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Published in:
Marine Biology Research

Link to article, DOI:
10.1080/17451000.2016.1210806

Publication date:
2016

Document Version
Publisher's PDF, also known as Version of record

Citation (APA):
Dutz, J., Støttrup, J. G., Stenberg, C., & Munk, P. (2016). Recent trends in the abundance of plaice Pleuronectes platessa and cod Gadus morhua in shallow coastal waters of the Northeastern Atlantic continental shelf – a review. Marine Biology Research, 12(8), 785-796. DOI: 10.1080/17451000.2016.1210806

Marine Biology Research

ISSN: 1745-1000 (Print) 1745-1019 (Online) Journal homepage: http://www.tandfonline.com/loi/smar20

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To cite this article: Jörg Dutz, Josianne G. Støttrup, Claus Stenberg & Peter Munk (2016) Recent trends in the abundance of plaice Pleuronectes platessa and cod Gadus morhua in shallow coastal waters of the Northeastern Atlantic continental shelf – a review, Marine Biology Research, 12:8, 785-796, DOI: 10.1080/17451000.2016.1210806

To link to this article: https://doi.org/10.1080/17451000.2016.1210806

Published online: 05 Oct 2016.

MARINE BIOLOGY RESEARCH, 2016
VOL. 12, NO. 8, 785–796
http://dx.doi.org/10.1080/17451000.2016.1210806

REVIEW ARTICLE

Recent trends in the abundance of plaice *Pleuronectes platessa* and cod *Gadus morhua* in shallow coastal waters of the Northeastern Atlantic continental shelf – a review

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ABSTRACT
Shallow, near-shore water habitats on the continental shelf of the Northeast Atlantic have been productive fishing areas in the past. Here, we review the present knowledge about (i) recent trends in the abundance of plaice and cod in these habitats and (ii) hypotheses regarding the factors responsible for any trends. At present, only a few studies exist on the trends of abundance of plaice or cod, namely from the Bay of Biscay, the North Sea and the Skagerrak/Kattegat. They suggest a declining abundance in coastal, shallow areas and – at least for plaice – a latitudinal gradient with an erosion of the southern distribution boundary in the Bay of Biscay and deepening of stocks in the North Sea. In contrast, no trend in shallow water abundance of plaice similar to a decline in deep-water stocks during the 1970s and their slow recovery during the 2000s is apparent in the Skagerrak/Kattegat. Although shallow habitats fundamentally differ from deeper areas by the prevalence of juvenile stages, the declining trends coincide with decreasing abundance/landings and spatial stock relocations in the deeper areas. Whether this indicates a common trend pointing at connectivity between shallow and deep water remains open. Fundamental differences exist in the suggested causes of the trends in different geographical areas. High fishing pressure together with low local recruitment apparently prevents the recovery of overexploited plaice and cod stocks in the Skagerrak/Kattegat. In contrast, the responses of juveniles and adult fish to increasing seawater temperature are the main hypotheses for changes in distribution and abundance of both fish species in the North Sea/Bay of Biscay. However, temperature alone cannot explain the observed decline of fish in coastal areas, and the causes may be more complex, involving nutrient loading, primary productivity or food availability, although at present, knowledge of these factors is insufficient.

ARTICLE HISTORY
Received 18 August 2015
Accepted 1 July 2016
Published online 5 October 2016

RESPONSIBLE EDITOR
Kjell Rong Utne

KEYWORDS
Cod distribution; plaice distribution; coastal systems; coastal fish abundance

Introduction

Coastal marine ecosystems are ecologically and socio-economically among the most valuable systems of the world, responsible for an important share of global goods and services. There is increasing concern about the sustainability of these resources in view of pressures originating from climate change and increasing human activity and demand (Worm et al. 2006; Brander 2010; McClanahan et al. 2015). Overexploitation and habitat destruction for centuries has led to severe degradation of coastal systems and a pronounced decline in invertebrate and vertebrate abundance and diversity (Jackson et al. 2001; Lotze et al. 2006; Harley et al. 2006).

In Denmark, coastal fishermen operating from small vessels or directly from beaches with gillnets, fish weirs or trawls have indicated declining fish abundance in coastal areas (Støttrup et al. 2014). Of 74 coastal fishermen, 68% and 54% reported that the abundance of cod (*Gadus morhua* Linnaeus, 1758) and plaice (*Pleuronectes platessa* Linnaeus, 1758) as major targeted species, respectively, has declined since the beginning of the last decade in coastal areas. This has reduced their fishing opportunities and forced them to move to more offshore fishing areas. A preliminary examination of the data from fishing surveys from the North Sea and Kattegat showed similar temporal changes in the spatial distribution of these two species (Støttrup et al. 2014). We found, therefore, a need for a more systematic overview about the available scientific information on the status of these two species in coastal areas of the Northeast Atlantic.

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Large-scale changes in fish distribution, abundance and community composition occur in offshore areas at various geographic scales (Drinkwater 2005; Rose 2005; ter Hofstede et al. 2010; Nicolas et al. 2011). These include latitudinal expansion of warm-water fish (Quéro 1998; Stebbing et al. 2002; Beare et al. 2004; Poulard & Blanchard 2005), contractions or shifts of mean latitude or northern/southern distribution boundaries (Brander et al. 2003; Perry et al. 2005), and significant deepening of whole fish assemblages (Dulvy et al. 2008; Simpson et al. 2011). Analyses focusing on physical variables and fisheries effort found that fishing alone is insufficient to explain the observed trends (Perry et al. 2005; Dulvy et al. 2008; ter Hofstede et al. 2010). In contrast, significant relationships among sea water temperature or climate indices such as the North Atlantic Oscillation Index (NAO) and trends in fish stocks suggest that warming of the oceans affects the distribution of fish by exceeding the thermal limits of boreal species or by expanding the habitats of species preferring warm temperatures (Roessig et al. 2004; Harley et al. 2006; Simpson et al. 2011).

Less-comprehensive knowledge on changes of the fish fauna exists for coastal habitats, which are not regularly monitored by international surveys and are often studied locally. Coastal habitats are defined as areas ranging from coastal wetlands to estuaries, bays and open water less than 30 m deep (Seitz et al. 2014). Many of the commercially important fish species occurring on continental shelves like cod and plaice use them temporally as feeding, spawning, or nursery grounds and are connected to coastal areas by larval transport, immigration and emigration (Seitz et al. 2014). Because of the connectivity of coastal and offshore populations, coastal stocks, in turn, most likely depend on abundance changes in deeper areas. Thus, causes of decline in coastal fish fisheries cannot be examined without reference to the general trends in fish stocks established in offshore areas.

In this review, we assembled findings from a range of relevant studies about changes in the abundance and distribution of plaice and cod in the shallow continental coastal water of the Northeast Atlantic. We specifically address the questions of (i) whether there is evidence of a decline of plaice and cod in coastal water, (ii) how trends, if any, compare to those in well-monitored offshore waters and (iii) whether causes of changes in abundance and distribution have been identified in the studies observing these trends. Scientific literature was compiled from searches made using Google Scholar by combining the species name with attributes of the habitat ('coastal', 'shallow', 'depth') or variation ('time-series', 'trend'). The review focuses on continental coastal waters of the NE Atlantic because relevant studies are limited to this area.

Plaice: trends in abundance and distribution

Shallow/coastal waters

Plaice is a temperate flatfish species found on sandy and muddy substrates in shelf waters of the eastern North Atlantic ranging from the Bay of Biscay to the Barents Sea (Rijnsdorp et al. 2010; ICES WKHVES 2012). Relatively few investigations have reported on long-term trends of plaice in shallow, coastal waters, namely from the Bay of Biscay, the continental coast of the North Sea and the Skagerrak/Kattegat (Table I, Figure 1). In the Bay of Biscay, trawl surveys in the Bay of Vilaine and the eastern part of the shelf in the years 1987–2001 showed a significant decrease in the abundance of juvenile plaice over time and their complete disappearance from shallow water toward the end of the observation period (Désaunay et al. 2006). In the North Sea, a 37-year time series from the Dutch demersal fish survey in coastal continental waters, conducted since 1970, revealed a decline in demersal fish species biomass together with a change in their community composition (Tulp et al. 2008; Bolle et al. 2009a; Tulp & Bolle 2009). Following peak abundance in the mid-1980s, a continuous decline of plaice and other species such as eel, eelpout, whiting and dab occurred until the mid-2000s in most areas of the Dutch and German Wadden Sea. This decline was primarily observed in the shallow Wadden Sea, but not in the deeper coastal zone or the shallow Westerschelde (Tulp

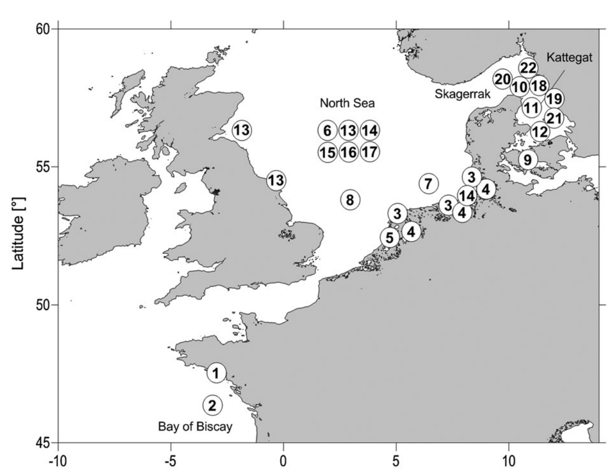

Figure 1. Locations of the studies on trends in abundance of plaice and cod on the northeastern continental shelf. Numbers refer to studies listed in Tables I and II.

Table I. Trends and potential causes of changes observed in plaice abundance in various areas of the Bay of Biscay, North Sea and Skagerrak/Kattegat.

Area	Years of data	Trend	Identified or hypothesized cause	Reference
Bay of Biscay				
Shallow, coastal				
1 Bay of Vilaine, eastern shelf	1981–2001	↓ since 1990s	Increasing winter temperatures	Désaunay et al. (2006)
Deep, offshore				
2 Eastern shelf	1987–2006	↓ since 1995	Recruitment failure related to temperature Amplification by fishing	Hermant et al. (2010)
North Sea				
Shallow, coastal				
3 Continental coast	1902–1909 1983–1987 1999–2003	↓ since 1983	Temperature in summer exceeding tolerance Increasing food requirements related to increased temperature Decrease in benthic productivity, e.g. *Limecola balthica* (Linnaeus, 1758)	van Keeken et al. (2007) Teal & van Keeken (2011)
4 Continental coast Wadden Sea	1970–2006	↓ since 1985	Increasing temperature (coast only) Oligotrophication, decreasing productivity Fishing on benthic prey, food reduction Increased predation Combination of factors, bioenergetics	Tulp et al. (2008), Tulp & Bolle (2009), Bolle et al. (2009a)
5 Wadden Sea (intertidal)	1975–2007	↓ since 1990s	Unexplained reduction in nursery function Decrease in offshore recruitment Interspecific competition	van der Veer et al. (2010, 2011)
Deep, offshore				
6 Entire	1974–2006	↓ 1990	Not identified	Rijnsdorp et al. (2010)
7 East–central	1913–2007	↓ 1990–2000s	Temperature and climate effects Decreased productivity, prey resources Habitat modification (closure of nursery grounds)	Engelhard et al. (2011)
8 Central	2000–2006	↓ since 2000	Not identified	Poos et al. (2013)
Skagerrak/Kattegat				
Shallow, coastal				
9 Kattegat Belt Sea	1904–2007	No trend identified		Sparrevohn et al. (2013)
Deep, offshore				
10 Skagerrak Eastern Kattegat	1901–2007	↓ since 1970, ↑ during 2000s	Increasing fishing mortality	Cardinale et al. (2010)
11 Danish Skagerrak Swedish Skagerrak SW Kattegat Swedish SE Kattegat	1901–2007	↓ since mid 1970s, ↑ during 2000s in Danish Skagerrak and SW Kattegat	Prolonged overexploitation Eradication of spawning aggregations	Cardinale et al. (2011)
12 Kattegat/Skagerrak	2002–2010	↓ since 2002 ↑ since 2007 in Skagerrak	No explanation	Ulrich et al. (2013)

Note: Downward arrow indicates decline, upward arrow indicates increase in abundance of plaice. Numbers in first column refer to the location of the study in Figure 1.

et al. 2008). The Wadden Sea is an important nursery area for plaice, especially in the intertidal and shallow subtidal zones (Zijlstra 1972; Zijlstra et al. 1982). Fyke net surveys showed that since the 1980s the abundance of plaice in age groups 1 and 2 and since the 1990s plaice in age group 0 also declined in these zones, which suggests a strong reduction of plaice in their nursery areas (van der Veer et al. 2011).

Information on trends of plaice in shallower, coastal areas in the Skagerrak/Kattegat is scarce. Recently, surveys targeting young flatfish in inshore Danish waters in the Kattegat/Øresund (depth < 4.5 m) conducted from 1904 to 2006 were analysed for changes in the relative abundances of sole and plaice to understand potential shifts in flatfish community composition (Sparrevohn et al. 2013). Strong increases in the ratio of sole to plaice in these nursery grounds were recorded from the mid-1980s, which indicated a shift in community composition. However, this trend was largely determined by a sixfold increase in the catch of sole, while no difference in the catches of juvenile plaice was observed (Sparrevohn et al. 2013).

Deep/offshore waters

In recent decades, considerable changes in landings and abundance of plaice have also been recorded for the deeper offshore water of the Bay of Biscay, the North Sea and the Skagerrak/Kattegat (Table I). In the Bay of Biscay, landings of plaice have moderately decreased since the 1990s (Rijnsdorp et al. 2010). This contrasts with a decrease in catches of plaice in 1995 observed in groundfish surveys during 1987–2006 (Hermant et al. 2010). Landings in the North Sea also decreased following a historical maximum in the mid-

1980s, with some increase since 2008 (ICES 2015; Rijnsdorp et al. 2010). Spawning biomass in the North Sea has basically the same trend as the catches; however, the increase in spawning stock since 2008 has been significant, and the spawning stock estimate for 2013 has passed the historical maximum of the mid-1980s (Figure 2; ICES 2015). Together with these long-term trends, changes in the geographical and water-depth distribution of the stock have occurred. These include a northward shift of the southern distribution boundary in the Bay of Biscay (Hermant et al. 2010) and a general increase in the mean depth of plaice in the North Sea with a deepening of ~4 m per decade as deduced from the English groundfish surveys 1977–2006 (Perry et al. 2005; Dulvy et al. 2008). In addition, commercial fisheries data indicate a large-scale relocation of distribution centres of plaice with a westward shift and drop in plaice abundance along the east–central North Sea and in Danish waters in the 1990s to the 2000s (Engelhard et al. 2011; Poos et al. 2013).

In the Kattegat/Skagerrak, landings of plaice continuously decreased from the mid-1970s until 2007 (Cardinale et al. 2010). The spawning stock biomass of plaice modelled from otter trawl surveys shows a decline from a peak in the mid-1960s until the mid-1970s (Cardinale et al. 2010). In contrast to the

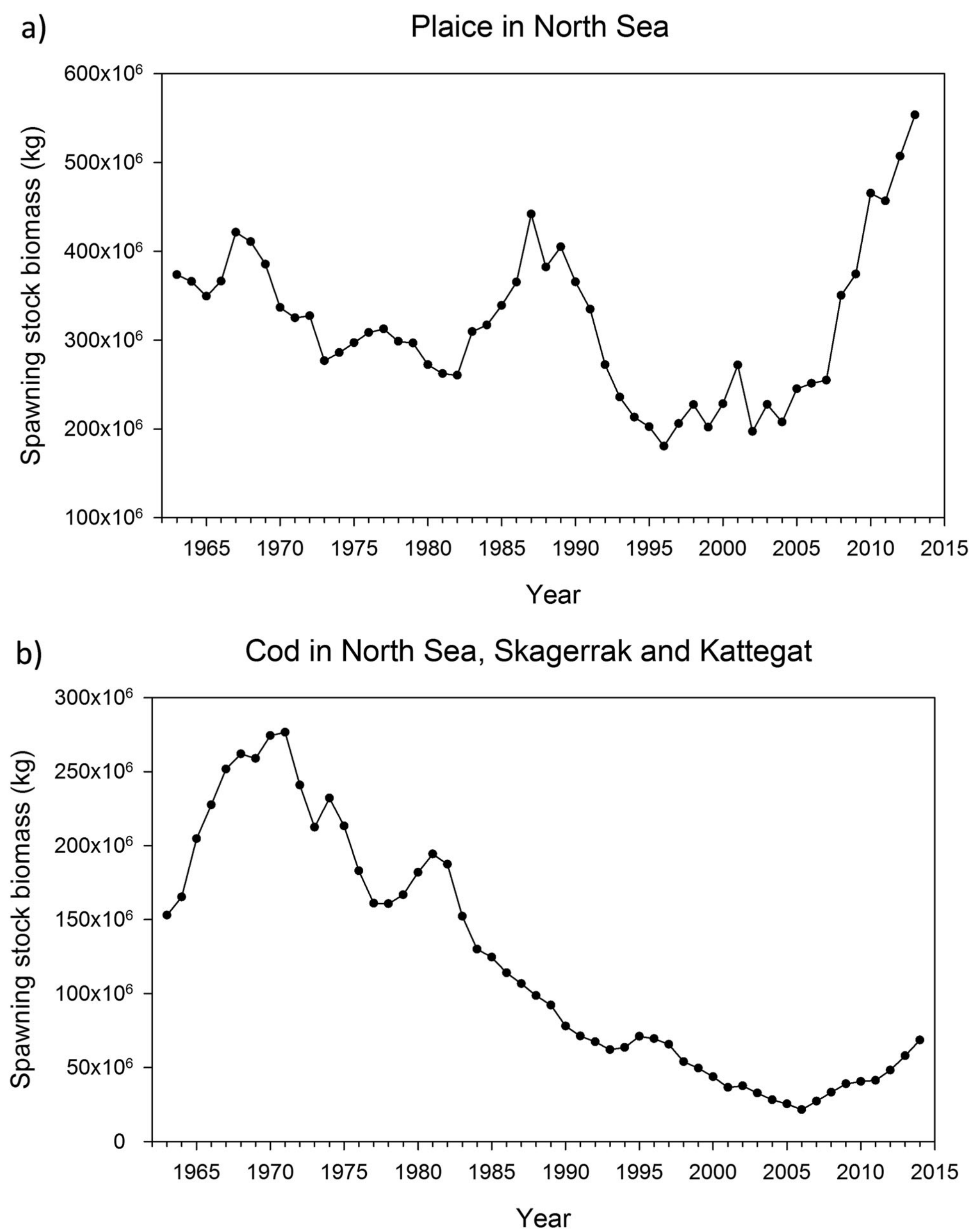

Figure 2. Spawning stock biomass estimates from standard assessment (ICES 2015). (a) Estimates for plaice in the North Sea during 1963–2013. (b) Estimates for cod in the North Sea and Skagerrak/Kattegat for the years 1963–2014.

landings, however, a gradual increase in the modelled biomass was already discernible from the mid-1970s and particularly following strong recruitment events in 1998–1999. This led to a spawning stock biomass at the end of 2000s representing 38% of the maximum biomass observed during the twentieth century (Cardinale et al. 2010). The general decline of the plaice abundance observed in the surveys was accompanied by a strong contraction of four different aggregations of plaice, namely a western component on the Danish Skagerrak coast and in the southwestern Kattegat and an eastern component along the Swedish Skagerrak coast and in the Swedish eastern Kattegat (Cardinale et al. 2011). The recent increase in plaice biomass, however, shows spatiotemporal heterogeneity, and is mainly related to a recovery of the western component, whereas the eastern component remains at a historically low level. The importance of the western component in the Skagerrak and Kattegat as a productive fishery area for plaice was also stressed by the analysis of recent landings by Danish and Swedish fisheries from larger vessels (> 12 m) (Ulrich et al. 2013). The observed trends, however, differ from the plaice biomass modelled by Cardinale et al. (2011). Although catches were reported to increase similarly in the Skagerrak, catches in the Kattegat have continuously decreased (Ulrich et al. 2013).

Synopsis

The literature survey shows that apart from studies in the Dutch coastal zone very limited data exist allowing insights into common trends of plaice in shallow and deep water over the species distribution range. In addition, a thorough comparison of common trends in habitats is hampered by the fact that some information about trends in deep water originates from landing of fisheries rather than surveys as in shallow water. This might lessen the identification of decreasing trends in the deeper areas. Apart from these restrictions, the available information suggests some latitudinal differences in trends. The survey data from the Bay of Biscay demonstrate the erosion of the southern distribution limit by the disappearance of plaice from both shallow and deep waters. The decline of plaice in shallow areas of the North Sea following the maximum abundance in the 1980s, in contrast, coincides with a general deepening and geographical relocation of plaice in the deeper North Sea indicated in groundfish surveys. This deepening, however, is not only a recent observation, but has occurred previously as a result of a gradual and age-dependent shift of juvenile plaice of age groups 0–2 to deeper waters along the Dutch, German and Danish continental coasts in the periods 1902–1909, 1983–1987 and 1999–2003 (van Keeken et al. 2007). In recent years, the deepening trend and the decline of plaice in the Wadden Sea apparently have persisted despite the stabilization of stocks in deep water (see ICES 2013, 2015). A recovery of plaice stocks after a decline during the 1970s occurred, at least in the western areas, in the Skagerrak/Kattegat region as well. Despite the limited information for this area, a decline in shallow, coastal areas is not yet apparent. The spatial heterogeneity in trends along the North Sea coast and the Skagerrak/Kattegat could indicate that the interaction of environmental factors and differential effects of the local habitat or interspecific interactions play an important role, as implied by Simpson et al. (2011) for the entire North Sea.

Potential causes for changes in abundance and distribution of plaice

Temperature effects

Temperature is one of the primary factors determining the distribution of fish. In several of the reports from the North Sea, offshore displacement and decreasing abundance were correlated with increasing surface or bottom seawater temperatures and/or climate indices such as the North Atlantic Oscillation (NAO) in shallow (Désaunay et al. 2006; van Keeken et al. 2007; Tulp et al. 2008) as well as deep habitats (Hermant et al. 2010; Engelhard et al. 2011). The mechanisms underlying this temperature effect remain uncertain, but might reflect temperature exceeding metabolic thermal optima and fish behaviour (Table I). At the boundary of their distribution, the sensitivity of plaice to increasing temperature might have caused their disappearance in the shallow Bay of Vilaine (Désaunay et al. 2006). Increases in the summer temperature beyond tolerance levels might also have forced the offshore movement of age groups 0–2 plaice in the shallow Wadden Sea (van Keeken et al. 2007). However, the continuous presence of juvenile flounder, which has a temperature tolerance similar to that of juvenile plaice (Fonds et al. 1992), probably excludes thermal sensitivity as the single cause of the disappearance of plaice in these shallower areas (van der Veer et al. 2011). Regarding long-term shifts, higher temperatures have been associated with a more northwestern and deeper distribution pattern of plaice in the North Sea, which suggests that fluctuations in the thermohaline circulation and temperature have affected adult plaice distribution in general (Engelhard et al. 2011).

Temperature sensitivity of population-dynamic processes may contribute to changes in abundance and distribution. Failure in recruitment because of higher temperatures in bottom waters of the shelf could have caused the decline of plaice in the shallow water of the Bay of the Biscay (Hermant et al. 2010). In the North Sea, year-class strength in plaice appears to be negatively correlated with sea temperature during the larval period, with strong classes arising during cold winters (Bolle et al. 2009b; van der Veer et al. 2009). This could be related to increasing mortality of eggs and larvae associated with increased food limitations imposed by increasing temperatures or temperature-mediated effects on predation pressure (van der Veer et al. 2009). In the shallow Wadden Sea, juvenile plaice growth was found to be maximal only shortly after settlement because otherwise food availability does not meet their increasing energy demands (van der Veer et al. 2010). Consequently, long-term increases in temperature will increase energy demands, cause an earlier offshore movement, and reduce the nursery function of the Wadden Sea (van Keeken et al. 2007; van der Veer et al. 2011).

Habitat changes

Several observations, however, question a prevailing role of temperature as the single determinant of the observed changes in plaice abundance and distribution, and point to an interplay with other factors such as food availability or competition. In the Dutch coastal area, general shifts in species composition and a decrease in demersal fish abundance were related to temperature in the coastal zone only and not in the Wadden Sea, in which the strongest decline in plaice was observed (Tulp et al. 2008; Bolle et al. 2009a). Moreover, in the shallow Westerschelde area, plaice stocks increased despite an increase in temperature. The decline of plaice in the Wadden Sea and the changes in the demersal fish composition were correlated with indicators of eutrophication and predators (Tulp et al. 2008). In the 1960s and 1970s, eutrophication likely resulted in an increase in primary and secondary production, and it may explain the observed increase in fish biomass. The growth rate of plaice was also positively correlated with eutrophication (Rijnsdorp & van Leeuwen, 1996; Teal et al. 2008). Consequently, the decline in abundance and growth in plaice stocks may be related to the more recent decline in productivity of the benthic system and associated changes in benthic biodiversity (Tulp et al. 2008). Changes in shrimp *Crangon crangon* (Linnaeus, 1758) abundance may also add to the decline (Tulp et al. 2008) because they are important predators of small juvenile plaice (Wennhage 2002; Gibson et al. 2002).

Influence of fishing and recruitment

Fishing mortality was investigated as an additional factor potentially complicating the assessment of the environmental impact on fish populations, because spatial differences in fishing effort can explain spatial changes in abundance (e.g. Perry et al. 2005; Dulvy et al. 2008). However, in shallow areas of the North Sea no effect of beam trawl fishery on the abundance of plaice in the Wadden Sea was found (Tulp et al. 2008). The shift of juvenile plaice to deeper water observed in coastal areas further contrasts with increasing offshore fishing intensity (van Keeken et al. 2007). Also, in the deeper areas of the North Sea fishing mortality was not correlated with changes in latitudinal, longitudinal, or depth distribution, and therefore cannot predict plaice distribution (Engelhard et al. 2011). Similarly, although a reduction in stocks of commercially targeted species was recorded in the Bay of Biscay, the analysis of trends in abundance of fish communities revealed no impact of exploitation (Hermant et al. 2010). Nevertheless, overfishing could amplify the effects of climate change (Perry et al. 2005; Hermant et al. 2010).

In the Kattegat/Skagerrak, analyses on the effects of fisheries focus exclusively on the data from the deeper groundfish surveys. Here, historical declines in plaice stocks have been attributed to high fishing pressure in the region (Cardinale et al. 2010, 2011). The recent increase in plaice biomass on the northwestern Danish Skagerrak coast, also recorded by Ulrich et al. (2013), occurs, however, in spite of an increasing trend in fishing effort, whereas the eastern stocks apparently have been eradicated by overexploitation. This increase may be due to large year-classes and strong recruitment in the last decade, which might reflect increased water temperature, reduced predation mortality because of declining cod stocks, or an increased productivity of benthic prey stimulated by trawling (Cardinale et al. 2010). This contrasts conclusions about a negative influence of increasing temperatures and trawling effects on food abundance in the shallow Wadden Sea area (Tulp & Bolle 2009).

Cod: trends in abundance and distribution

Shallow/coastal waters

Reports about trends in abundance of cod in shallow and coastal areas along the continental coast of the Northeast Atlantic are scarce. Few studies exist from the North Sea and Skagerrak/Kattegat (Table II, Figure 1). Estimates of the stock spawning biomass from the Scottish groundfish survey or the International Bottom Trawl survey in the North Sea indicate a decline of cod in coastal areas along the British east coast from the

Table II. Trends and potential causes of changes observed in cod abundance in various areas of the North Sea and the Skagerrak/Kattegat.

Area	Years of data	Trend	Identified or hypothesized cause	Reference
North Sea				
Shallow, coastal				
13 British east coast	1983–2005	↓ since 1983	Environmental changes Fishing pressure	Holmes et al. (2008)
14 Continental coast	1971–2010	↓ since 1993	Predation by/competition with herring Temperature effects on recruitment	Hjermann et al. (2013)
4 Continental coast Wadden Sea	1970–2006	↓ since 1980s ↑ since 1995 in coastal zone	Seal predation Prey removal by beam trawl fishery Oligotrophication, reduced food Decreased cod recruitment offshore	Tulp et al. (2008); Tulp & Bolle (2009)
Deep, offshore				
15 Entire	1970–2003	↓ since mid 1980s	Overfishing Temperature effects on production and recruitment	Brander (2007)
16 Entire	1983–2005	↓ since 1983	Environmental changes Fishing pressure	Holmes et al. (2008)
17 Entire	1929–1999	↓ since mid 1980s	Not identified	Lescrauwaet et al. (2010)
6 Entire	1973–2005	↓ since mid 1980s	Increased fishing effort Temperature/food effects on recruitment	Rijnsdorp et al. (2010)
Skagerrak/Kattegat				
Shallow, coastal				
18 Eastern Skagerrak	1968–1980 1975–1999 2000–2001	↓ since 2000	Increased fishery exploitation Lacking recruitment offshore	Svedäng (2003)
19 Inshore Skagerrak/ inshore Kattegat	1955–1997/ 1975–1999	↓ since 1970s	Exploitation of local stocks and disappearance of spawning aggregations Variable recruitment from North Sea	Svedäng & Bardon (2003)
Deep, offshore				
20 Eastern Skagerrak Eastern Kattegat	1978–1999	↓ since 1982 ↓ since 1978	High fishing pressure	Svedäng & Bardon (2003) Cardinale & Svedäng (2004)
21 Kattegat/Öresund	1981–2008 1981–2000, 2004–2008	↓ since 1981	High fishing pressure	Svedäng et al. (2010)
22 Skagerrak/Eastern Kattegat	1907–2007	↓ since 1980s ↑ since 1998	Fishery exploitation	Bartolino et al. (2012)

Note: Downward arrow indicates decline, upward arrow indicates increase in abundance of cod. Numbers refer to the location of the study in Figure 1.

mid-1980s (Holmes et al. 2008) or the Danish, German and Dutch coasts from the early 1990s (Hjermann et al. 2013). Dutch surveys covering the continental coast and Wadden Sea area have confirmed the decrease in stocks in shallow areas (Tulp et al. 2008; Bolle et al. 2009a). Here, cod declined following increased abundance during the 1970s–1980s in most areas ranging from the western Dutch Wadden Sea to the North Frisian Wadden Sea (Tulp et al. 2008). The decline of cod, however, was spatially heterogeneous and was particularly strong in the eastern Wadden Sea and northern Frisian waters compared with the western Dutch Wadden Sea (Bolle et al. 2009a).

In the Skagerrak and Kattegat, knowledge about coastal cod stocks is restricted to the eastern, Swedish coast. A severe reduction in abundance was previously recorded in landings by fishermen, sport fishermen and the mixed *Nephrops* fishery in coastal waters during the 1980s (Svedäng 2003; Svedäng & Bardon, 2003).

Deep/offshore waters

Cod is one of the most important commercial fish species, but in recent decades stock size estimated from groundfish surveys and landings have declined almost throughout the species range, following the gadoid outburst from the late 1960s to the mid-1980s (Brander 2007; Holmes et al. 2008; Lescrauwaet et al. 2010; Rijnsdorp et al. 2010). This tendency is more prominent for North Sea cod, in which the spawning stock biomass has declined from a maximum of 277 $\times$ 10^6 kg in 1971 to a minimum of 22 $\times$ 10^6 kg in 2006. Since this low, there has been some increase in the biomass (Figure 2; ICES 2015). Similar to that seen in plaice, the decline of the cod stock was accompanied by distributional changes identified from international bottom trawl surveys in deeper waters of the North Sea (Hedger et al. 2004). The analysis of trends in the spatial distribution in the years 1980–1999 revealed that the bulk of mature cod was distributed in the shallower waters of the German Bight during 1980–1989, but shifted toward the deeper northern areas in the following decade (Hedger et al. 2004). This generally agrees with a northward shift in the mean latitude of cod distribution and increase of mean depth in the North Sea (Perry et al. 2005; Dulvy et al. 2008).

The analysis of otter trawl surveys revealed that cod stocks in the Skagerrak and Kattegat have also declined rapidly since the early 1980s (Cardinale & Svedäng 2004; Bartolino et al. 2012). During the last decade, however, spawning stock biomass showed a moderate increase in the western Skagerrak (Bartolino et al. 2012). In the eastern Kattegat, in contrast, biomass continuously declined and reached historically low levels in several subpopulations (Svedäng et al. 2010; Bartolino et al. 2012). Older age groups in particular declined and disappeared in the northern and western Kattegat and along the Swedish west coast, in contrast to increased age diversity found in the Öresund, where trawling is prohibited (Svedäng & Bardon, 2003; Svedäng et al. 2010).

Synopsis

The few known trends in the abundance of cod in shallow, coastal areas of the North Sea and the Skagerrak/Kattegat identified in various surveys largely follow those of landings and surveys of cod in deeper water. However, the observed decline in coastal waters appears to be much more pronounced than offshore. This is apparent from a greater decline of cod in inshore areas compared with offshore areas along the British east coast (Holmes et al. 2008) or the Danish and German coasts (Hjermann et al. 2013) based on survey data. In the Skagerrak/Kattegat, large fish virtually disappeared in coastal waters compared to offshore areas (Svedäng 2003; Svedäng & Bardon 2003). However, this decline preceded the decline in offshore areas by 5–10 years. Because these data are based on landings of sport fishermen, this needs to be interpreted with caution.

Potential causes for changes in abundance and distribution of cod

Temperature effects

Few studies have so far explicitly analysed the causes of the decline of cod in near-shore or coastal areas, so reasons for the decline remain largely unclear. Therefore, very little is known about the effects of temperature on cod abundance or distribution in coastal, shallow areas and most information originates from analyses of stocks in deeper areas, even in those studies including coastal areas (Holmes et al. 2008, Hjermann et al. 2013). A decreasing abundance and spatial shifts in the North Sea cod stock have been linked primarily to increasing seawater temperature and, therefore, climate warming (Hedger et al. 2004; Perry et al. 2005; Dulvy et al. 2008). The exact mechanisms, however, are not clear. The southern North Sea might have become too warm to support a resident population. However, the effect of temperature is not evident in the distributional patterns of adult cod. Righton et al. (2010) made direct observations of habitat occupation of adult cod, showing that they will be able to tolerate warming seas within a wide range, but they suggest that climate change will affect cod populations at earlier life-history stages, as well as cod prey species. Direct effects of temperature on development, growth and survival could have reduced the recruitment (Hedger et al. 2004; Rijnsdorp et al. 2010). This effect was shown by Planque & Frédou (1999) when they combined analyses of recruitment variability of several cod stocks in a single meta-analysis. They demonstrated that recruitment of Atlantic cod is linked to interannual fluctuations in temperature in such a way that for stocks located in warm water, as also seen in the North Sea and Skagerrak/Kattegat, the relationship is negative, but for stocks located in cold water the relationship is positive.

Habitat changes

In the study of the long-term dynamics of demersal fish in the coastal zone and the Wadden Sea, the decline of cod in coastal waters was negatively correlated with the abundance of predators (seals) and beam trawl effort and positively correlated with run-off and nutrient load, but these correlations were not significant (Tulp et al. 2008; Bolle et al. 2009a). The causes of the particularly strong decline of coastal cod detected in the Scottish and International Bottom Trawl surveys also remain unknown (Holmes et al. 2008; Hjermann et al. 2013). The simultaneous decline of cod in the Wadden Sea and deeper areas during the 1980s, however, could indicate that the dynamics of cod stocks in shallow water are strongly influenced by processes acting on North Sea stocks in general (Tulp et al. 2008; Bolle et al. 2009a).

Influence of fishing and recruitment

Fisheries exploitation together with effects of climate change are the major but controversial causes of the decline in North Sea cod populations (Horwood et al. 2006; Brander, 2007; Rijnsdorp et al. 2010; Engelhard et al. 2014). Again, knowledge is largely restricted to deeper, offshore areas. North Sea cod stocks have been subjected to extensive fishing pressures. A latitudinal gradient in fishery effort with greater trawling in the southern and the central North Sea than in the Northern North Sea could cause overall distribution shifts and deepening of the mean depth of cod stocks, if the species has several subpopulations of which only some are highly exploited (Dulvy et al. 2008; Rijnsdorp et al. 2010; Engelhard et al. 2014).

In the Skagerrak and Kattegat, fishing pressure was identified as the most important variable explaining adult fish abundance in shallow and deep areas, but there was no correlation with environmental factors and climate indices (Cardinale & Svedäng 2004; Svedäng et al. 2010; Bartolino et al. 2012). Very high fishing pressure in the Skagerrak and Kattegat, as well as along the eastern Swedish coast, has likely caused the eradication of local spawning aggregations and has largely increased the dependence on transport of recruits from the North Sea (Svedäng et al. 2010; Bartolino et al. 2012). Therefore, recruitment depends strongly on the reproduction of the North Sea stock and favourable wind and temperature conditions (Cardinale & Svedäng 2004). Such intermittent and variable transport was demonstrated by cod larvae surveys and genetic studies (Knutsen et al. 2004; Svedäng & Svenson 2006). The recent increase in adult cod abundances in the western area of the Skagerrak, therefore, may result from a major contribution from the neighbouring North Sea cod population to the Skagerrak rather than recovery of the local aggregations (Bartolino et al. 2012). The decline recorded in landings from inshore areas at the Swedish east coast of the Skagerrak/Kattegat might be similarly caused by a lacking recruitment of overfished stocks from offshore areas (Svedäng 2003; Svedäng & Bardon 2003).

Conclusions

In comparison to an increasing knowledge about long-term changes in the fish fauna in offshore waters of the northeastern Atlantic continental shelf, near-shore studies systematically investigating trends in abundance, distribution, or community composition in relation to water depth or distance from shore are limited to a few case studies in areas such as the Dutch Coast/Wadden Sea (Tulp et al. 2008; Bolle et al. 2009a) or the western Swedish coast of the Skagerrak/Kattegat (Svedäng et al. 2010; Bartolino et al. 2012). In addition, few studies at present address potential drivers of changes in coastal ecosystems (e.g. Collie et al. 2008; Tulp et al. 2008; van der Veer et al. 2011). This essentially reflects limited data availability as a result of restricted spatial overlap of shallower coastal areas with regular, large-scale bottom-trawl monitoring surveys or a lack of records of fish caught by the smaller fishing vessels exploiting coastal areas during short fishing trips (1–3 days).

The few observations available for shallow, near-shore areas generally appear to integrate broadly into the large-scale changes recently described for North Atlantic fish fauna. However, common trends need to be interpreted with caution because shallow areas often harbour the early year-classes of fish, which use the areas as nursery grounds and, therefore, trends and the effects of environmental factors or fisheries influencing the abundance in both habitats might principally differ. In the North Sea, the observed decline in some coastal areas matches the long-term trends in the erosion of southern distribution boundaries, in north- or westward shifts in distribution centres, or in the contraction of demersal fish stocks extracted from bottom-trawl surveys. Notably, the considerable increase in the mean depth of demersal fish in the North Sea and in the Wadden Sea would provide a fundamental explanation for decreasing catches in near-shore fishing grounds, particularly in the case of plaice. The shallow-water emigration and spatial stock redistribution might represent a general latitudinal trend along the continental shelf that restricts the presently dense coastal populations of cod and plaice largely to the north and into western Skagerrak. This process needs to be investigated further, especially with regard to the potential role of a spatial relocation of spawning stocks for the recruitment of juvenile stages in shallow nursery areas, which is the least-understood process.

The various factors causing the changing trends in abundance and distribution in near-shore and also offshore shelf waters are not fully understood at present. Although common factors such as temperature or fisheries are often invoked as major factors in both coastal and offshore areas, changes will affect the different age groups in the habitats differently. Fundamental differences apparently exist in the significant variables identified for changes in plaice and cod abundance in the North Sea and the Skagerrak/Kattegat. In the latter, a continuously high fishing pressure, together with a strong dependence of local recruitment on transport from the North Sea, seemingly prevents the recovery of overexploited plaice and cod stocks (e.g. Cardinale et al. 2011; Bartolino et al. 2012). At present, however, it is unclear whether this affects inshore and offshore abundance of juveniles similarly. In contrast, changes in distribution and abundance in the North Sea are largely attributed to changing environmental factors (Tulp et al. 2008; Dulvy et al. 2008; Simpson et al. 2011). In particular, direct and indirect responses of juvenile and adult fish to increasing seawater temperature dominate the present discussion on the causative effects. However, temperature alone cannot explain the observed decline of fish in coastal areas, and the causes may be more complex, involving long-term trends not only in climate but also in nutrient loading, food availability, and changed larval transport or immigration/emigration patterns. In addition, the impact of anthropogenic activity, such as eutrophication, pollution, or habitat destruction, has to be considered when evaluating changes in local fish stocks.

Acknowledgements

We are grateful to the anonymous reviewers for valuable comments on earlier versions of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The work was supported by the EU and the Danish Ministry for Food through the European Fisheries Fund (EFF): Kyst-fisk-I (reference no. 33010-12-p-0230).

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