et al. 2015) based on number of years found as core (≥ 20 y) or transient species (< 20 y), by mode of life (pelagic, demersal, benthopelagic) using Fishbase (www.fishbase.org) and their biogeographic guild (northern and southern species) after Daan (2006). All information is presented in Appendix A. The environmental parameters that were considered were also in line with the previous analysis (van der Veer *et al*. 2015) and included water temperature, salinity, obtained from long-term monitoring programmes at the NIOZ sampling jetty, located < 1 km east of the kom-fyke (van Aken 2008ab).

3.2. Data analysis

3.2.1. Trends in presence/absence of species

Species were split up according to their biogeographic guild into northern (N), southern (S) or in between (NS) and according to the number of years found in core and transient species. Subsequently, trends in northern species were compared with those for southern species for both core and transient species. Data for spring were taken because they represented to longest period of fishing (spring: 3 months; autumn: 2 months).

3.2.2. Trends in biomass

For each species, mean daily catch (kg wet mass d^{-1}) was determined for spring and autumn. Subsequently, total mean daily catch was estimated for both northern and southern species. Next, to correct for trends over time, the ratio of the total mean daily catch of the northern and the southern species was computed. Similar as for trends in presence/absence of species, data for spring were taken.

The min/max auto-correlation factor analysis showed a first axis represented a decrease from the 1960s followed by stabilization from the mid-1990s and a second trend with an increase with a maximum around 1980 followed by a steady decrease (Fig. 2). Increased water temperature was listed as potential explanatory factor for the first axis (van der Veer et al. 2015). Therefore, for all species canonical correlations between trends in mean biomass and the first axis were computed and the correlation coefficient were compared between northern and southern species, whereby for northern species positive relationships were expected and for southern species negative ones.

3.2.3. Trends in first appearance and last occurrence

For each species, the first day of appearance and the last day of occurrence in each year were determined. If this corresponded with the first and/or the last day of fishing, that year was excluded from further analysis. Long-term changes in first appearance and last occurrence were described by a series of models. The first model (M_0) is a linear model which checks for a possible interaction between temperature and salinity:

$$M_0 : F_t = a + Temperature_t + Salinity_t + Temperature_t * Salinity_t + \varepsilon_t$$

The second model M_1 hypothesised that temperature and salinity have additive effects on the date of first/last/ occurrence:

$$M_1 : F_t = \alpha + f(Temperature_t) + f(Salinity_t) + \varepsilon_t$$

where F_t is the date of occurrence in year t ; t = 1960, ..., 2011. The terms $f(Temperature_t)$ and $f(Salinity_t)$ are smoothing functions of temperature (index of seawater temperature) and salinity respectively. The next models hypothesised that either temperature or salinity in winter (M_2 and M_3) or in spring (M_4 and M_5) drives changes in day of first occurrence, and in in autumn (M_6 and M_7) drives changes in day of last occurrence, and they all used a single smoothing function for the covariate. It may well be that other factors are important and therefore we also considered models of the form:

$$M_8 : F_t = \alpha + f(Year_t) + \varepsilon_t$$

whereby *f*(*Year*) is a smoother of time and represents the long-term trend in the data (model M_8). Cross-validation was used to estimate the optimal amount of smoothing and a thin-plate regression spline was applied (Wood, 2006). The residual terms ε_t were assumed to be normally distributed and to have mean 0 and variance σ^2. All models were fitted and compared with each other using the corrected Akaike's Information Criterion (AICc) (Burnham and Anderson 2002). Finally, the models were also compared with linear regression models fitted using the same covariates.

Models for first day of appearance were run for the spring sampling (until day 175) with mean winter values for temperature and salinity; for last day of occurrence the autumn sampling was taken (after day 175) and mean spring, summer or autumn values were used for temperature and salinity instead of winter values.

3.2.4. Trends in peak occurrence

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. The long-term changes in the timing of peak occurrence were analysed with the same model M_8 as for first occurrence.

3.3. Statistical analysis

Data explorations and calculations were carried out in R version 3.0.2 (R Core Team, 2014). The data were explored following the protocol described by Zuur *et al.* (2010). Scatterplots of first occurrence versus time and versus the covariates showed clear non-linear patterns and therefore generalised additive models (GAM) were applied (Wood, 2006) using a Normal distribution with log-link. GAM assumes homogeneity, normality and independence of residuals. To verify these assumptions, residuals of the models were inspected for temporal correlation using the auto-correlation function. Normality and homogeneity of variance of the residuals was also verified using histograms and plots of residuals versus fitted values. The GAM's were applied with the gam functions in the mgcv package (Wood, 2006). Plots were created with the ggplot2 package (Wickham, 2009).

4. Results

4.1. Environmental conditions

The environmental variables showed different temporal patterns (Fig. 3). Both sea water temperature and salinity varied considerably over the years, whereby both winter, spring and summer temperature did show an increase time in contrast to salinity.

4.2. Trends in phenology

4.2.1 Trends in presence/absence of species

Core species were the dominant group for both northern and southern species in spring (Fig. 4). Transient species were found only incidentally with a frequency of between 0 and a few species per year. Both northern and southern species a showed a significant trend over time, respectively (GAM $p<0.001$, $r^2= 0.48$ and $p<0.001$, $r^2=0.39$), with a dome-shaped curve with a decreasing trend for the 1990-ties onwards for the northern species and a trend with an increase in the 1980-ties followed by a stabilization for the southern species. As a consequence, the ratio between northern and southern species also showed a significant relationship ($p<0.001$, $r^2= 0.48$) with an increase until about 1980 followed by a steady decrease (Fig. 5).

4.2.2. Trends in biomass

Mean total daily biomass showed a similar pattern for both the northern and the southern species with maximum values around 1980 followed by a steady decrease to a few kg d^{-1} in recent years (Fig. 6). The ratio of mean total daily biomass between northern and southern species varied considerably over the years between 1 and 6, especially until 1990. Hereafter, the ratio dropped to below 1.0, indicating that biomass of southern species became dominant. These changes in the ratio over time were significant ($p<0.001$, $r^2= 0.48$).

Boxplot of the canonical correlations between trend in mean biomass and the first axis did not show significant differences between northern and southern species (Fig. 7), although on average correlations were more positive for northern species which for southern species also negative values were found (Fig. 8).

The strongest correlations were found for individual species near their southern (the eelpout *Zoarces viviparous*) or northern (the seabass *Dicentrarchus labrax*) edge of the distribution in the Wadden Sea, showing the strongest respectively decrease ($r^2=-0.70$) and increase in biomass ($r^2=0.60$) with climate change.

4.2.3. Trends in first appearance, last occurrence and peak occurrence

Number of observations was too low to analyse trends in first appearance and last occurrence in transient species. Only core fish species (occurring in more than 20 years; see Fig. 3 in Van der Veer et al. 2015) were included (47 species). Some species had to be removed from the analysis (pelagic: *Alosa fallax, Clupea harengus, Osmerus eperlanus, Sprattus sprattus;* demersal: *Anguilla anguilla, Chelon labrosus, Ciliata mustela, Gadus morhua, Limanda limanda, Myoxocephalus scorpius, Platichthys flesus, Pleuronectes platessa, Salmo trutta trutta, Zoarces viviparous*). These species were relatively abundant over the years and often already caught at both the first day of fishing and the last day of fishing (Fig. 9). For the remaining species (Fig. 10) the criterion of at least 20 observations was applied for first day of appearance and the last day of occurrence. As a consequence, first day of appearance and last day of occurrence could be analysed for respectively 31 and 27 species. An overview of the differences between the 1980's and the last decade is presented in Appendix 1 – 3.

4.2.3.1. First day of appearance

In total 31 species (9 pelagic, 4 benthopelagic and 18 demersal) were analysed for trends in first day of occurrence. Significant relationships were found in 19 species (Table 1). Most relationships found were with either winter or spring temperature (12), compared to 6 with either wither or spring salinity and two with a significant year effect. In most cases inverse relationships were observed (12 versus 5 times), implying an earlier first day of occurrence with higher temperature or salinity.

First day of occurrence showed an inverse relationship with winter or spring temperature in 5 out of 9 pelagic species, in two cases in interaction with winter salinity. For the 17 demersal species, in 4 cases an inverse relationship with winter or spring temperature was found and in 2 cases a positive relationship. In three cases a relationship with salinity was found. No clear differences between northern and southern species were found, except for the fact that in two cases winter temperature was a significant factor for southern species.

None of the southern species did show a negative relationship between first day of appearance and year (Model M_6). Also no negative relationships with year were found for the northern species.

4.2.3.2. Last day of occurrence

For 25 species (8 pelagic, 17 demersal), trends in last day of occurrence could be analysed (Table 2). Significant relationships were found in 14 species. Most relationships found were with year (6). Furthermore, relationships were present with winter temperature and salinity (2), winter (1) and spring (1) temperature and winter (1) and spring (3) salinity. In most cases positive relationships were found implying that last day of occurrence increased with temperature, salinity or over the years.

No trends were found in 11 species. For 4 pelagic and 1 demersal species, last day of occurrence increased significantly over time (Table 2). This group included three northern species and 2 southern species. However, in two of the northern species (*Belone belone* and *Scomber scombrus*) last day of occurrence decreased in recent years. Most northern species did not show any relationship at all.

4.2.4. Trends in peak occurrence

For the For 33 species, trends in peak occurrence in relation could be analysed. Significant relationships were found in 4 species (Table 3), of which 3 were negative relationships (*Belone belone*, *Scomber scombrus*, *Syngnatus acus* and *Trigla lucerna*). No relationship with species type (northern versus southern species, pelagic versus demersal species) could found.

5. Discussion

The expectations of a potential impact of climate change on fish phenology is in the western Dutch Wadden Sea in relation to climate change are based on physiological mechanisms and principles and various observations of recent shifts in fish population that were attributed to global change, especially warning (a.o. Rijnsdorp *et al*. 2009).

The fact that 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) implies that climate change and especially global heating will seriously effect fish phenology. On the other hand, any predictions or analysis is complicated by these species and stage specific requirements. 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. Build on this, quantitative frameworks and budgets have been build, first static energy budgets (Hoar & Randell 1969, Brown 1979, Brett & Gloves 1979) and more recently dynamic energy budgets that are able to 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 for most species and stages is the availability 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). As a result, predictions of the impact of climate change remain restricted to qualitative hypotheses (c.f. Rijnsdorp *et al*. 2009). Special attention should be given to irreversible non-genetic adaptation, whereby environmental conditions experienced during early development affect temperature and salinity tolerance later on during juvenile and adult stage (Kinne 1962, van der Veer *et al*., 2000). The present study still represents a black box approach and lacks underlying species-specific quantitative mechanisms.

The conceptual framework in this study is restricted to differences in species complex whereby the focus is on especially effect of mode of living (pelagic versus benthopelagic and demersal species) and biogeographic guild (northern cold water adapted versus southern (warm water adapted species) on both transient and core species. Transient species were thought to represent species to be near the edge of the distribution in the Wadden Sea and therefore being most sensitive to climate change. However, despite the relatively long time series of 50 years, for almost all transient species the number of observations were too low to permit any analysis at all. The remaining core species –those being present in at least 20 years- are representing species whereby the Wadden Sea is not at the edge of their distributional range (see www.fishbase.org). A group of 14 core species had to be removed from the analysis because these species were present and often already caught at both the first day of fishing and the last day of fishing. The remaining core species were not equally representing pelagic, benthopelagic and demersal species, nor northern versus southern species. It is unclear to what extend this has affected the results.

For the remaining core species, three aspects were tested in relation to climate change: trends in presence/absence of species, trends in biomass and trends in first appearance, last occurrence and peak occurrence. Overall, the mode of living (pelagic versus demersal) did not seem to be of influence maybe because of the low number of species or because (seasonal) mobility in both groups is large enough to cope with environmental conditions. In contrast biogeographic guild suggests shifts in the fish community in the western Wadden Sea. Despite a decrease in both northern and southern species especially in biomass, the relative contribution of southern species has increased from the 1980-ties onwards parallel with increased water temperature and in line with the expectations. However, these shifts were not apparent in first day of appearance and last day of occurrence. None of the southern species showed a negative relationship in first day of appearance over time and only one northern species did. Shifts in last day of occurrence occurred in more species (6), however without any relationship to biogeographic guild.

The various relationships with temperature and salinity are not in line with the expectations. Any impact of climate change would act on earlier appearance or later departure from the Wadden Sea, however under the assumption that thermal preferences and tolerance did remain the same. Shifts in the temperature conditions experienced during egg and larval stages might via irreversible non-genetic adaptation (Kinne, 1962; van der Veer *et al*., 2000) have change thermal preferences and tolerance.

At the species level, the fish community has already shown some clear shifts: species near their southern (the eelpout *Zoarces viviparous*) or northern (the seabass *Dicentrarchus labrax*) edge of the distribution in the Wadden Sea, and showing respectively the strongest decrease and increase in biomass with climate change. Therefore, the next step might be to focus on individual species. However, the question remains whether future changes in species composition and phenology can be predicted from physiological requirements and performance of the individual species? Also whether trends in presence/absence of species, trends in biomass and trends in first appearance and last occurrence are the most sensitive parameters or whether further analyses should focus more on biological parameters (such as growth) and biological interactions such as predator-prey interactions.

Finally, it remains open for discussion whether the impact of climate change can be studied at a more detailed level than species composition. In spring when water temperatures are rising, immigrating fish are blocked offshore until April by lower water temperatures inside the Wadden Sea and in a similar way in autumn by lower water temperatures offshore until October (van Aken, 2008b). This raises the question what exactly will be the temperature trigger for these migrating temperate fish communities.

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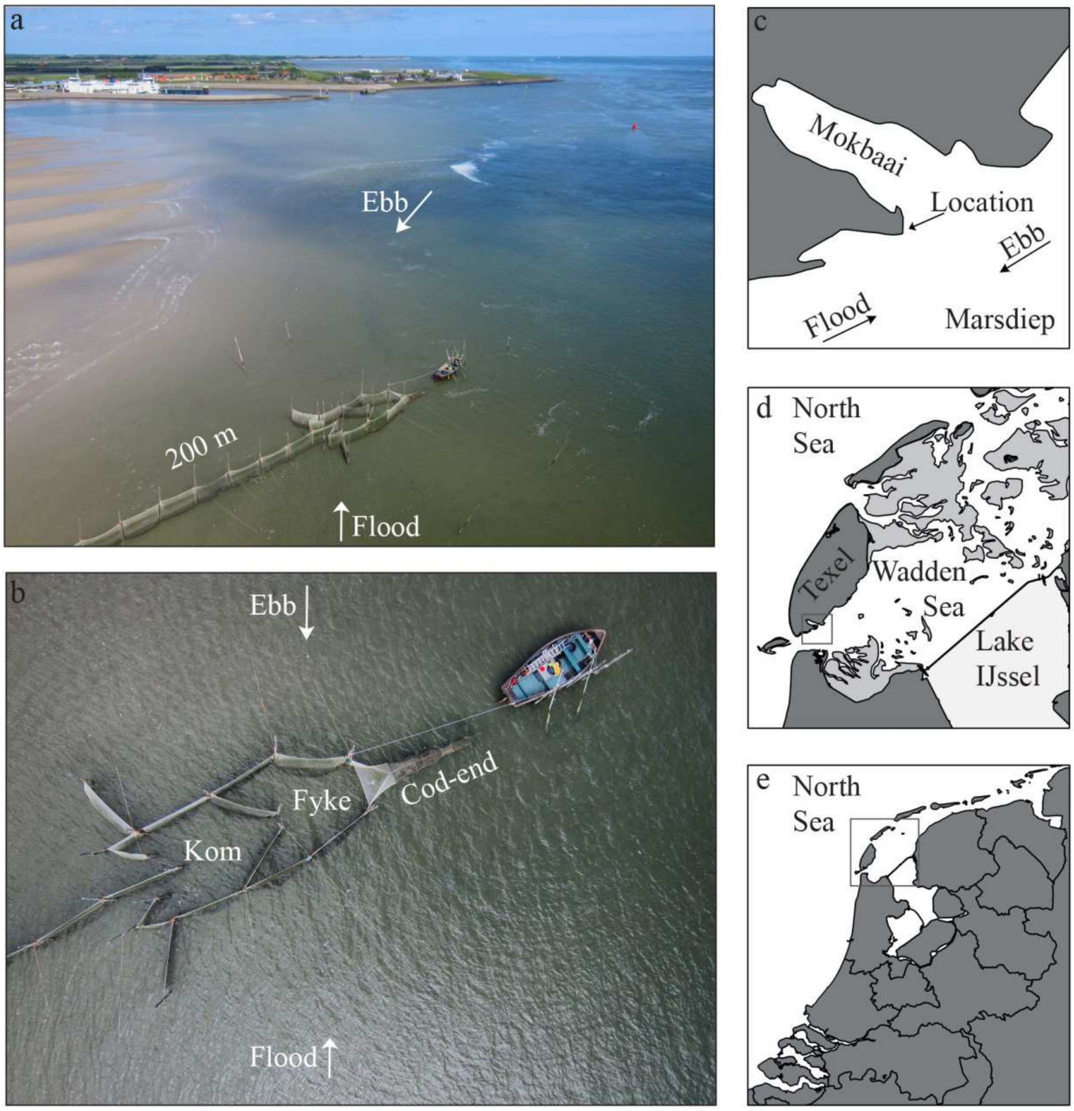


Figure 1 The NIOZ kom-fyke in the western Dutch Wadden Sea. Dark gray areas are land, light gray areas are intertidal flats. (a): aerial photograph showing the location of the kom-fyke; (b): aerial photograph showing the design of the kom-fyke. (c): location of the study area in the Netherlands; (d): location of the study area in the western Wadden Sea; (e): location of the kom-fyke (arrow). 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.

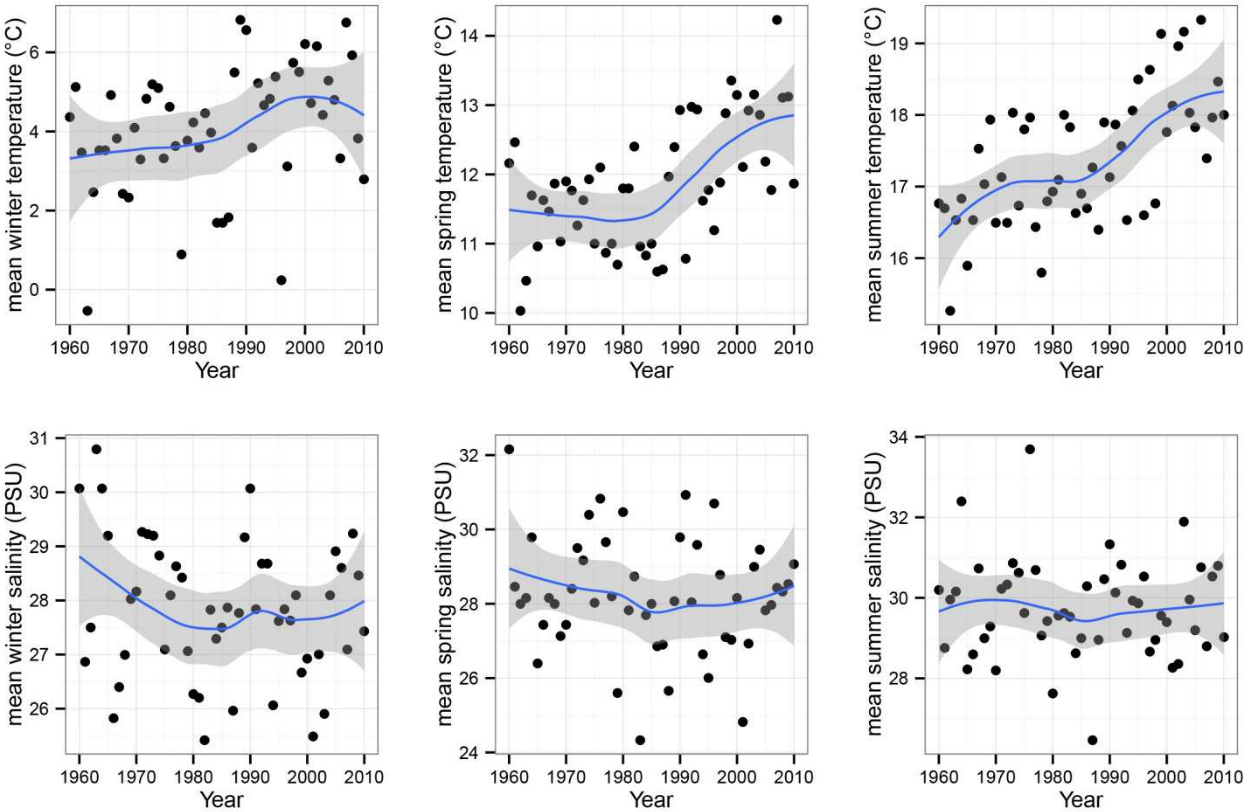


Figure 2 Trends in environmental conditions in the western Dutch Wadden Sea between 1960 and 2011. Seasonal means are for the following months: winter: January - March, spring: April - June, summer: July - September. For references see text. The solid line through the data is a LOESS smoother (LOESS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

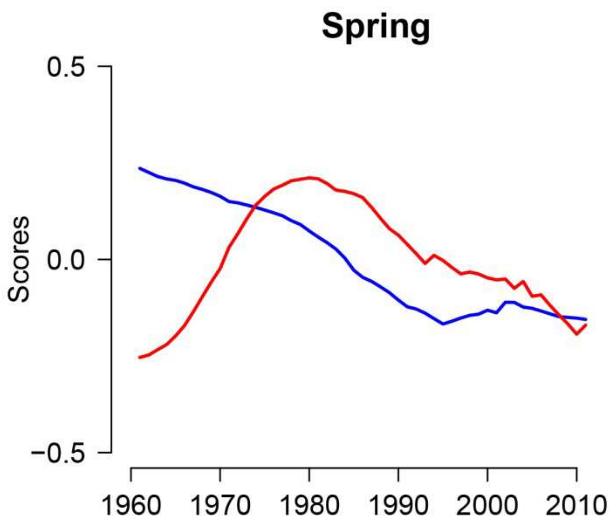


Figure 3. Min/max auto-correlation factor analysis. First (blue) and second (red) MAFA axes of the common trends in the time series of the biomass of the fish species that occurred in the kom-fyke in at least 10 years for spring.

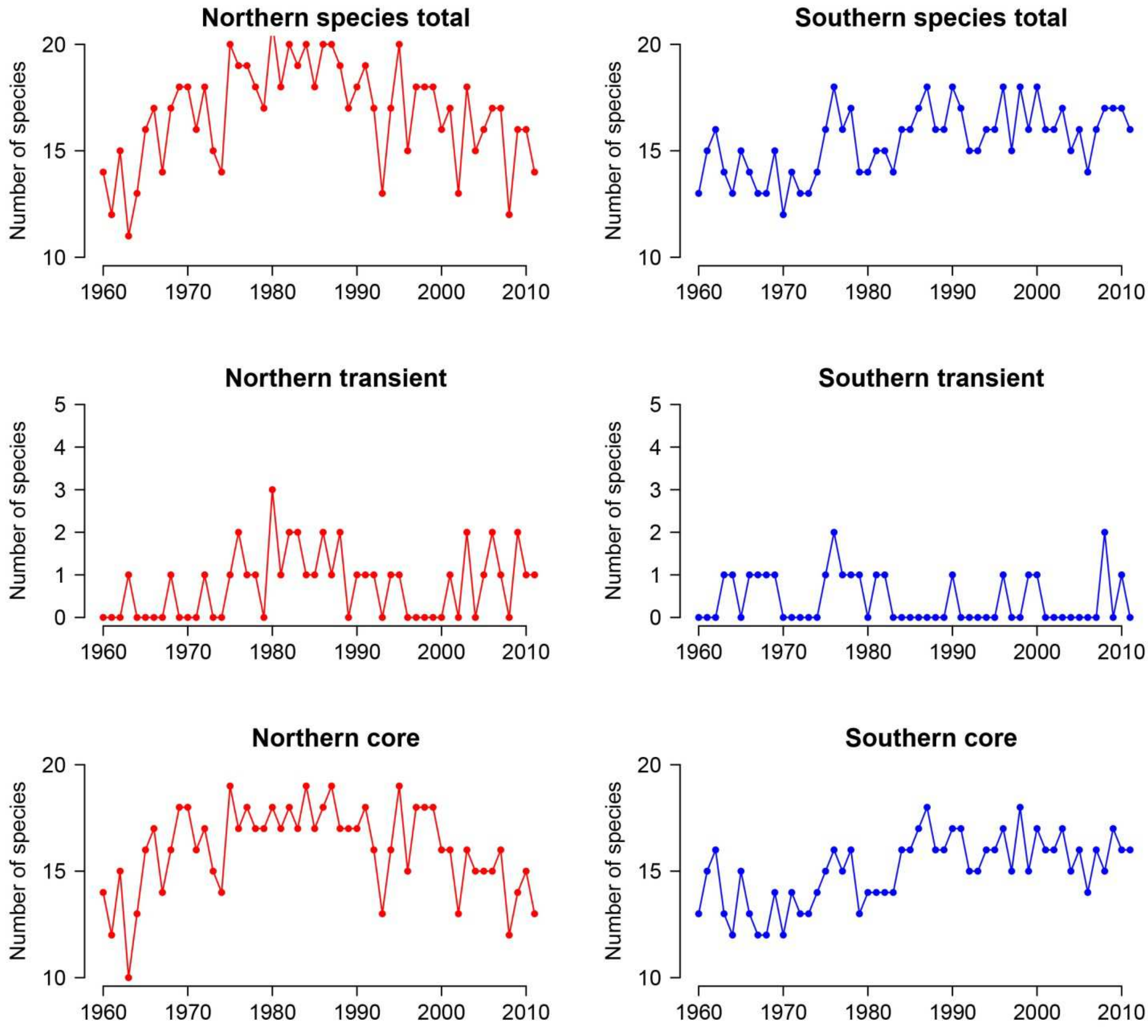


Figure 4. Trends in number of northern (left panel) and southern species (right panel) found in spring for all (top panel), transient (middle panel) and core species (lower panel).

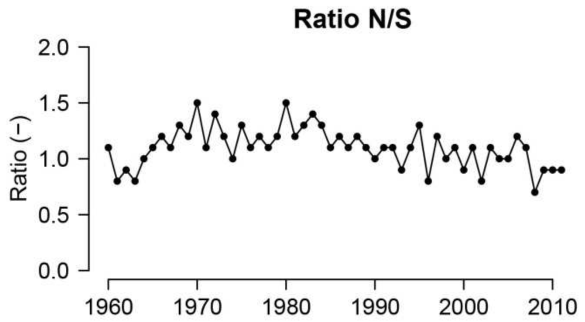


Figure 5. Ratio (-) between number of northern and southern species found in spring.

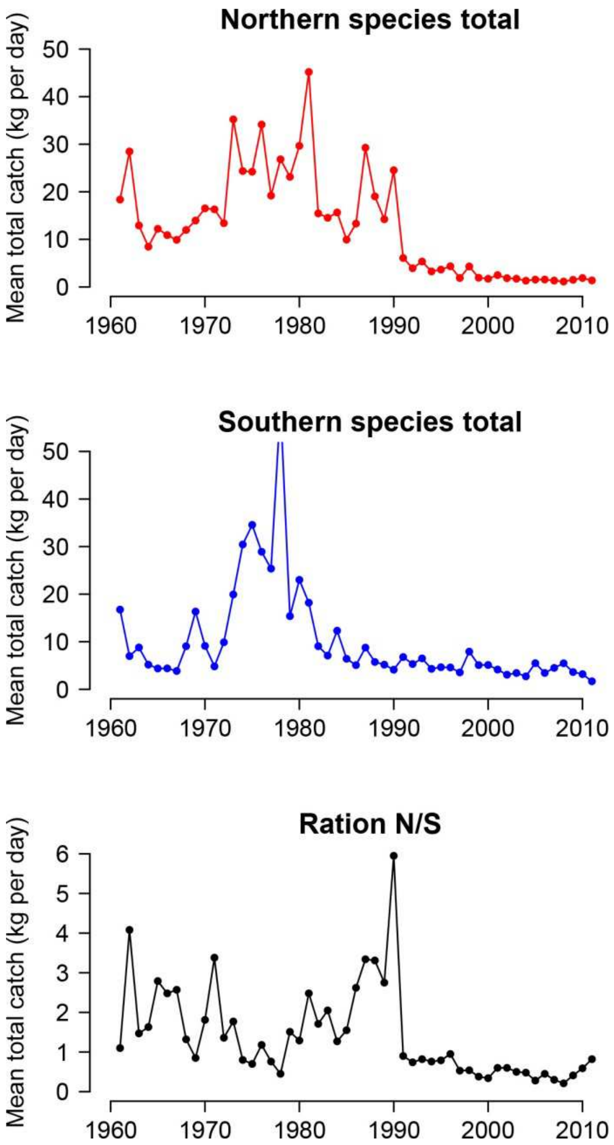


Figure 6. Mean total daily catch (kg wet mass d^{-1}) of all northern (top panel) and southern species (middle panel) in spring, together with the ration between total biomass of northern and southern species (lower panel).

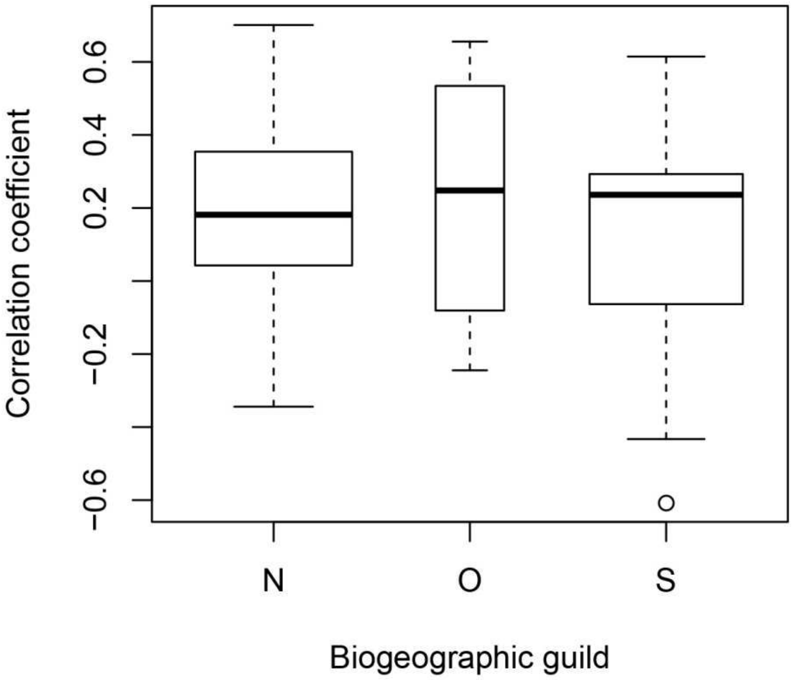


Figure 7. Boxplot of canonical correlations coefficients between trends in mean biomass of individual species and the first MAFA axis for trend in total biomass for northern (N),north-southern (O) and southern species (S) in spring.

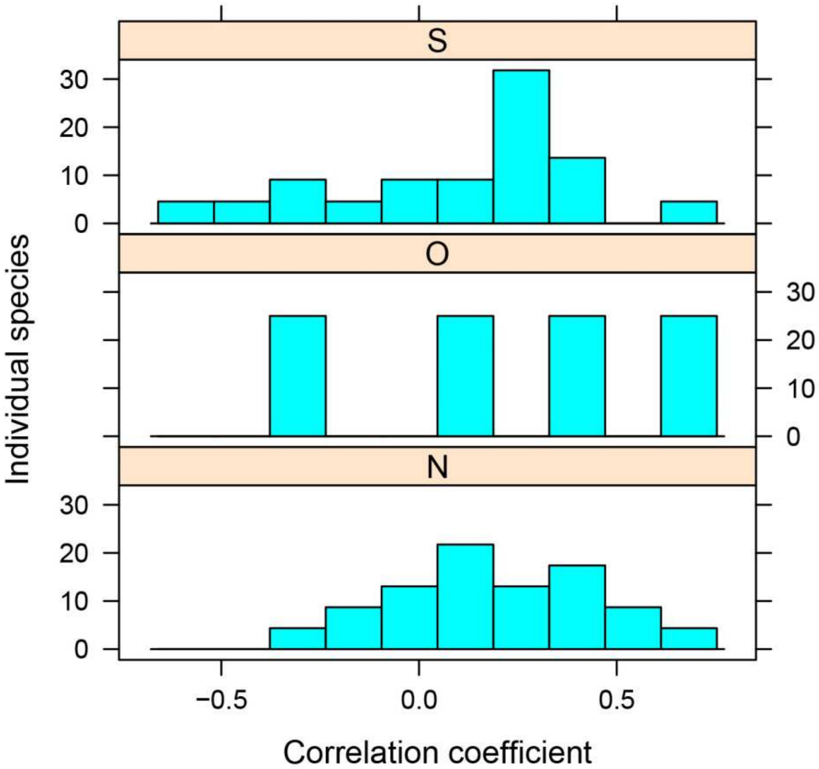


Figure 8 Frequency distribution of canonical correlations coefficients between trends in mean biomass of individual species and the first MAFA axis for trend in total biomass for northern (N),north-southern (O) and southern species (S) in spring.

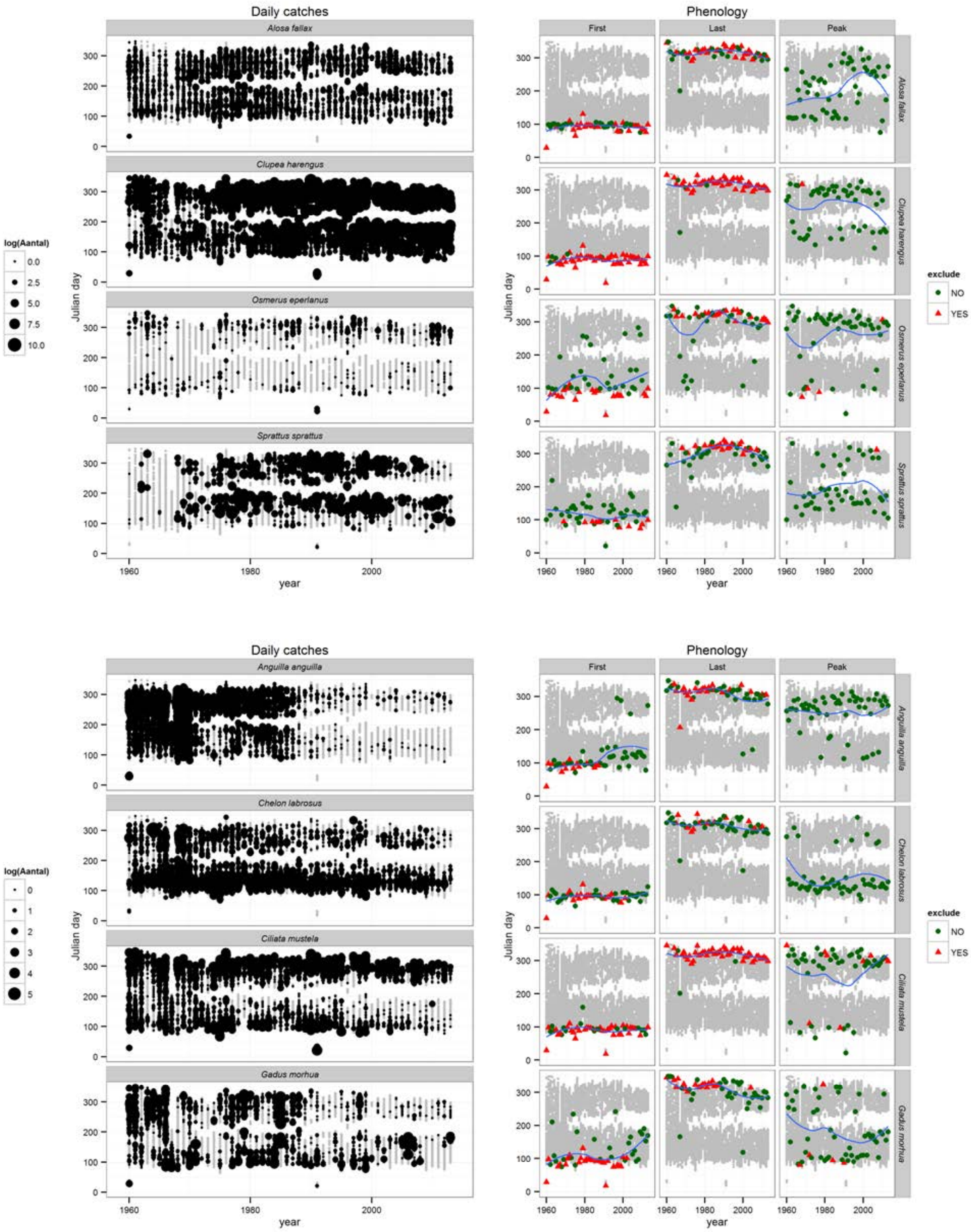


Figure 9 The NIOZ kom-fyke: Trends in abundance (left) and day of first, last and peak appearance (right) for core fish species in the western Dutch Wadden Sea with first, last or peak day of occurrence often corresponding with first or last day of fishing (red triangles). These species were excluded from further analysis.

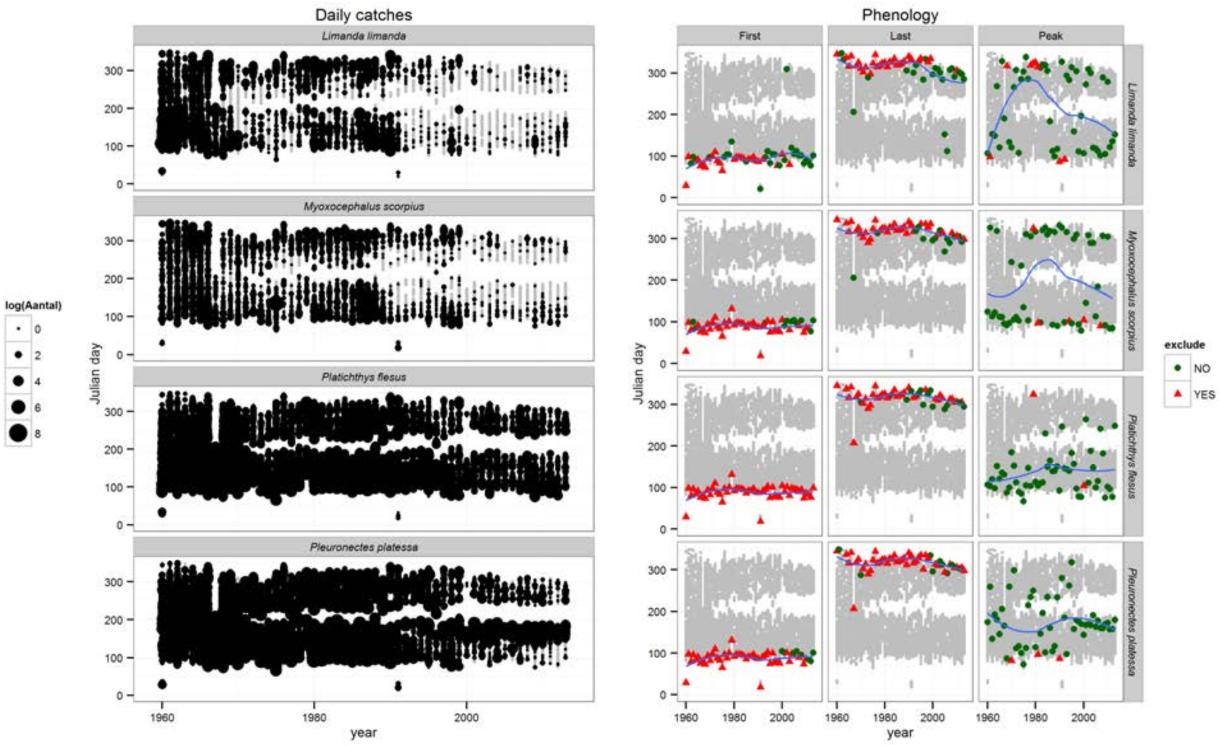


Figure 9 -continuation-

The NIOZ kom-fyke: Trends in abundance (left) and day of first, last and peak appearance (right) for core fish species in the western Dutch Wadden Sea with first, last or peak day of occurrence often corresponding with first or last day of fishing (red triangles). These species were excluded from further analysis.

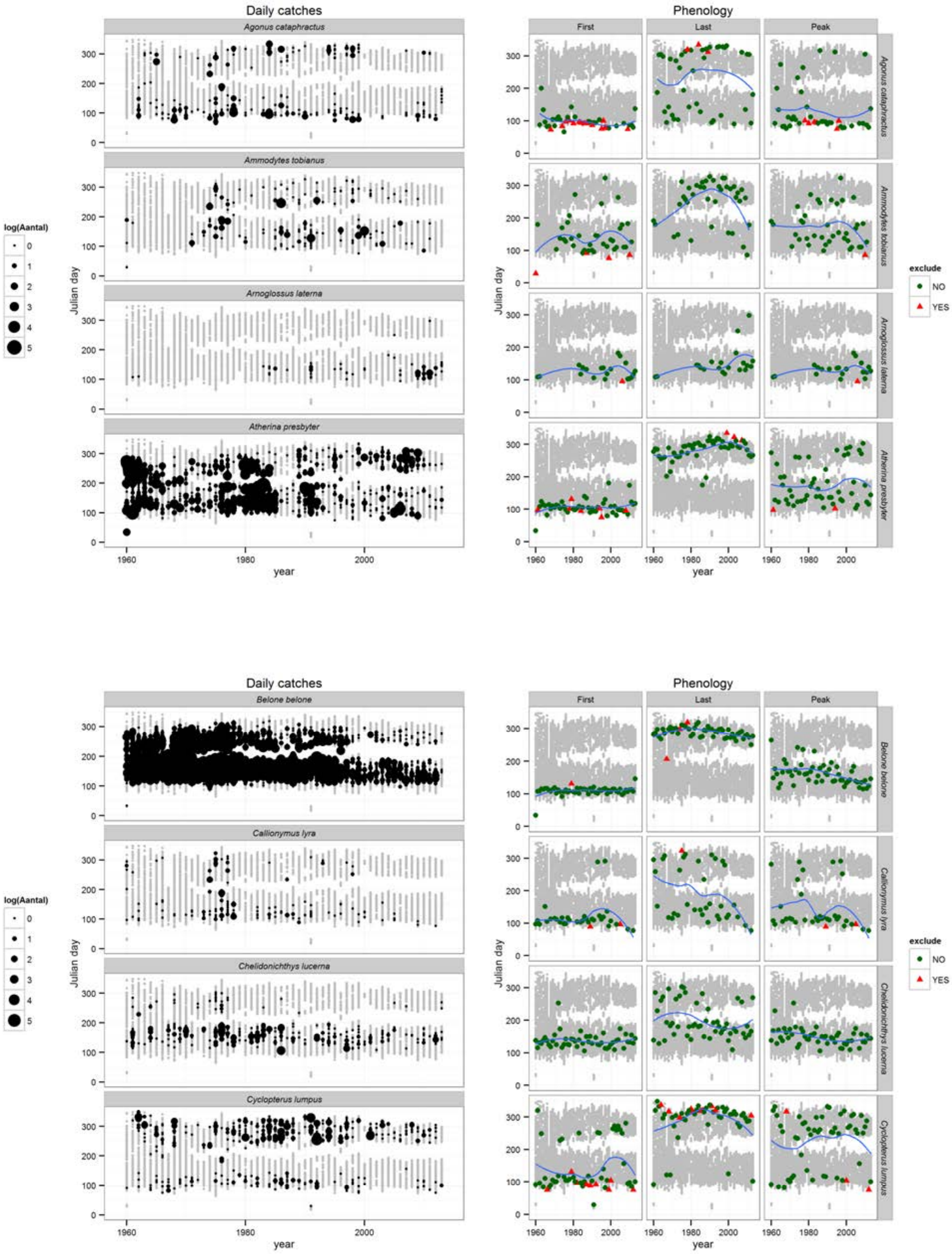
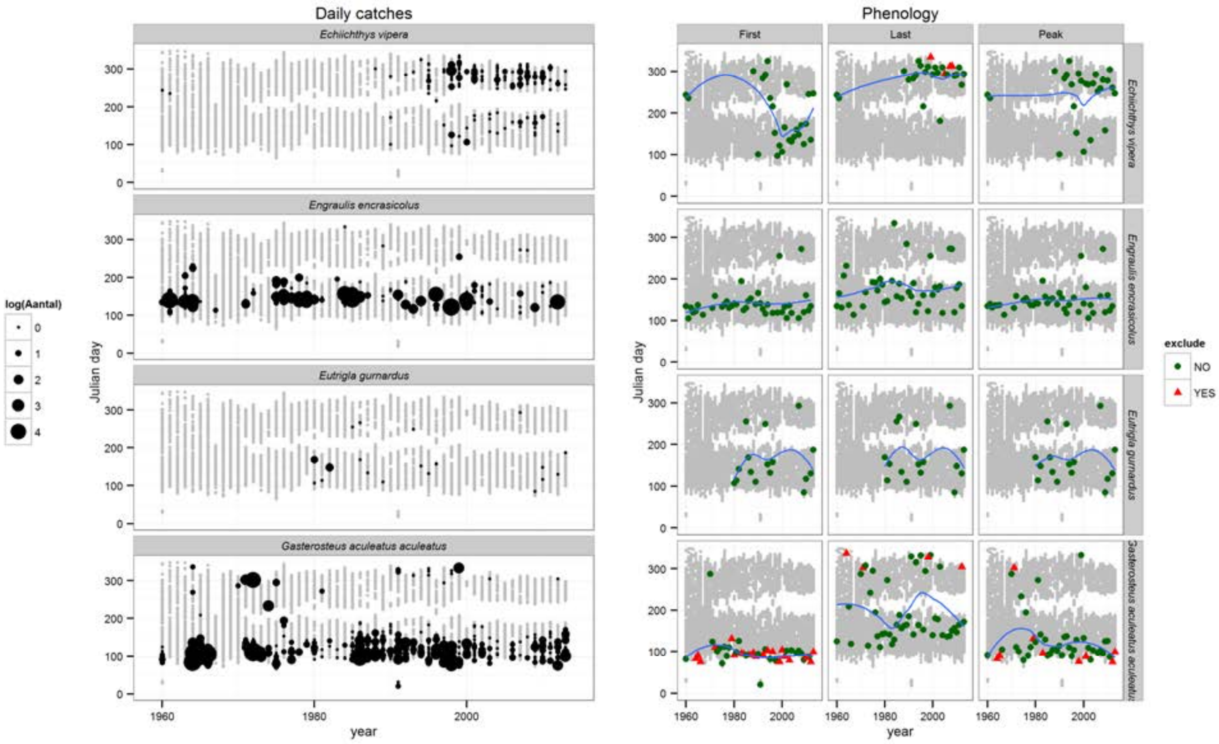


Figure 10 The NIOZ kom-fyke: Trends in abundance (left) and day of first, last and peak appearance (right) for core fish species in the western Dutch Wadden Sea. In case first, last or peak day of occurrence corresponded with first or last day of fishing, the observation was excluded from further analysis (red triangles).



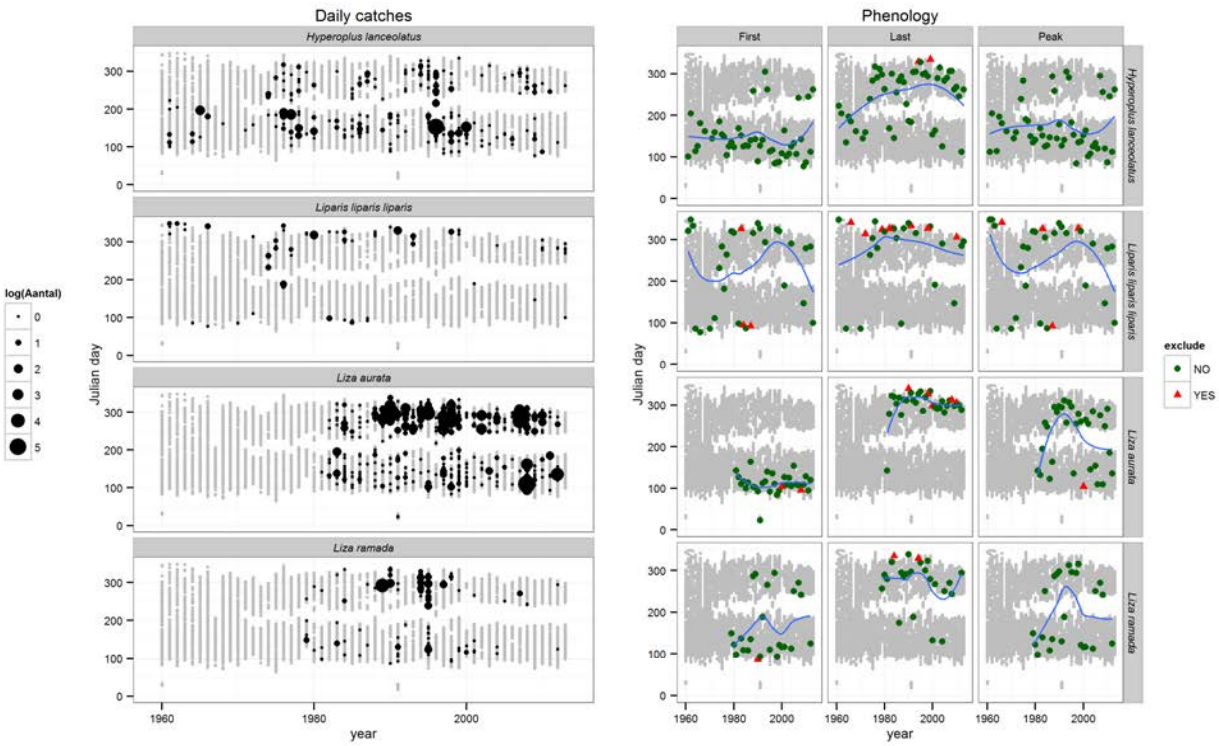
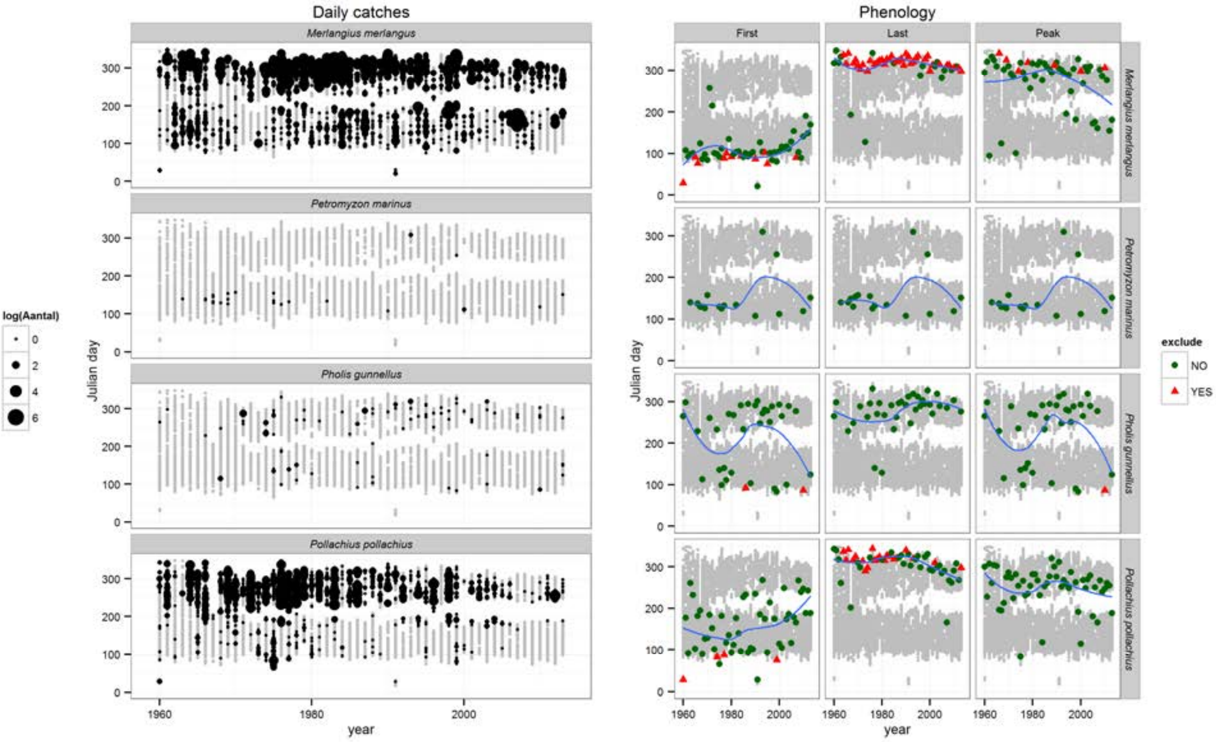


Figure 10 -continuation-

The NIOZ kom-fyke: Trends in abundance (left) and day of first, last and peak appearance (right) for core fish species in the western Dutch Wadden Sea. In case first, last or peak day of occurrence corresponded with first or last day of fishing, the observation was excluded from further analysis (red triangles).


Daily catches
Phenology
Merlangius merlangus
Petromyzon marinus
Pholis gunnellus
Pollachius pollachius
First
Last
Peak
log(Aantal)
0
2
4
6
Julian day
year
exclude
NO
YES

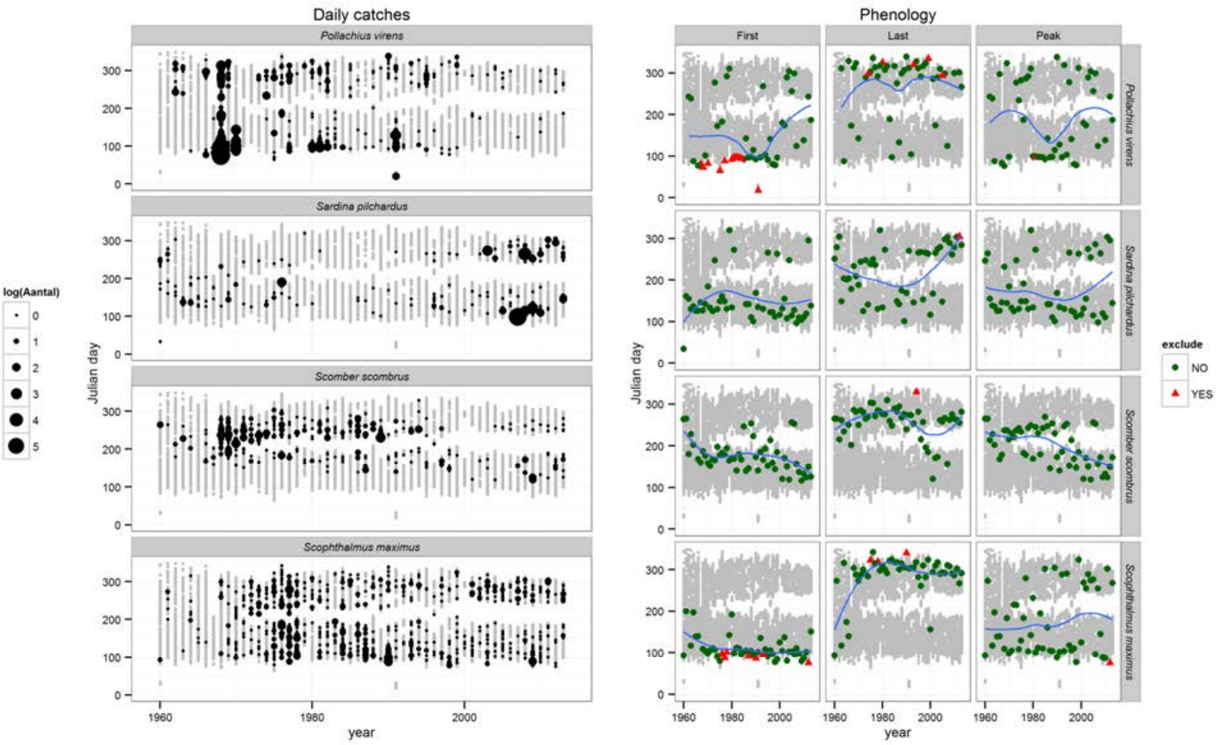
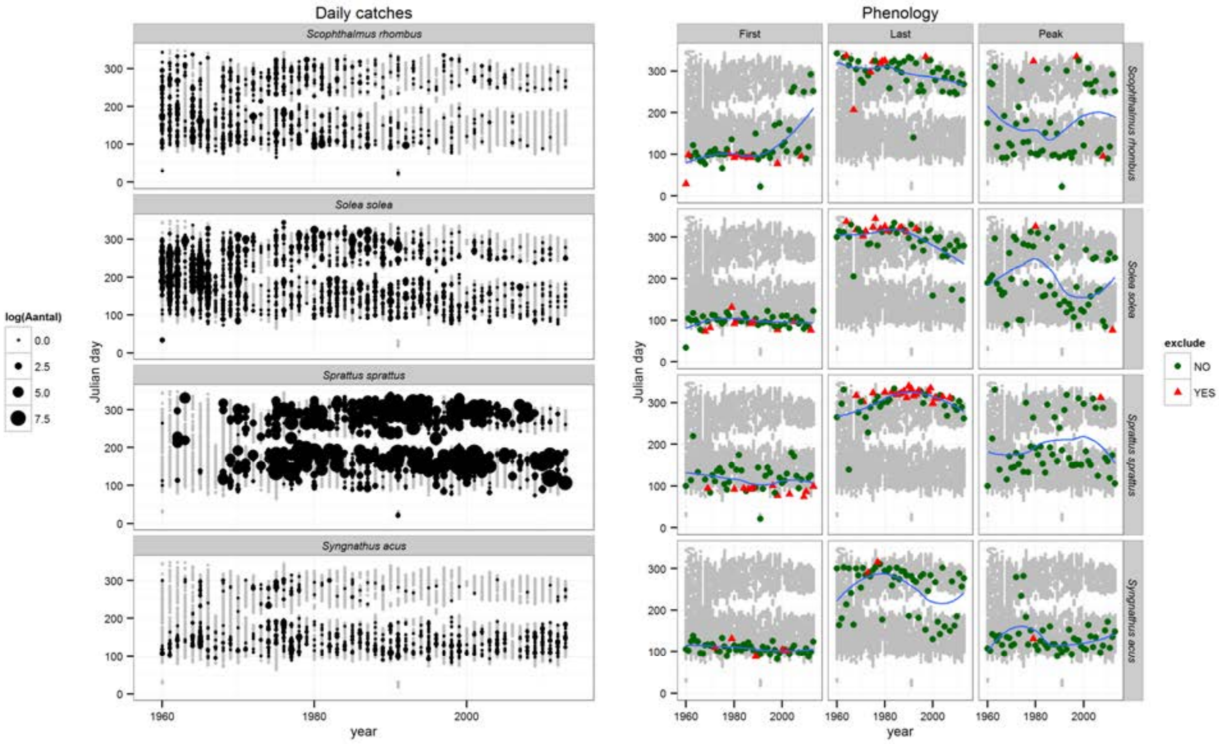

Daily catches
Phenology
Pollachius virens
Sardina pilchardus
Scomber scombrus
Scophthalmus maximus
First
Last
Peak
log(Aantal)
0
1
2
3
4
5
Julian day
year
exclude
NO
YES

Figure 10 -continuation-

The NIOZ kom-fyke: Trends in abundance (left) and day of first, last and peak appearance (right) for core fish species in the western Dutch Wadden Sea. In case first, last or peak day of occurrence corresponded with first or last day of fishing, the observation was excluded from further analysis (red triangles).



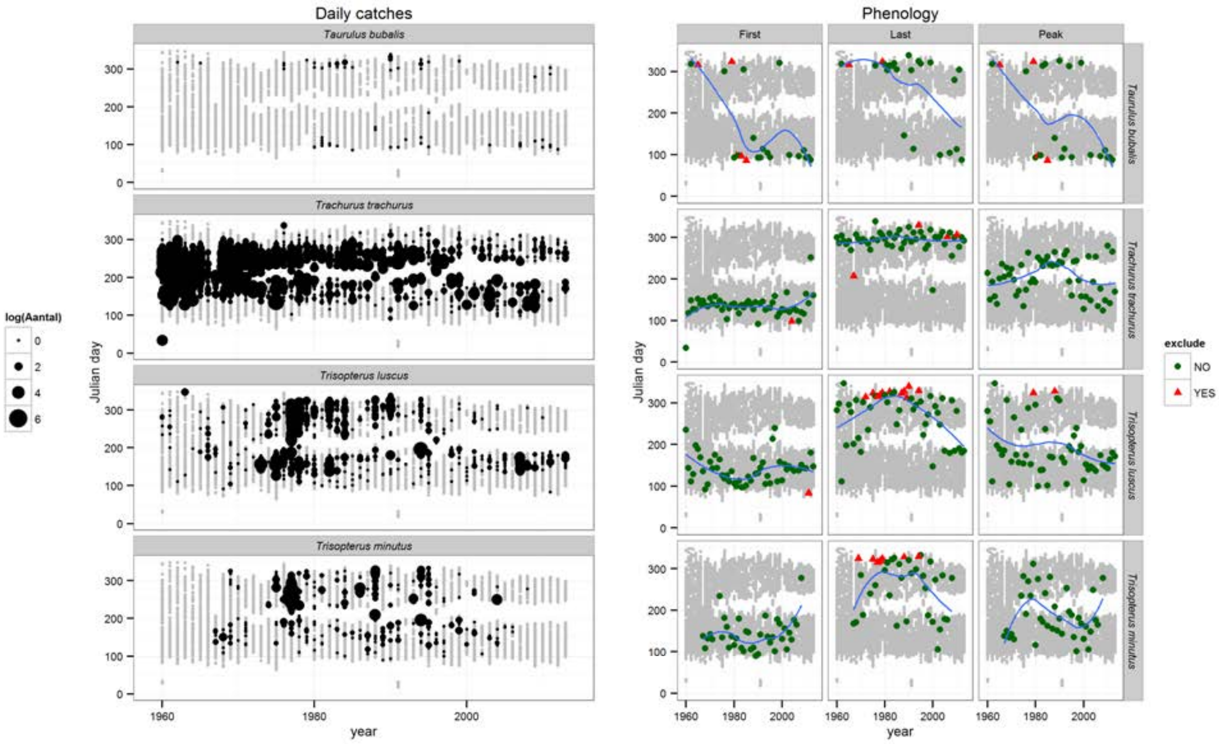


Figure 10 -continuation-

The NIOZ kom-fyke: Trends in abundance (left) and day of first, last and peak appearance (right) for transient fish species in the western Dutch Wadden Sea. In case first, last or peak day of occurrence corresponded with first or last day of fishing, the observation was excluded from further analysis (red triangles).

Table 1 Model results (environmental variables: wt: winter temperature; ws: winter salinity; st: spring temperature; ss: spring salinity; year: year) for trends in first day of appearence for various core species, together with mode of living (P: pelagic; BP: benthopelagic; D:demersal) and biogeographic guild (N:northern; NS: in between N en S; S: southern species). For explanation of the various models, see tekst. Green: significant linear model; Yellow: significant GAM model. *: p<0.05; **: p<0.01; *: p<0.001.

Species	Mode of living	Biogeographic guild	M1 (wt ws)	M2 (wt)	M3 (ws)	M4 (st)	M5 (ss)	M6 (year)
Belone belone	P	N	. ** - 0.15					
Scomber scombrus	P	N				* - 0.11		
Atherina presbyter	P	S						
Engraulis encrasicolus	P	S	*** ** -0.24					
Liza aurata	P	S						
Liza ramada	P	S						
Sardina pilchardus	P	S				* -0.11		
Sprattus sprattus	P	S						
Trachurus trachurus	P	S				* -0.09		
Ammodytes tobianus	BP	N						
Cyclopterus lumpus	BP	N		* 0.29				
Merlangius merlangus	BP	S						** 0.35
Gasterosteus aculeatus aculeatus	BP	NS						
Hyperoplus lanceolatus	D	N						** -0.19
Liparis liparis liparis	D	N					* + 0.37	
Pholis gunnellus	D	N				** -0.64		
Pollachius pollachius	D	N				** +0.21		
Pollachius virens	D	N						
Scophthalmus maximus	D	N						
Taurulus bubalis	D	N					* -0.35	
Trisopterus minutus	D	N			. +0.25			
Arnoglossus laterna	D	S						
Callionymus lyra	D	S						
Chelidonichthys lucerna	D	S	* -0.10					
Echiichthys vipera	D	S		* -0.21				
Eutrigla gurnardus	D	S				** -0.50		
Scophthalmus rhombus	D	S				* +0.11		
Solea solea	D	S				* +0.13		
Syngnathus acus	D	S		*** -0.37				
Trisopterus luscus	D	S						

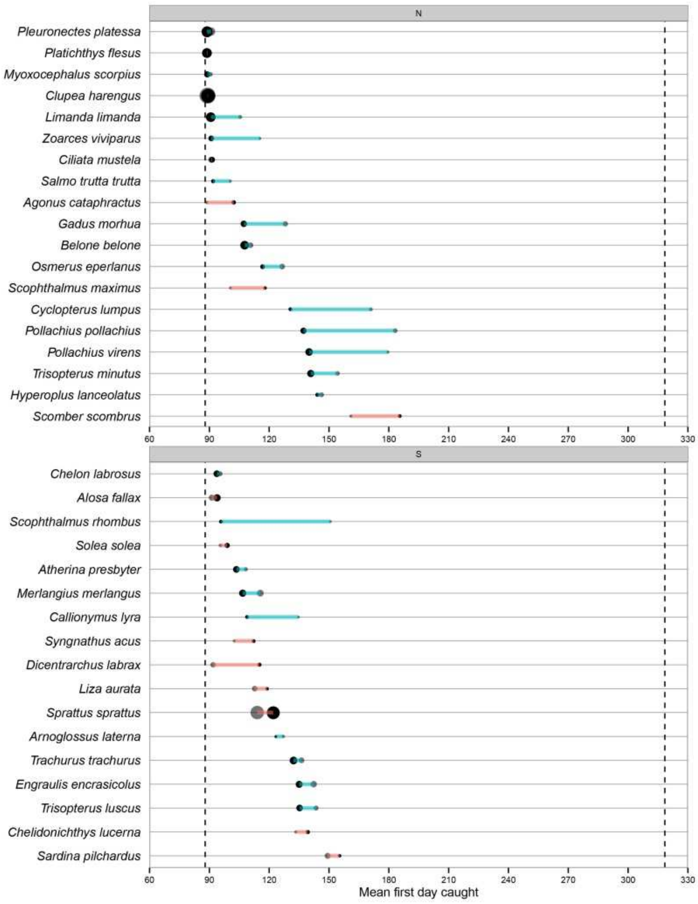
Table 2 Model results (environmental variables: wt: winter temperature; ws: winter salinity; st: spring temperature; ss: spring salinity; at: autumn temperature; as: autumn salinity; year: year) for trends in last day of occurrence for various core species, together with mode of living (P: pelagic; BP: benthopelagic; D:demersal) and biogeographic guild (N:northern; NS: in between N en S; S: southern species). For explanation of the various models, see tekst. Green: significant linear model; Yellow: significant GAM model. *: p<0.05; **: p<0.01; *: p<0.001.

			M1	M2	M3	M4	M5	M6	M7	M8
Species			(wt ws)	(wt)	(ws)	(st)	(ss)	(at)	(as)	(year)
Belone belone	P	N								*** 0.35
Scomber scombrus	P	N								*** 0.35
Alsosa fallax	P	S								** 0.33
Engraulis encrasicolus	P	S								
Liza aurata	P	S								
Liza ramada	P	S								
Sardina pilchardus	P	S								** + 0.32
Trachurus trachurus	P	S			* +0.10					
Ammodytes tobianus	D	N					** -0.23			
Cyclopterus lumpus	D	N				* 0.22				
Hyperoplus lanceolatus	D	N								** 0.44
Pholis gunnellus	D	N		** +0.20						
Pollachius virens	D	N					** 0.43			
Scophthalmus maximus	D	N								
Taurulus bubalis	D	N								
Arnoglossus laterna	D	S								
Callionymus lyra	D	S								
Chelidonichthys lucerna	D	S								
Echiichthys vipera	D	S					** -0.34			
Eutrigla gurnardus	D	S								
Scophthalmus rhombus	D	NS								*** -0.28
Solea solea	D	S	* -0.41							
Syngnathus acus	D	S								
Trisopterus luscus	D	S								
Gasterosteus aculeatus aculeatus	D	NS	* * 0.41							

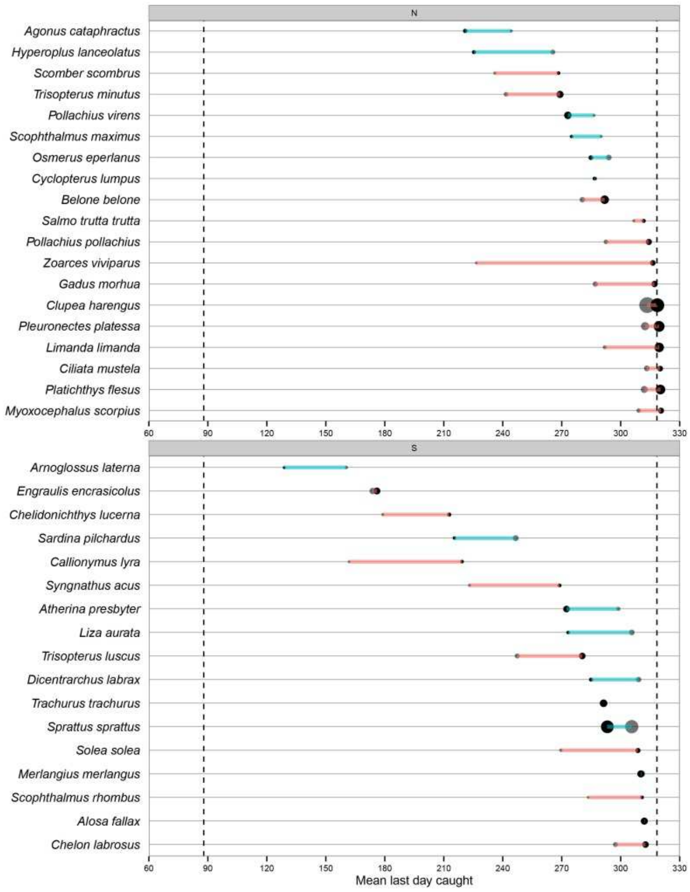
Table 3 Model results (environmental variable: year: year) for trends in day of peak occurrence for various core species, together with mode of living (P: pelagic; BP: benthopelagic; D:demersal) and biogeographic guild (N:northern; NS: in between N en S; S: southern species). For explanation of the various models, see tekst. Green: significant linear model; Yellow: significant GAM model. *: p<0.05; **: p<0.01; *: p<0.001.

Species			M8 (year)	
Belone belone	P	N	***	0.21
Scomber scombrus	P	N	***	0.28
Alosa fallax	P	S	**	0.13
Chelidonichthys lucerna	D	S	**	0.13

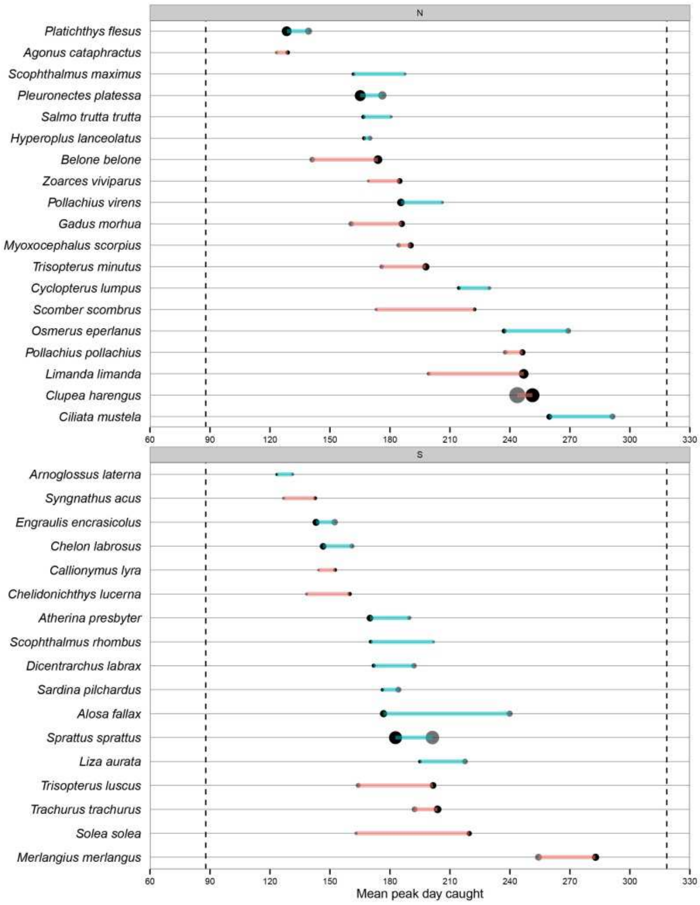
Appendix 1. Shift in day of first appearance (day number) between the period before 1985 and the last decade (2001-2011) for selected northern species (top panel) and southern species (lower panel). Blue line: later first appearance; red line: earlier first appearance. For more information see text.



Appendix 2. Shift in day of last occurrence (day number) between the period before 1985 and the last decade (2001-2011) for selected northern species (top panel) and southern species (lower panel). Blue line: later last occurrence; red line: earlier last occurrence. For more information see text.



Appendix 3. Shift in day of peak occurrence (day number) between the period before 1985 and the last decade (2001-2011) for selected northern species (top panel) and southern species (lower panel). Blue line: later peak occurrence; red line: earlier peak occurrence. For more information see text.



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