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Changes in distributional patterns of plaice *Pleuronectes platessa* in the central and eastern North Sea; do declining nutrient loadings play a role?

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ABSTRACT

Since the beginning of the 1990s, there has been a change in the relative distribution of smaller age-classes of plaice *Pleuronectes platessa* (age 1–3) in the North Sea. The abundances have increased in deeper, more offshore areas, while coastal abundances have been stagnant or declining. For the same time period available time series data on nutrient conditions in the coastal North Sea area show that the freshwater nitrogen loading has decreased by about 50%. While nutrient concentrations in the ambient environment have been shown to influence growth in juvenile plaice through influence on their prey, we here inspect the potential linkage between distributional changes in plaice and the decline in nutrient loading. We compare plaice observations in coastal areas in the eastern North Sea, which have experienced large changes in eutrophication, with observations for the Dogger Bank, a large sandbank in a shallow offshore area of the North Sea. The Dogger Bank, was used as a reference location assuming this area has been less influenced from coastal eutrophication but similar regional climate conditions, and here we found no changes in the abundances of juvenile plaice. The increase in the use of offshore habitats as nursery areas by juvenile plaice in the North Sea appears not related to water depth per se but driven by specific processes dominating in near-shore areas and may be related to changes in nutrient loadings. This point to the importance of separating more general depth-related factors from conditions specific for near-shore areas, such as nutrient loadings in coastal waters and export offshore. The concurrent changes in environment and in distribution of juvenile plaice may have implications for environmental and fisheries management.

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1. Introduction

Marine coastal areas in the North Sea have long been regarded as important nursery areas for juveniles of several marine fish species including plaice *Pleuronectes platessa* (Linnaeus, 1758) a demersal boreal species abundant in the North Sea (van Beek et al., 1989: van der Veer et al., 2016). Adult plaice are generally found in deeper waters where they perform migrations between summer feeding areas in the north and winter spawning areas in the south (Rijnsdorp and Pastoors, 1995; Bolle et al., 2009).

In recent decades, considerable changes were reported in the landings, abundance and distribution of plaice in the North Sea (Tulp et al., 2008; Rijnsdorp et al., 2009). In particular the decline and ultimately total absence of age 1 plaice in the coastal nurseries in Southern North Sea (van Keeken et al., 2007; Teal et al., 2012; Poos et al., 2013) have initiated investigations on the potential underlying processes. The changes have been linked to warming of the coastal and shelf seas, when higher temperatures may have rendered coastal habitats less suitable for species with relatively low upper temperature tolerance limits for growth,

or for species with high juvenile fish energy demands (van der Veer et al., 2011). Such increase in energy demands, coupled with a decreased benthic productivity (Tulp et al., 2008) and competition for food from other flatfish and gobiids (van Hal et al., 2010; Freitas et al., 2012) may have exacerbated the changes and caused the juveniles to move offshore at an earlier age.

Changes in growth rate of plaice have also been reported. Growth rate in juvenile plaice in coastal areas was positively correlated to eutrophication from the mid-1950s to the 1980s (Rijnsdorp and van Leeuwen, 1996). During this period increased primary and secondary production in the coastal North Sea coincided with increased input of nitrates and phosphate (Colijn et al., 2002). For the intermediate sizes (15–30 cm) of plaice the increased growth rate could be attributed to both eutrophication and effect of beam trawling because these sizes are found in deeper waters where fishing takes place. Beam trawling is believed to enhance food availability directly by damaging benthic organisms and indirectly by causing a shift from "low-productive, long-lived species to high-productive, short-lived species" (Rijnsdorp and van Beek, 1991). After the 1980s growth rates began to decline. Boddeke and Hagel (1991) proposed the decline in phosphate loading as an explanation but found it debatable, since all other parameters related to primary production remained constant during the 1980s. The

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observed lower growth rates may, however, also be due to intraspecific competition caused by the appearance of two strong recruiting year-classes in 1981 and 1985 (Rijnsdorp and van Leeuwen, 1996).

Coastal eutrophication takes place when there is excess loading of organic matter to a system (Nixon, 1995). In coastal waters eutrophication typically results from excessive supply of inorganic nutrients via major European rivers, which subsequently stimulates primary productivity and increases the supply of organic matter to the benthos, and lead to a suite of other ecosystem effects. Among these effects are increasing abundances of deposit feeders especially in estuarine systems (Josefson and Rasmussen, 2000). With the implementation of the EU Urban Waste Water Directive (1991), a new era began for European coastal waters when the nutrient loading to coastal systems was targeted by a series of reductions. Reductions in nutrient loadings have been observed in Danish coastal waters, accompanied by a decrease in total benthic macrofauna (Rieman et al., 2016).

With this study we aimed to examine if the continued decline in the abundance of juvenile plaice along the coastal North Sea has been correlated to reductions in nutrient loadings and thus related to prey conditions. To this we used nutrient concentrations as a metric of system productivity. The effects of eutrophication generally decrease with distance from the coast. We therefore expected any impact associated with nutrient loading to be greatest in near-shore areas. The trends in distribution of plaice in near-shore shallow areas were therefore compared with trends in plaice distribution in an offshore shallow area (Dogger Bank), where direct coastal eutrophication effects should be comparatively minimal.

Considerable reductions in nutrient concentrations in coastal waters of the South West North Sea have occurred. We hypothesise that the subsequent reduced supply of organic matter to the benthos (oligotrophication) will have a detectable influence on plaice distributions. We explored the correlations between nutrient conditions and the distribution of plaice of different age-classes in the shallow and deeper coastal areas of the North Sea. We further examined whether the observed correlations were restricted to the coastal areas and potentially could be attributed to nutrient conditions, by correlating nutrient conditions and the distribution of plaice in different age-classes in shallow coastal areas with those in shallow offshore areas.

2. Material and methods

2.1. Nutrient trend analysis

Data on total nitrogen (TN), total phosphorus (TP), silicate (Si) were obtained from the ICES data website (http://www.ices.dk). Salinity and temperature measurements nearest to the bottom were also obtained from the ICES database. In order to investigate the recent trends in winter nutrient environment in the Danish west coast, which is one of the most important determining factor of spring production for those areas, we used first quarter (Q_1) data on nutrients and salinity within the area framed in latitude 54° N to 57°N and longitude 6°E to 8°E between 1985 and 2011 (Fig. 1).

To examine the trends in nutrient conditions, linear regressions of the relationships between salinity and nutrients were carried out using a General Liner Model approach: $N = a \times$ (salinity $*$ year) $+ b*/$ year) $+ c*$(salinity), where N is concentrations of TN, TP and Si (μM), slope a and intercept b are constants determined for each year. Years where the regressions were not significant (i.e. no linear trend), or there was insufficient data for the regression analysis, were removed. These were 1993 and 2009 for TN, 1991, 1993, 2007 and 2009 for TP and 1993 for Si. As we consider the water column in coastal areas is vertically well-mixed in winter, whole profile data from surface to bottom were used, except salinity data <28, to eliminate the effect of episodic extremely high and very localised nutrient discharge. This lower salinity was chosen as there were very few years with samples with lower salinity and these few samples showed high nutrient concentrations,
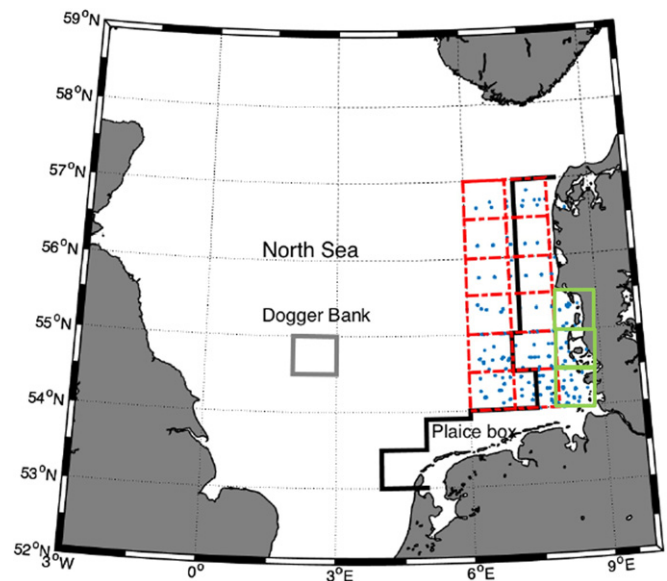

Fig. 1. We will provide a map with better resolution. Overview of the study area in the North Sea. Dogger Bank and Danish Wadden Sea ICES squares are marked in grey and green respectively. Plaice box is marked in black. The ICES squares marked in red cover the Coastal and Offshore areas. The blue dots represent the stations for the nutrient data. Data from ICES database. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

skewing the subsequent regressions. Although both N and P represent essential elements which have been affected by anthropogenic impact, recent trends in concentrations of TN and TP in the North Sea coastal waters were not the same. Their supply over the study period has changed due to changing fertilizer use practices, independent N and P regulatory measures and changing wastewater treatment strategies (Bouraoui and Grizzetti, 2011; Burson et al., 2016; Rieman et al., 2016). Trends in concentration of Si however differ in such that in this region they are essentially not affected by human activity but dominated by yearly precipitation and related river discharge, i.e. catchment hydrology. We therefore used the ratio of TN to Si to remove the contribution from dry and wet years. Therefore, as detailed in the results section, we finally used intercept of TN regression b_{TN} and ratio to intercept of Si b_{TN}/b_{Si} as indicator of nutrient loading without climate inter-annual variability.

2.2. Fish data

In order to examine the trends in CPUE (catch per unit effort, number per hour) of plaice in the Danish west coast, we used ICES NS-IBTS (North Sea International Bottom Trawl Survey) data sampled by standard GOV (Grande Ouverture Verticale) gear between 1991 and 2015. We used winter (first quarter, Q_1) and summer (third quarter, Q_3) data sorted by age-classes in 12 ICES survey rectangles on the Danish west coast and one rectangle at Dogger Bank (Fig.1). Dogger Bank was included to be able to compare trends in a shallow offshore area to a shallow coastal area. Further, to illustrate trends in abundances as one approaches the coastline, data for three ICES rectangles in the Danish Wadden Sea were included (Fig. 1). Each rectangle is 0.5° latitude × 1.0° longitude which is roughly 30 × 30 nautical miles.

Data of 12 rectangles on the Danish west coast were integrated into two groups, those closer to shore named "Coastal" and those further offshore named "Offshore" to compare the difference in trends between coastal and offshore. Ratio of Coastal to Offshore (CPUE$_{Coastal}$/CPUE$_{Offshore}$) were calculated for each age class and log-transformed [log 10 (CPUE$_{Coastal}$/CPUE$_{Offshore}$)] to satisfy the assumption of normality and homogenous variance. The Dogger Bank to Offshore ratio [log10

(CPUE$_{DB}$/CPUE$_{Offshore}$)] was also calculated to refer the trend in the North Sea and effect of depth.

2.3. Correlation analysis between nutrients and fish

In order to examine whether nutrient conditions had significant impact on the recent trend of coastal-offshore distribution of plaice, regression analyses were performed on the log10-transformed relative CPUE [log10 (CPUE$_{Coastal}$/CPUE$_{Offshore}$)] against nutrient indexes, intercept of nitrogen regression line b_{TN} and ratio of intercept of silicate regression b_{TN}/b_{Si}. To examine time lag effect of nutrient environment, nutrient indices of first quarter for any given year Q$_1$(t) were correlated with relative CPUE [log10 (CPUE$_{Coastal}$/CPUE$_{Offshore}$)] of third quarter in the same year Q$_3$(t), and first quarter in the next year Q$_1$(t + 1), which correspond to half year and one year delay, respectively.

3. Results

3.1. Trends in nutrient environment

Fig. 2 presents the salinity and temperature data for the Coastal and Offshore areas, the Danish Wadden Sea areas and for Dogger Bank for Q$_1$ and Q$_3$. Salinities at Dogger Bank and in the Offshore areas were consistently ≥ 34 in Q$_1$ and Q$_3$ except 2001 in Q$_3$. In the coastal areas this varied from 33 to 35 and was generally below 32 in the Danish Wadden Sea areas. No evident trends in temperature in the different areas were

evident during the study period, although, as one approached the coastline, temperatures were slightly colder during winter (Q$_1$) and warmer during summer (Q$_3$) in most years. Fig. 3 presents the nutrient data downloaded from the ICES database and plotted against salinity. A clear temporal trend in the TN vs Salinity can be observed in this data which is apparent as the slope of the relationship decreasing with time from the 1990s (green), through the 2000s (shades of blue) and into the last decade (purple to red). TP and Si also have linear relationships to salinity but no clear temporal trend is apparent in Fig. 3 due to the spread in the data. Fig. 4 shows the time series of slope, a, and intercept, b, from the linear regression analysis between salinity and TN, TP and Si. Both the slope and intercept of TN salinity relationships, a_{TN} and b_{TN}, showed a significant increasing and decreasing trend, respectively, across the whole period (Fig. 4a and b). Similar trends were found for the TP salinity relationships, however, only for the time period up to 2000 (Fig. 4c and d). For the remaining 11 years of the period no significant change in the slopes and intercepts of the TP regressions was detected. The results for silicate contrasted those for TN and TP. Although significant relationships between Si and salinity were found every year, there were no trends in the intercept or slopes of the regression over the time period (Fig. 4e and f). The nutrient salinity relationships can be influenced by both changes in the freshwater concentrations (essentially the intercept of the regressions) and changes in the concentrations in the marine environment (i.e. the North Sea). The average nutrient concentrations at salinities > 34 were calculated in order to examine if a trend was apparent. For all three nutrients no
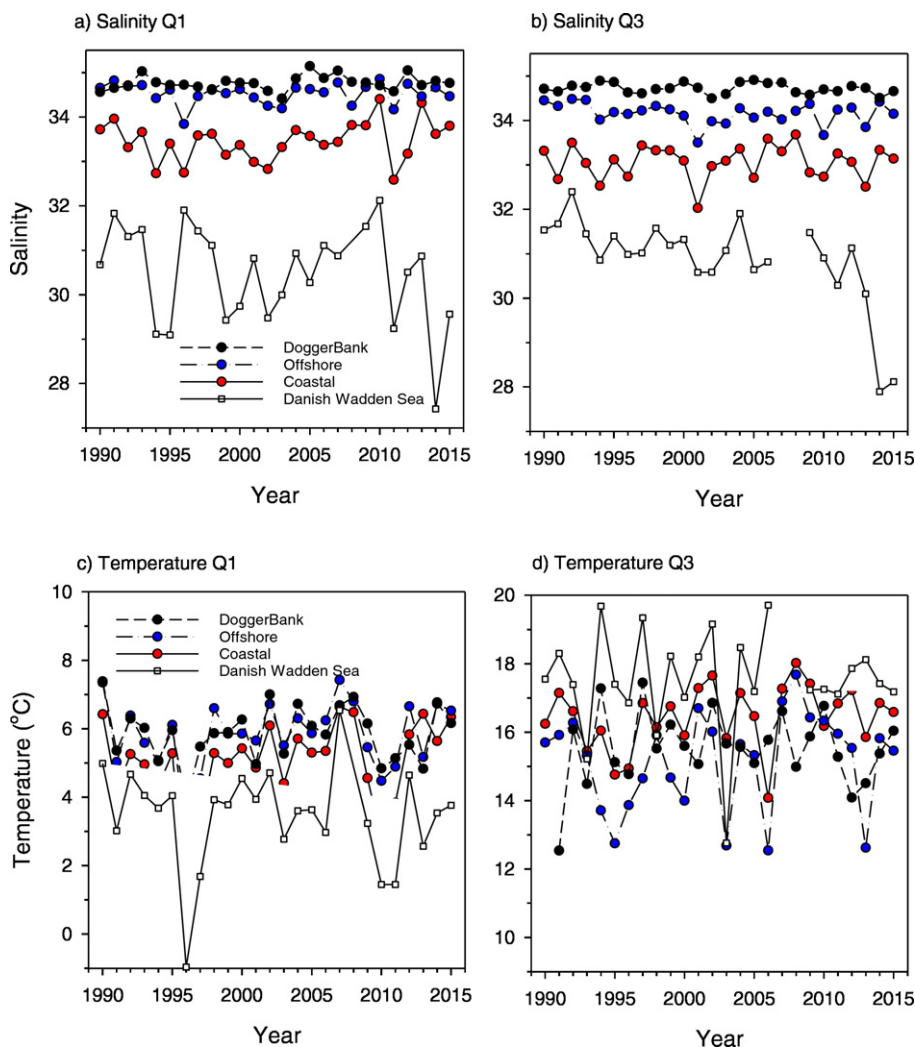

Fig. 2. Data series for salinity (psu) and temperature (°C) for investigated areas (see Fig. 1) in Q$_1$ and Q$_3$. Data from ICES database, values are measurements nearest to bottom.
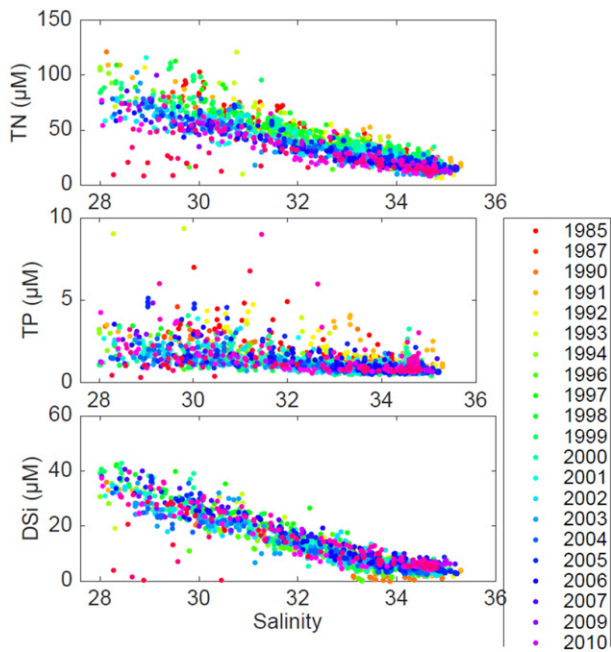
Fig. 3. Regressions of the nutrient data plotted against salinity. Above total nitrogen (TN), middle total phosphor (TP) and below Silicate (DSi). Data from ICES database. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

significant systematic change in the marine winter nutrient concentrations was detected. This indicates that the trends in the salinity relationships (slopes) were solely driven by the variable freshwater nutrient concentrations.

3.2. Trends in CPUE of plaice

Time series of logarithm transformed plaice CPUE in ICES survey rectangles for the Danish Wadden Sea, Coastal and Offshore areas of the Danish west coast and the Dogger Bank, all in the first quarter (Q_1) and third quarter (Q_3) are shown in Fig. 5. Data were plotted for age 1, age 2, age 3 and fish ≥ age 4 were integrated as age 4 +. The Danish Wadden Sea data provided evidence of a temporal decrease in all ages of plaice (Fig. 5 a, b). Hence the declining trend in abundance of plaice becomes more apparent as one approaches the coastline. Decreasing trends in abundances of age 2 and 3 plaice were observed for Q_1 in the coastal areas, whereas the other age groups showed no trends (Fig. 5c). Increasing trends in abundances were observed for all ages in Coastal Q_3 (Fig. 5d) and in both seasons in the Offshore (Fig. 5e, f) and Dogger Bank areas (Fig. 5g, h). The differences in trends of abundances changes between Coastal and Offshore and Offshore and Dogger Bank were further investigated by direct comparison (below).

3.3. Coastal to offshore ratio of plaice CPUE

Fig. 6 (a and b) shows the time series of logarithm transformed Coastal to Offshore ratio of plaice CPUE for all age-classes in first quarter Q_1 and third quarter Q_3. Statistics of time series trend analysis for those ratios were summarized in Table 1. Significant trends of decrease were observed for all age-classes in the first quarter and for age 1 and 2 in the third quarter. Moreover the slopes of decrease were steeper in younger age-classes. The time series of the logarithm transformed Dogger Bank to Offshore ratios of plaice CPUE for all age-classes in both quarters and are also shown in Fig. 6 (c and d). There were no significant trends in the Dogger Bank to Offshore ratios for the young age-classes age 1–3 and a significant increasing trend for the larger plaice (age 4 +; Table 1).

3.4. Correlation between nutrient indexes and CPUE ratio

Relationships between b_{TN} and relative CPUE (Coastal/Offshore) in the third quarter for the same year, Q_3 (t), and the first quarter for the following year, Q_1 (t + 1), are shown in Fig. 7a and c. These relationships between nutrient indexes and relative CPUE of Q_3 (t) and Q_1 (t + 1) correspond to approximately half year time lag and one year time lag from the winter nutrient conditions, respectively. Relationships between b_{TN}/b_{Si} ratio and relative CPUE were also examined for same time lag (Fig. 7b and d). Age 1 and 2 correlated to winter nutrient conditions (Fig. 7a) and the older age-classes, age 2, 3 and 4 + showed positive significant correlations (Fig. 7c). In correlations between b_{TN}/b_{Si} and Q_3 (t), age 1 and age 2 showed significant positive correlation similar to the correlation against b_{TN} (Fig. 6b). In correlations between b_{TN}/b_{Si} and Q_1 (t + 1) (Fig. 7d), age 2, 3 and 4 + showed significant correlations similar to the correlations to b_{TN}.

4. Discussion

4.1. Trends in nutrient indices

The riverine supply of nitrogen, phosphorus and silicate to coastal waters plays a central role in coastal productivity (Skogen et al., 2004). Winter runoff in particular, delivers large quantities of nutrients as a result of greater precipitation and limited winter plant growth in the river catchments. In offshore waters winter vertical mixing of bottom waters with higher nutrient concentrations is the dominant supply. Both processes replenish surface nutrient concentrations that provide the basis for the very productive spring phytoplankton bloom. During the last 30 years water quality regulations have had a considerable effect on riverine nutrient loadings (Conley et al., 2000; Radach and Pätsch, 2007). These effects are also clearly apparent in our dataset. The trends reveal the success of water quality management measures implemented in the countries along the Southern North Sea coast. The TN intercept (b_{TN}) decreased linearly from 488 μmol/L in the late 1980s to 295 μmol/L in 2011; a 40% decrease in regionally integrated winter freshwater TN concentrations. TP freshwater concentrations were similarly reduced by approximately 50% although the reductions were limited to the years before 2000. This reflects the earlier implementation of measures to limit P discharge from point sources and the continued focus on reducing diffuse N loadings in Europe and agree well with earlier reports on nutrient concentration reductions measured directly in river waters in the region (Behrendt et al., 2002; Radach and Pätsch, 2007; Amann et al., 2012).

By the strong relationship between nutrient concentrations and salinity our results illustrate that the surface coastal waters pre-spring phytoplankton bloom nutrient concentrations in the study region have been considerably reduced for TN and TP, while silicate concentrations have not changed (see Fig. 3). The shift in N:P accompanying the initial decline in TP led to changes in the phytoplankton community (Burson et al., 2016) along the Dutch and Danish coasts. The more recent declines in TN will most likely alter the TN:Si ratios. Our results show a slight increase in TN:Si offshore, which may be due to transport of excess Si from coastal areas. The contrasting behaviour of silicate relative to TN and TP reflects the fact that silicate concentrations are more controlled by hydrological changes in the catchment (e.g. damming) rather than anthropogenic discharge. As a result the silicate relationships reflect year-to-year hydrological differences driven mostly by climate. The fact that no significant temporal trend in the silicate-salinity relationships is found indicates that the trends for TN and TP observed are not climatically driven. In the correlations between nutrient indices and relative CPUE in Q_3 (t), significance against b_{TN}/b_{Si} were stronger than in the case of b_{TN} in all significant age-classes. This indicates that b_{TN}/b_{Si} is a useful index to distinguish between anthropogenic and hydrological forced changes in regions of freshwater influence.
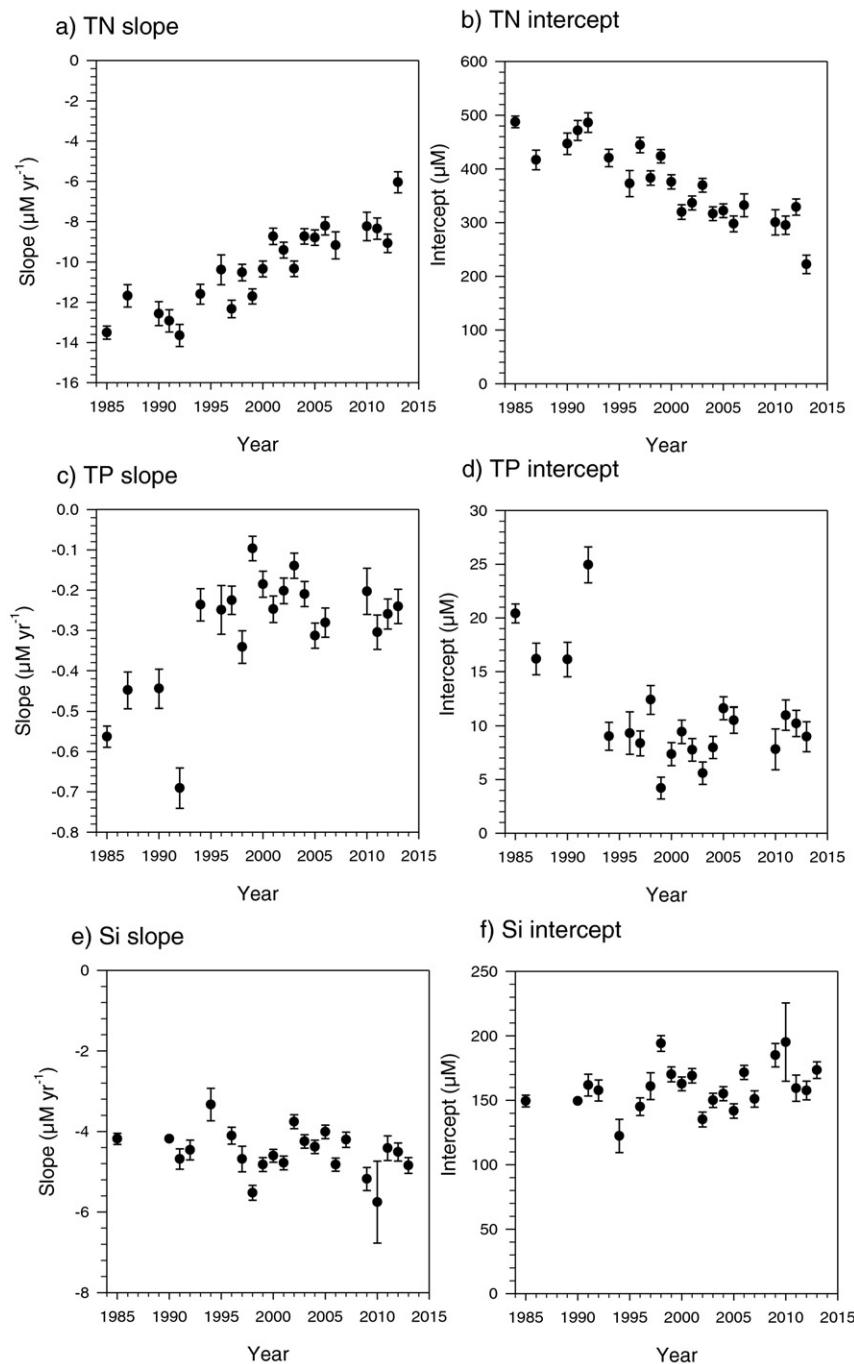
Fig. 4. Slopes and intercepts for regressions of nutrients 1985–2014, a–b) total nitrogen (TN), c–d) total phosphor (TP) and e–f) Silicate (Si). All in µM yr^{-1}. Dots represent the regression coefficients. The error bars represent the standard error of each coefficient. The regression was done in one step using a GLM (general linear model). Years with no significant linear relationships are not shown. These were 1993, 2009 and 2014 for TN, 1991, 1993, 2007, 2009 and 2014 for TP, and 1993 and 2014 for Si.

The ~50% reduction in nutrient concentrations that these coastal waters have experienced has implications for the overall productivity here. The intensity of the spring phytoplankton bloom in the region is largely determined by winter nutrient concentrations (Skogen et al., 2004). Increasing light levels, high nutrient concentrations and water column stratification in the spring initiate the phytoplankton bloom. The bloom is often dominated by large phytoplankton organisms such as diatoms, which sink and provide an important supply of organic material to the benthic fauna which are the main prey for demersal fish. Consequently, the winter nutrient concentration reductions may have an effect on fish species that rely on the benthos as prey.

4.2. Trends in of plaice mean CPUE in coastal, offshore and Dogger Bank

Coastal shallow areas along the North Sea have historically provided nursery habitat for plaice (Zijlstra et al., 1982) and produce up to 90% of the recruits of North Sea plaice (van Beek et al., 1989). Up to the 1980s three age-classes of plaice (age 0, 1, and 2) were abundant in these coastal areas during the summer growth season (van der Veer et al., 2011). These areas have undergone major changes in the last decades due to climate change, changes in human activities such as fishing and eutrophication, and changes in the abundance of top predators such as seals and birds (Leopold et al., 1998; Philippart et al., 2007). Larger
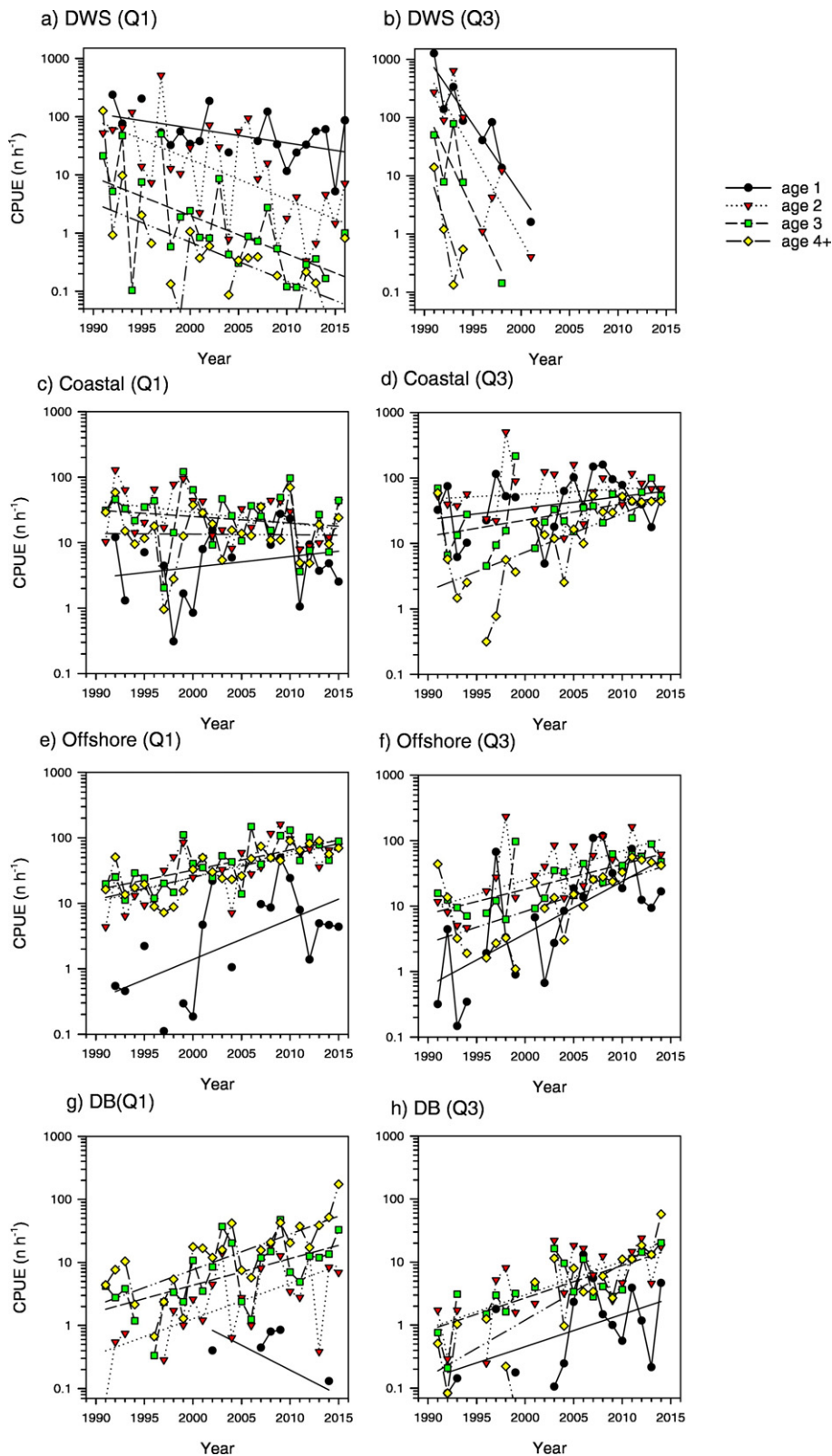
Fig. 5. Time series of mean CPUE (n h^{-1}) for each plaice age class in ICES survey rectangles as in Fig. 1, for: a–b) Danish Wadden Sea area (DWS), c–d) Coastal areas off the Danish west coast, e–f) Offshore areas and g–h) Dogger Bank area (DB). All for the first quarter (Q1) and third quarter (Q3).

vessel fisheries were banned from 1989 along the Southern North Sea (Plaice Box, ICES, 1994) to reduce discards of juvenile plaice, based on the differential spatial distributions of juvenile and adult plaice. The lack of positive results was attributed to concurrent changes in the distribution in particular an offshore movement of juvenile plaice and

instigated studies on the potential causes for this directed movement (Beare et al., 2013) the latter of which were also recently reviewed in Dutz et al. (2016).

The offshore movement that we exemplify by the present comparison of specific coastal and more offshore areas has been attributed to
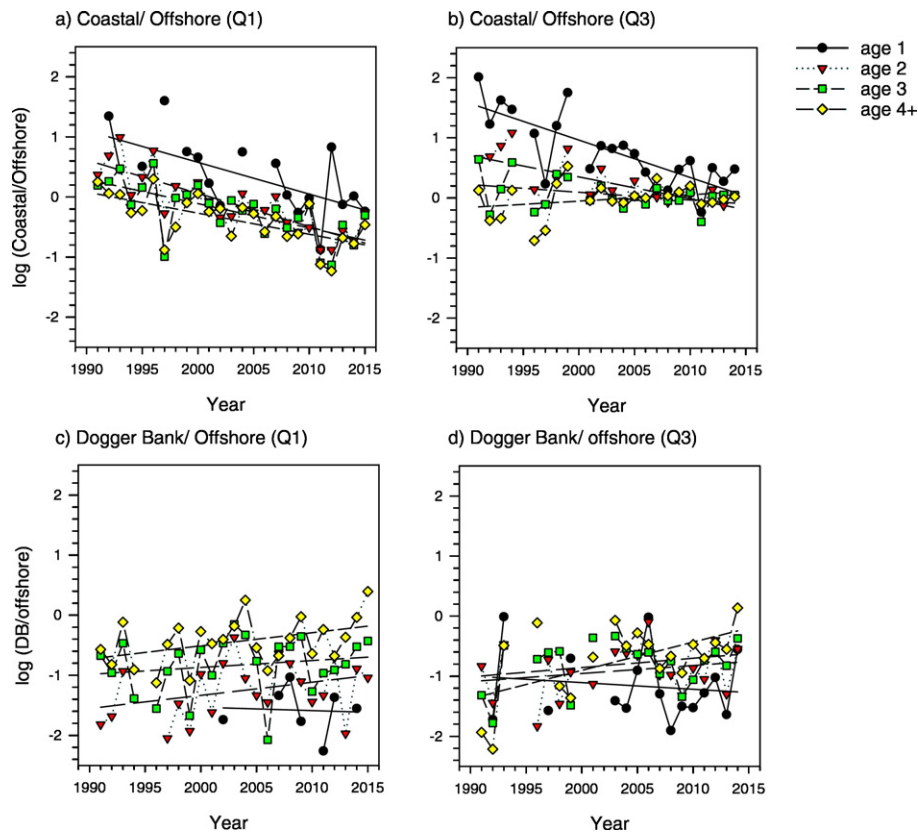
Fig. 6. Time series of logarithm transformed ratios of plaice CPUE for four age classes. a–b) Coastal to Offshore ratios, and c–d) Dogger Bank to Offshore. All for first quarter (Q_1) and third quarter (Q_3). Statistics of time series analysis for these ratios are summarized in Table 1.

increased sea surface temperatures that may affect juvenile plaice in two ways: The high summer temperatures may exceed the upper temperature tolerance limits for growth, which is >20 °C for plaice (van der Veer et al., 2009), or the higher temperatures increase energy demands (van der Veer et al., 2011) requiring a higher benthic productivity. Benthic production has been shown to be a limiting factor for juvenile

Table 1
Statistics of the relationship between year and the Coastal to Offshore ratio of plaice CPUE, and the Dogger Bank to Offshore ratio of plaice for the age groups 1, 2, 3 and 4 +. Q_1: Survey during first quarter of the year, Q_3: Survey during third quarter. Ns = not significant.

	Slope	Intercept	R^2	n	p	Significance
Coastal/Offshore						
Q_1						
Age 1	−0.053	106.2	0.41	18	0.004	***
Age 2	−0.055	110.7	0.69	25	0.0001	***
Age 3	−0.041	80.9	0.44	25	0.0003	***
Age 4 +	−0.035	70.2	0.43	25	0.0004	***
Q_3						
Age 1	−0.062	125.7	0.60	22	0.0001	***
Age 2	−0.036	76.2	0.52	22	0.0002	***
Age 3	−0.013	26.3	0.13	22	0.099	ns
Age 4 +	0.011	−21.5	0.08	22	0.212	ns
Dogger Bank/Offshore						
Q_1						
Age 1	−0.006	9.5	0.003	18	0.90	ns
Age 2	0.022	−45.0	0.11	22	0.13	ns
Age 3	0.016	−24.0	0.03	24	0.40	ns
Age 4 +	0.022	−44.2	0.17	24	0.046	*
Q_3						
Age 1	−0.011	20.9	0.02	16	0.65	ns
Age 2	0.013	−27.5	0.001	20	0.33	ns
Age 3	0.016	−31.9	0.08	20	0.23	ns
Age 4 +	0.047	−95.1	0.33	19	0.010	*

* $p < 0.05$.
*** $p < 0.0005$.

growth and survival in some nursery areas (Nash et al., 2007). Both temperature tolerance and limited food availability would cause the fish to move either towards colder regions or, in the case of increased energy demands in situations where food availability is poor, the fish may move to other areas where food availability is higher to maximize their scope for growth (van der Veer et al., 2009).

Coastal areas are highly productive and, with eutrophication, the benthic community switched to opportunistic highly productive species in the decades up to the 1980s (Rijnsdorp and Vingerhoed, 2001). This increased productivity correlated positively with growth rate in plaice during that period (Rijnsdorp and van Leeuwen, 1996). After the 1980s growth rates in juvenile plaice decreased and P was proposed as a main driver, due to the decrease in riverine loadings of P during this period (Brockmann et al., 1990; Boddeke and Hagel, 1991). Also, since the 1980s, decreases in benthic productivity associated with reductions in nutrient loadings were suggested as one of the main drivers for the observed changes in the distribution patterns (Tulp et al., 2008). Further, long-term annual variations in size of juveniles were related to nutrient concentrations (used as a proxy for system productivity) on Dutch, German and Danish coasts (Teal et al., 2008). P concentrations have since remained at a stable comparatively low level since around 2000, whereas N loadings have decreased significantly during the subsequent decades. Most likely N levels have now become the important determining factor for benthic production in these coastal areas. This is supported by the findings of this study where CPUE of plaice has increased both offshore and on Dogger Bank, but not coastal along the Danish west coast. The declining tendency in the Coastal areas were, however, only seen for age 2 and 3 in Q_1, but became more defined in the more coastal Wadden Sea area for all ages and both Q_1 and Q_3. This could reflect a decline in habitat quality as one approaches the coast in recent years. Temperature and food availability are among the primary factors determining habitat quality (Gibson, 1994) and fish distribution patterns (Rijnsdorp et al., 2009). However, we did not detect
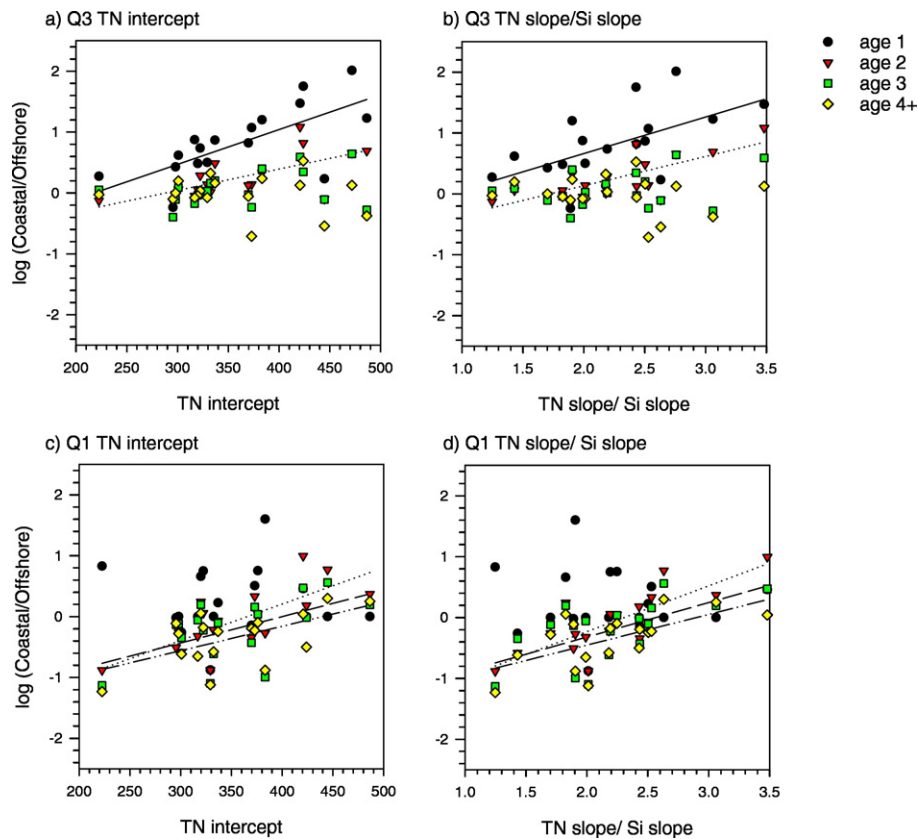
Fig. 7. Correlation between the relative CPUE (CoastalOffshore) for four yearclasses of plaice and nutrient regression parameters. a–b) in the third quarter for the same year $Q_3(t)$ and c–d) in the first quarter of the following year $Q_1(t + 1)$. Regression lines are only plotted for significant relationships ($p < 0.01$). Age 1 correlated to winter nutrient conditions. Older ages correlated to previous year.

trends in temperature during the study period and therefore the decline in use of coastal nursery habitat by juvenile plaice may be due to limited food availability inshore.

The increased use of the offshore areas may be related to improved food conditions in these areas. The reductions in TP at the start of our study period and decline in TN midway during the study period may have led to an excess of silicate in coastal waters and potentially a greater export to offshore waters. Although Si did not increase, the TN:Si ratio decreased in the offshore areas. The improved TN:Si ratio may have stimulated diatom growth thus resulting in a more efficient transfer of energy and matter from primary producers to fish. The overall depth of the coastal area and Dogger Bank areas are similar. The Dogger Bank, being offshore, is presumably exposed to a similar climatic forcing (cold years, warm years, etc.), but differs in the fact that it is not influenced by riverine anthropogenic eutrophication to the same extent, at least, as the coastal areas; although it is acknowledged that in some years coastal temperatures may be higher, as predicted by a coupled hydro-dynamical and ecosystem model (Teal et al., 2012). This was the reason for our choice of this area as a reference site for the coastal area. The difference in the development of fish abundance in the coastal area relative to that in the Dogger Bank can thus be attributed to processes that are more strongly related to coastal areas. This was supported our results of similar trends for Dogger Bank and Offshore abundances of plaice.

In the coastal area off the Danish coast the estimated average CPUE's were variable with different trends among age-classes and between the two surveys, hence differences in ratios of coastal to offshore were mainly driven by the increasing trend in the offshore area. However a significant decline in especially age 1 plaice are seen in the coastal nurseries in the southern North Sea (Teal et al., 2012; Poos et al., 2013) and intertidal western Dutch Wadden Sea (van der Veer et al., 2011). The results thus indicate that the coastal nursery habitat is unable to support

the increasing North Sea population (ICES, 2013), and that the younger plaice age groups must broaden their depth distribution to search a larger area for food as predicted by MacCall's (1990) habitat basin model and by the Dynamic Energy Budget theory, where fish will change their distribution in an attempt to maximize their scope for growth (van der Veer et al., 2009).

A shift of larger plaice (20–39 cm) towards deeper waters already took place before the 1980s (van Keeken et al., 2007) and may explain why no significant decreasing trends were observed in this study for age 4 + plaice. Our data time series dates back to 1991, i.e. it starts after the reported offshore shift of the larger plaice. The increase in population size of plaice was also reflected in an increase in abundance of age 4 + fish, but only offshore, which indicates no further changes in the distribution of the older plaice in this part of the eastern North Sea.

Apparent correlations do not in themselves point to cause-effect relationships and underlying processes need to be better understood to enhance the predictive powers of studies on the distribution of different size-classes of fish. However, these results indicate that the considerable measures to improve water quality in European waters could influence higher trophic levels. Parallel to the benefits observed in fisheries as a result of the initial stages of eutrophication (Nielsen and Richardson, 1996), subsequent oligotrophication might be influencing fish abundances and their distributions. Thus, there is a need for further exploration of hypotheses on physiological responses to observed changes in species distribution aiming at assessing the effects of anthropogenic forcing and/or climate change on local or regional scale.

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References

Amann, T., Weiss, A., Hartmann, J., 2012. Carbon dynamics in the freshwater part of the Elbe estuary, Germany: implications of improving water quality. Estuar. Coast. Shelf Sci. 107, 112–121.

Beare, D., Rijnsdorp, A.D., Blaesberg, M., Damm, U., Egekvist, J., Fock, H., Kloppmann, M., Röckmann, C., Schroeder, A., Schulze, T., Tulp, I., Ulrich, C., van Hal, R., van Kooten, T., Verweij, M., 2013. Evaluating the effect of fishery closures: lessons learnt from the plaice box. J. Sea Res. 84, 49–60.

Behrendt, H., Kornmilch, M., Opitz, D., Schmoll, O., Scholz, G., 2002. Estimation of the nutrient inputs into river systems – experiences from German rivers. Reg. Environ. Chang. 3, 107–117.

Boddeke, R., Hagel, P., 1991. Eutrophication of the Dutch Coastal Zone, a Blessing in Disguise. ICES C.M. 1991/E: 7.

Bolle, L.J., Dickey-Collas, M., van Beek, J.K.L., Erftemeijer, P.L.A., Witte, J.I.J., van der Veer, H.W., et al., 2009. Variability in transport of fish eggs and larvae. III. Effects of hydrodynamics and larval behaviour on recruitment in plaice. Mar. Ecol. Prog. Ser. 390, 195–211.

Bouraoui, F., Grizzetti, B., 2011. Long term change of nutrient concentrations of rivers discharging in European seas. Sci. Total Environ. 409, 4899–4916.

Brockmann, U.H., Laane, R.W.P.M., Postma, J., 1990. Cycling of nutrient elements in the North Sea. Neth. J. Sea Res. 26, 239–264.

Burson, A., Stomp, M., Akil, L., Brussard, P.D., Huisman, J., 2016. Unbalanced reduction of nutrient loads has created an offshore gradient from phosphorus to nitrogen limitation in the North Sea. Limnol. Oceanogr. 61, 869–888.

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

Conley, D.J., Kaas, H., Møhlenberg, F., Rasmussen, B., Windolf, J., 2000. Characteristics of Danish estuaries. Estuaries 23, 820–837.

Dutz, J., Støttrup, J.G., Stenberg, C., Munk, P., 2016. Potential causes of the observed decline of plaice *Pleuronectes platessa* and cod *Gadus morhua* in shallow coastal waters of the North Sea, the Skagerrak, and the Kattegat – a review. Mar. Biol. Res. http://dx.doi.org/10.1080/17451000.2016.1210806.

Freitas, V., Kooijman, S.A.L.M., van der Veer, H.W., 2012. Latitudinal trends in habitat quality of shallow-water flatfish nurseries. Mar. Ecol. Prog. Ser. 471, 203–214.

Gibson, R.N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Neth. J. Sea Res. 32, 191–206.

ICES, 1994. Report of the Study Group on the Plaice Box, Charlottenlund, 12–15 April 1994. ICES C.M. 1994/Assess: 14.

ICES, 2013. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak, 24–30 April 2013. ICES C.M. 2013/ACOM:13.

Josefson, A.B., Rasmussen, B., 2000. Nutrient retention by benthic macrofaunal biomass of Danish estuaries : importance of nutrient load and residence time. Estuar. Coast. Shelf Sci. 50, 205–216.

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

MacCall, A.D., 1990. Dynamic geography of marine fish populations. Washington Sea Grant Program. Univ. Washington Press, Seattle, pp. 1–153.

Nash, R.D.M., Geffen, A.J., Burrows, M.T., Gibson, R.N., 2007. Dynamics of shallow-water juvenile flatfish nursery grounds: application of the self-thinning rule. Mar. Ecol. Prog. Ser. 344, 231–244.

Nielsen, E., Richardson, K., 1996. Can changes in the fisheries yield in the Kattegat (1952–1992) be linked to changes in primary production? ICES J. Mar. Sci. 53, 988–994.

Nixon, S., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41, 199–219.

Philippart, C.J.M., Beukema, J.J., Cadee, G.C., Dekker, R., Goedhart, P.W., van Iperen, J.M., et al., 2007. Impacts of nutrient reduction on coastal communities. Ecosystems 10, 95–118.

Poos, J.J., Aarts, G., Vandemaele, S., Willems, W., Bolle, L.J., van Helmond, A.T.M., 2013. Estimating spatial and temporal variability of juvenile North Sea plaice from opportunistic data. J. Sea Res. 75, 118–128.

Radach, G., Pätsch, J., 2007. Variability of continental riverine freshwater and nutrient inputs into the North Sea for the years 1977–2000 and its consequences for the assessment of eutrophication. Estuar. Coasts 30, 66–81.

Rieman, B., Carstensen, J., Dahl, K., Fossing, H., Hansen, J.W., Jakobsen, H.H., Josefson, A.B., Krause-Jensen, D., Markager, S., Stæhr, P.A., Timmermann, K., Windolf, J., Andersen, J.H., 2016. Recovery of Danish coastal ecosystems after reductions in nutrient loading: a holistic ecosystem approach. Estuar. Coasts http://dx.doi.org/10.1007/s12237-015-9980-0.

Rijnsdorp, A.D., Pastoors, M.A., 1995. Modelling the spatial dynamics and fisheries of North Sea plaice (*Pleuronectes platessa* L.) based on tagging data. ICES J. Mar. Sci. 52, 963–980.

Rijnsdorp, A.D., van Beek, F.A., 1991. Changes in growth of North Sea plaice *Pleuronectes platessa* L. and sole *Solea solea* (L.) in the North Sea. Neth. J. Sea Res. 27, 441–457.

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

Rijnsdorp, A.D., Vingerhoed, B., 2001. Feeding of plaice *Pleuronectes platessa* L. and sole *Solea solea* (L.) in relation to the effects of bottom trawling. J. Sea Res. 45, 219–229.

Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Möllmann, C., Pinnegar, J.K., 2009. Resolving the effect of climate change on fish populations. ICES J. Mar. Sci. 66, 1570–1583.

Skogen, M.D., Soiland, H., Svendsen, E., 2004. Effects of changing nutrient loads to the North Sea. J. Mar. Syst. 46, 23–38.

Teal, L.R., de Leeuw, J.J., van der Veer, H.W., Rijnsdorp, A.D., 2008. Effects of climate change on growth of 0-group sole and plaice. Mar. Ecol. Prog. Ser. 358, 219–230.

Teal, L.R., van Hal, R., van Kooten, T., Ruardij, P., Rijnsdorp, A.D., 2012. Bio-energetics underpins the spatial response of North Sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) to climate change. Glob. Chang. Biol. 18, 3291–3305.

Tulp, I., Bolle, L.J., Rijnsdorp, A.D., 2008. Signals from the shallows: In search of common patterns in long-term trends in Dutch estuarine and coastal fish. J. Sea Res. 60, 54–73.

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

van der Veer, H.W., Cardoso, J., Peck, M.A., Kooijman, S., 2009. Physiological performance of plaice *Pleuronectes platessa* (L.): a comparison of static and dynamic energy budgets. J. Sea Res. 62, 83–92.

van der Veer, H.W., Koot, J., Aarts, G., Dekker, R., Diderich, W., Freitas, V., et al., 2011. Long-term trends in juvenile flatfish indicate a dramatic reduction in nursery function of the Balgzand intertidal, Dutch Wadden Sea. Mar. Ecol. Prog. Ser. 434, 143–154.

van der Veer, H.W., Jung, A.S., Freitas, V., Philippart, C.J.M., Witte, J.I.J., 2016. Possible causes for growth variability and summer growth reduction in juvenile plaice *Pleuronectes platessa* L. in the western Dutch Wadden Sea. J. Sea Res. 111, 97–106.

van Hal, R., Smits, K., Rijnsdorp, A.D., 2010. How climate warming impacts the distribution and abundance of two small flatfish species in the North Sea. J. Sea Res. 64, 76–84.

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

Zijlstra, J.J., Dapper, R., Witte, J.I.J., 1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. Neth. J. Sea Res. 15, 250–272.