



# Shifts in the timing of spawning in sole linked to warming sea temperatures

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## ABSTRACT

Phenotypic traits such as peak spawning time may vary within and differ between populations in relation to environmental factors, such as temperature. Sole (*Solea solea*) is a valuable, commercially exploited species that spawns in late winter or spring. The date of peak spawning was estimated for each year for seven stocks from monthly fish samples collected from commercial fisheries since 1970. Four out of seven stocks showed a significant long-term trend towards earlier spawning (Irish Sea, east-central North Sea, southern North Sea, eastern English Channel) at a rate of 1.5 weeks per decade. The other three stocks (Bristol Channel, western English Channel and western-central North Sea) failed to show a relationship, but the available time series were limited for these stocks (<10 years). Sea surface temperature during winter significantly affected the date of peak spawning, although the effect differed between stocks. The implications of the effect of winter temperature on the timing of spawning for the population dynamics are discussed.

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## 1. Introduction

Commercial stocks are under pressures imposed by the fishing industry as well as atmospheric temperature rises that have caused the oceans to warm (review: Rijnsdorp et al., 2009). A growing body of evidence shows that many fish populations are responding to climate change in a variety of ways, including decreased or increased productivity of stocks (Brander, 2007; Planque and Frédou, 1999), population expansions, contractions, and shifts in distribution (Engelhard et al., 2011; Perry et al., 2005; Rindorf and Lewy, 2006) or towards deeper waters (Dulvy et al., 2008). Climate change will continue to affect fishery resources in the future, challenging managers to develop sustainable exploitation strategies (Cheung et al., 2009). Importantly, heavily fished species are predicted to be less resilient to climate change possibly due to the additional stress of fishing, which can reduce the age, size, and genetic diversity of a stock (Ainsworth et al., 2011; Brander, 2007; Ottersen et al., 2006). These shifts in distribution and changes in the abundance of stocks could cause economic losses as fisheries are at risk of collapsing and of crossing political or management area boundaries (Roessig et al., 2005).

Relatively little remains known about the possible effects of climate change on the phenology or timing of life-history events of fish populations. In some species low temperatures were correlated with delayed spawning, for example cod, *Gadus morhua* (Hutchings

and Myers, 1994) and capelin, *Mallotus villosus* (Carscadden et al., 1997). Along the same line, higher temperatures have been associated with earlier spawning in North Sea mackerel, *Scomber scombrus* (Jansen and Gislason, 2011) and is suggested for North Sea sole, *Solea solea* (van der Land, 1991). The opposite effect was found in flounder, *Platichthys flesus*, off south-west Britain: in years that were up to 2 °C cooler than normal, fish migrated some 1–2 months earlier from estuarine overwintering habitats to open-sea spawning grounds (Sims et al., 2004), probably as an avoidance reaction to the extreme cold of inshore waters; the fish may also move away earlier to warmer offshore water so their gonad maturation is not impeded (Pawson et al., 2000). It is important to improve our insight into the effects of climate change on the timing of spawning. There are both direct implications for fishery management such as the effectiveness of fishery closures during spawning seasons (Halliday, 1988; Kraus et al., 2009) and indirect effects such as the likelihood of a mismatch between the timing of larval development and the availability of planktonic food sources (Cushing, 1990; Genner et al., 2010).

Here we provide evidence for a shift towards significantly earlier timing of spawning in sole, *S. solea*, over the past 40 years, as a probable response to climate change. The distribution of sole ranges from the shallower parts of the Mediterranean and the north-west coast of Africa in the south, to the Irish Sea and North Sea in the north (Whitehead et al., 1986). We compare various stocks or substocks inhabiting the North Sea, English Channel, Bristol Channel and Irish Sea, where these are of crucial value to the beam trawl fisheries of Europe (Horwood, 1993; van Keeken et al., 2007). These stocks cover broadly similar habitats but are exposed to different annual temperature regimes. As there is evidence that following maturation sole do

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not migrate large distances (e.g., [Rijnsdorp et al., 1992](#)), the extent of mixing between stocks or substocks is probably limited. This is supported by distinct genetic structuring of North-East Atlantic sole into at least three populations, namely the Kattegat/Skagerrak region, the North Sea and the Bay of Biscay, and a likely fourth one, in the Irish/Celtic Sea; with further evidence of finer-scale genetic structuring ([Cuveliers et al., 2012](#)). Between sole stocks, differences in the average date of peak spawning are known to exist, ranging from late March in the Bristol Channel to mid-May in the Irish Sea and late May in the eastern-central North Sea ([Fox et al., 2000](#); [Horwood, 1993](#); [Rijnsdorp and Vingerhoed, 1994](#)). Sea temperatures during winter, when gonads are ripening, have been suggested to influence the timing of spawning in sole ([Rijnsdorp and Witthames, 2005](#)).

Specifically, we test the following three hypotheses:

- (1) Winter sea temperatures in sole habitats have risen significantly in the past 40 years;
- (2) There have been significant shifts in the peak spawning dates of sole; and
- (3) Shifts in peak spawning are related to trends and interannual variability in winter sea temperatures.

## 2. Methods

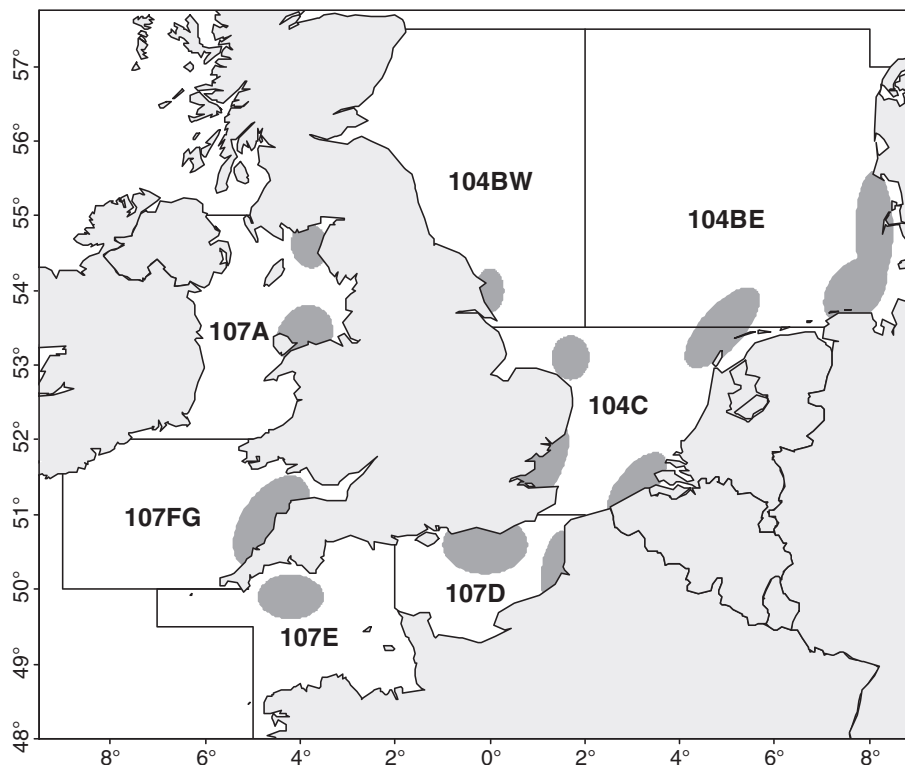
### 2.1. Study populations

This study covers much of the northern portion of the distribution range of sole by including stocks or substocks that correspond to the following ICES fishing regions ([Fig. 1](#)): Irish Sea (Division 107A), Bristol Channel (Divisions 107F and 107G combined as 107FG), Western Channel (Division 107E), Eastern Channel (Division 107D), southern North Sea or Southern Bight (Division 104C), west-central North

Sea (Division 104B west of 2E, 104BW) and east-central North Sea or German Bight (Division 104B east of 2E, 104BE). As each of these sampled divisions contains one or several spawning sites, data from the respective rectangles within these regions are considered to belong to the corresponding sole stock (as in [Rijnsdorp and Vingerhoed, 1994](#)).

### 2.2. Temperature data

Data on winter sea surface temperature (SST) were collated for each of the seven sole substocks. Given that sole tend to show highest densities on shallow grounds with most populations spawning in coastal waters, we used temperature data from coastal monitoring sites situated close to the corresponding sole spawning grounds. Temperatures at inshore sites will likely show greater variations than further offshore; still, interannual variability in coastal winter SST may be considered representative for the variability in winter temperatures experienced by the soles, given the high degree of mixing of waters during winter, and given that cold winters are characterised by colder-than-average coastal as well as offshore water temperatures ([MacKenzie and Schiedek, 2007](#)). For six substocks, SST data held at the Centre for Environment, Fisheries and Aquaculture Science (Cefas) were used, which maintains time-series of monthly temperature recordings at multiple locations around the English and Welsh coasts, as well as on the Isle of Man (see [www.cefas.defra.gov.uk/our-science/observing-and-modelling.aspx](http://www.cefas.defra.gov.uk/our-science/observing-and-modelling.aspx)). For the seventh substock inhabiting the east-central North Sea (104BE), the SST time-series for the Marsdiep (Texel, The Netherlands) was used, maintained by the Royal Netherlands Institute for Sea Research (NIOZ: [www.nioz.nl/nioz0](http://www.nioz.nl/nioz0)) ([van Aken, 2008](#)). Winter temperature was defined as the mean temperature for the first quarter (January–March). See [Table 1](#) for an overview of coastal temperature time-series corresponding to the different sole substocks.



**Fig. 1.** Map of ICES fishing regions corresponding to 7 sole stocks as distinguished in this study. ICES Division 104B was subdivided into 104BE and 104BW to correspond with the relatively small sole spawning population off north-east England and the much larger stock inhabiting the German Bight, respectively. Sole from Divisions 107F and 107G was combined and referred to as 107FG.

**Table 1**

Coastal temperature recording sites corresponding with seven sole substocks examined in this study.

Substock (ICES region)	Time-span	SST monitoring site
Irish Sea (107A)	1983–2009	Port Erin, Isle of Man
Bristol Channel (107FG)	1984–1992	Newlyn, Cornwall
Bristol Channel (107FG)	1993–2008	Ilfracombe, Devon
Western Channel (107E)	1983–2009	Weymouth, Dorset
Eastern Channel (107D)	1983–2009	Eastbourne, East Sussex
Southern North Sea (104C)	1970–2009	Southwold, Suffolk
West-central North Sea (104BW)	1983–2009	Scarborough, North Yorkshire
East-central North Sea (104BE)	1970–2010	Marsdiep, The Netherlands

### 2.3. Sole spawning data

The data on sole came from market sampling programmes in ports in England and the Netherlands, where random samples of fish landed by commercial fishing vessels are taken and biological data collected. For English ports, data were collected by Cefas during 1983–2010, and included 60,711 samples of adult female sole where information on the stage of sexual maturity was available. Owing to difficulty in the maturity staging of male soles, this study includes female fish only. The method of sampling collection is described by Bromley (2000, 2003). An additional 88,424 samples collected at Dutch ports by the Institute for Marine Resources and Ecological Studies (IMARES), collected from 1970–2010, were added. The study included any fish caught during quarters 1, 2 and 3 of the year, covering a time window from well before to well after the known spawning seasons of sole in these regions (Fox et al., 2000; Rijnsdorp and Vingerhoed, 1994).

A 5-stage maturity classification was followed, as is currently common usage in several European marine research institutes (see Table 2). During earlier sampling years, maturity of soles had been staged according to a more detailed maturity classification schedule, as in Bromley (2003). Where this was the case, these samples were here re-classified according to the 5-stage maturity key to allow consistency in the time-series.

### 2.4. Calculating mean spawning week

In order to model the seasonality of spawning in sole we calculated for each week of the year, where samples were available, the proportion of spawning females amongst the total number of sampled adult females. 'Adult' females included all maturing, hyaline, running and spent fish but excluded any immature fish. 'Spawning' females were defined as the combined number of hyaline and running fish. For each substock and for each year, the mean spawning week  $T$  was estimated according to:

$$T = \frac{\sum_i p_i w_i}{\sum_i p_i}$$

where  $p_i$  is the proportion of adult females in week  $i$  that are in spawning stage, and  $w_i$  is the week number.

**Table 2**

Stages of sexual maturity of female sole (Bromley, 2000).

Stage	Description
Immature	Ovaries small, thin-walled and yellowish in colour
Maturing	Full, pink-coloured ovaries with no hyaline eggs
Hyaline	Ovaries contain few to many hyaline eggs but will not run even under pressure
Running	Eggs can be extruded under light pressure
Spent	Ovaries contain very few opaque eggs, which are being reabsorbed; large quantities of slime

The method is analogous with calculating a spatial 'centre of gravity of distribution' but in this case has been used to calculate a temporal 'centre of gravity of distribution' (Bevington, 1969).

The sampling of soles was usually done during weeks distributed regularly throughout the year, but this was not always the case. In some years, sampling in some stocks tended to be concentrated either very early or very late in the year; or sampling effort was very low. To account for a possible sampling bias, the mean sampling week number was calculated by substock and year. We excluded those cases where the mean sampling week was <15 or >35 (sampling limited to the very begin or end of the year, respectively). We also excluded those cases where the sampling intensity of a stock in any given year was very low (<10 observations of spawning fish, or limited to <5 weeks).

### 2.5. Temperature trends

Temperature data were analysed using linear modelling (lm) with R 2.13.1. The model framework included average first quarter temperatures as a response with year as a fixed effect. This assessed whether there were significant temperature changes through time around the coast. Linear mixed-effects models (using the lme4 package in R 2.13.1- <http://CRAN.R-project.org/package=lme4>) were used to model the effects of years and regions on temperature changes. The models included region as a random effect and was originally modelled with no fixed effects but were then repeated with year as a fixed effect. The most accurate model was judged to be the one with the lowest Akaike Information Criterion (AIC) value when fitted with maximum likelihood (ML).

### 2.6. Spawning date shifts

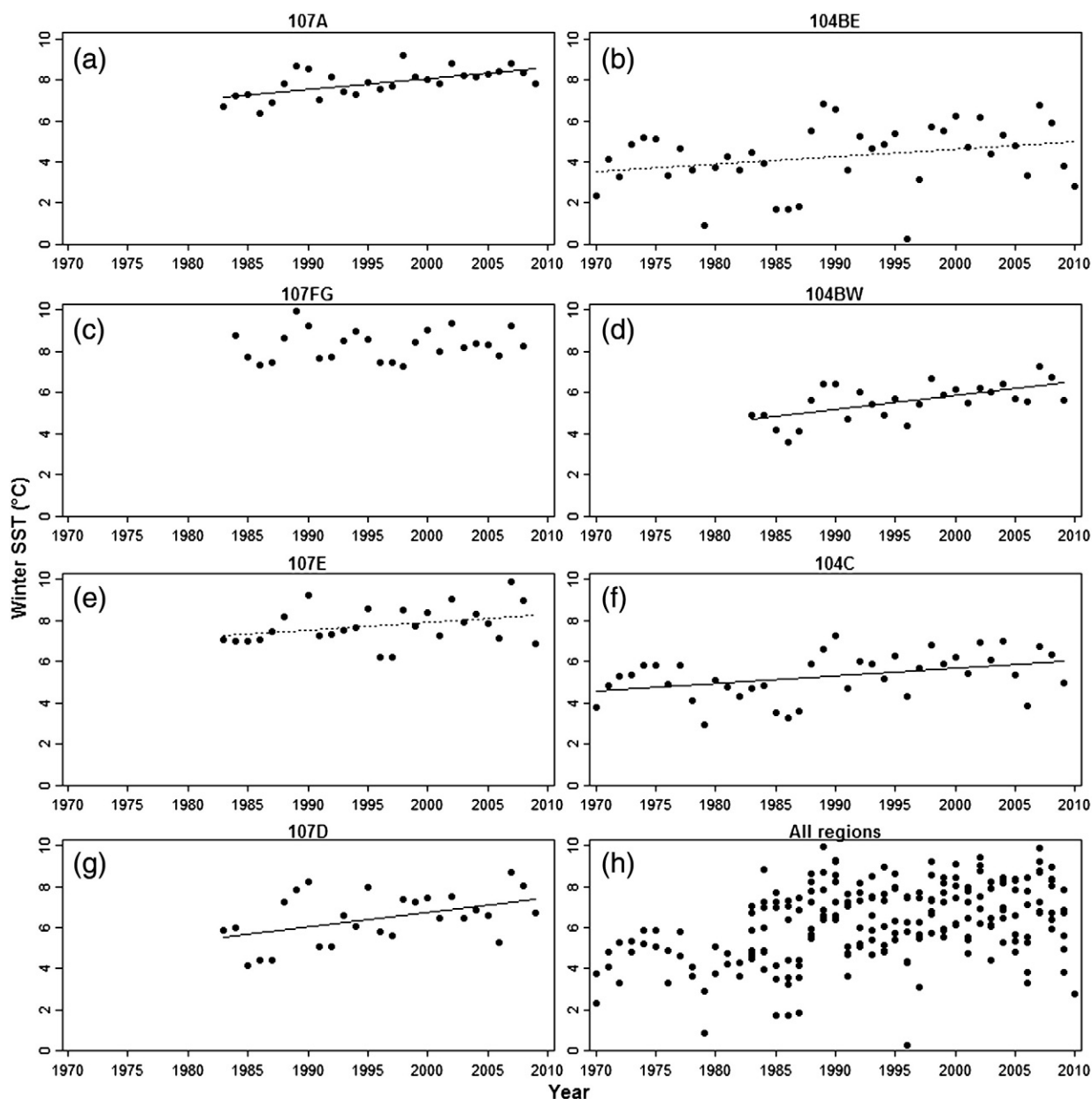
Shifts in spawning date were analysed by linear regression, with the mean spawning week as the response variable and either year or temperature as the fixed effect. This assessed whether there were significant shifts in spawning dates of sole, firstly over a temporal scale and secondly in response to temperature. Linear mixed-effects were modelled using the lme4 package in R 2.13.1 to test the effects of temperature, years and regions on spawning dates. With the spawning date as the response variable combinations of region, year and region and year were included as random effects. The selection procedures for the best models were determined by the lowest AIC value.

## 3. Results

### 3.1. Trends in winter sea temperature

When data from the seven coastal temperature time-series were combined, evidence was found for a significant overall rise in winter sea surface temperatures between 1970 and 2010 (Fig. 2). The winter SST in areas 107A, 104BW, 104C and 107D increased significantly by an average of 0.053 °C, 0.068 °C, 0.04 °C and 0.072 °C per year respectively (Fig. 2a, d, f, g; linear regressions, all  $p < 0.05$ ). The temperature trends in regions 104BE ( $p = 0.086$ ; Fig. 2b) and 107E ( $p = 0.087$ ; Fig. 2e) only approached statistical significance, and for region 107FG there was no evidence of a temperature rise ( $p = 0.659$ ; Fig. 2c).

A selection of linear mixed-effects models on the combined effects of year and region on winter SST is presented in Table 3. The model with lowest AIC, model 2, suggested significant SST differences between regions (variance component = 1.73). Generally, winter SST was higher in the deeper southern and western regions (107FG, 107E, 107A) than in the shallower northern and eastern regions (104BE, 104BW, 104C). Further, the overall increase in SST was significant, and amounted to 0.043 °C for all areas combined (equivalent to a 1 °C increase in 23 years).



**Fig. 2.** (a–g) Trends in winter SST for coastal monitoring sites corresponding with sole substocks in seven regions, and for all regions combined (h). Trend lines are shown where the change in temperature over time was significant ( $p < 0.05$ , continuous lines) or approached significance ( $0.05 < p < 0.1$ , dotted lines), based on linear regression. (h) Winter SST for all regions combined saw a significant temperature increase ( $p < 0.001$ ), based on a linear mixed effects model where region was included as random effect (Table 3).

### 3.2. Trends in the timing of spawning of sole

There were both geographical differences in the average timing of spawning between sole stocks and long-term trends towards earlier spawning over time (Fig. 3). Generally the timing of spawning was earliest in the south-western stocks of the Bristol Channel (107FG) and western English Channel (107E), intermediate in the Irish Sea

(107A) and eastern English Channel (107D) and latest in the North Sea stocks (104C and especially 104BW and 104BE).

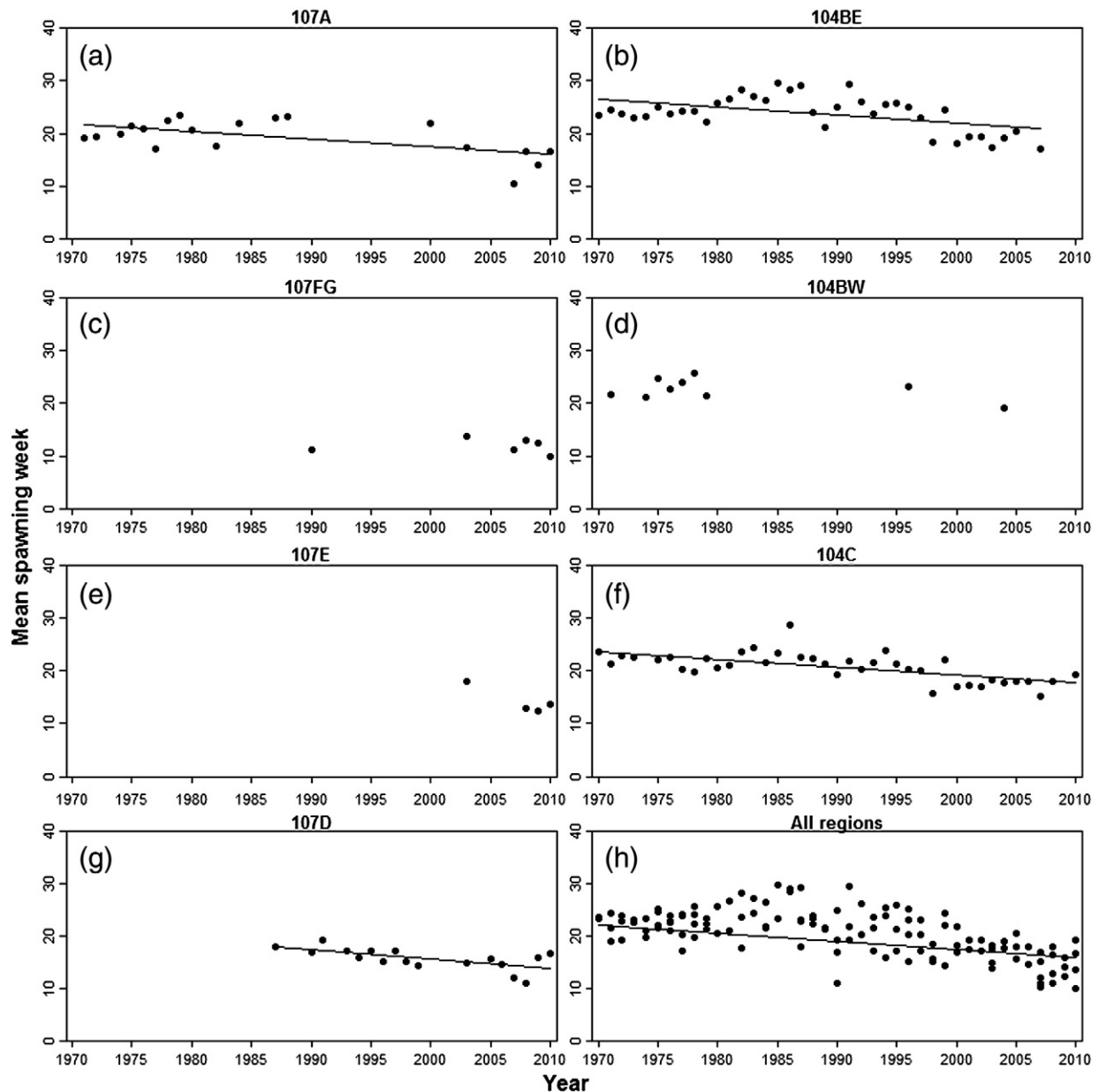
Four out of seven stocks showed a significant long-term trend towards earlier spawning over the time-periods where data were available: these were the Irish Sea ( $p = 0.009$ ), east-central North Sea ( $p = 0.002$ ), southern North Sea ( $p < 0.00001$ ), and eastern Channel ( $p = 0.0051$ ) stocks. For the other three stocks trends were not significant as the reliable estimates of peak spawning week were limited to a few years there was a limited power of detection. However, the long-term trend towards earlier spawning for all stocks combined (Fig. 3h) was significant, as shown by a linear mixed-effects model that accounted for differences between regions as a random effect (effect of year:  $p < 0.00001$ ) with spawning shifting from the end of May (week 22) in 1970 to mid-April (week 16) in 2010. This amounts to a rate of advancement in timing of 1.50 weeks per decade, or very approximately 1 day each year.

**Table 3**

Linear mixed-effects models examining the effect of year on winter SST, as monitored at coastal sites in 7 regions (included as random effects) corresponding with sole stocks. Models based on ML and REML yield consistent results.

Model	Random effect	Fixed effect	Coefficient + SE	AIC, ML
Model 1	Region			680.5
Model 2	Region	Year	$0.043 \pm 0.008$	652.1





**Fig. 3.** Long-term variability in the mean peak spawning week of sole, shown for seven sole substocks (a–g) and for all stocks combined (h). Trend lines are shown where significant ( $p < 0.05$ ) shifts in the mean spawning week over time were found, based on linear regressions for the individual substocks, and on linear mixed-effects models for all regions combined (with substock included as random effect).

### 3.3. Relationships between winter SST and timing of spawning of sole

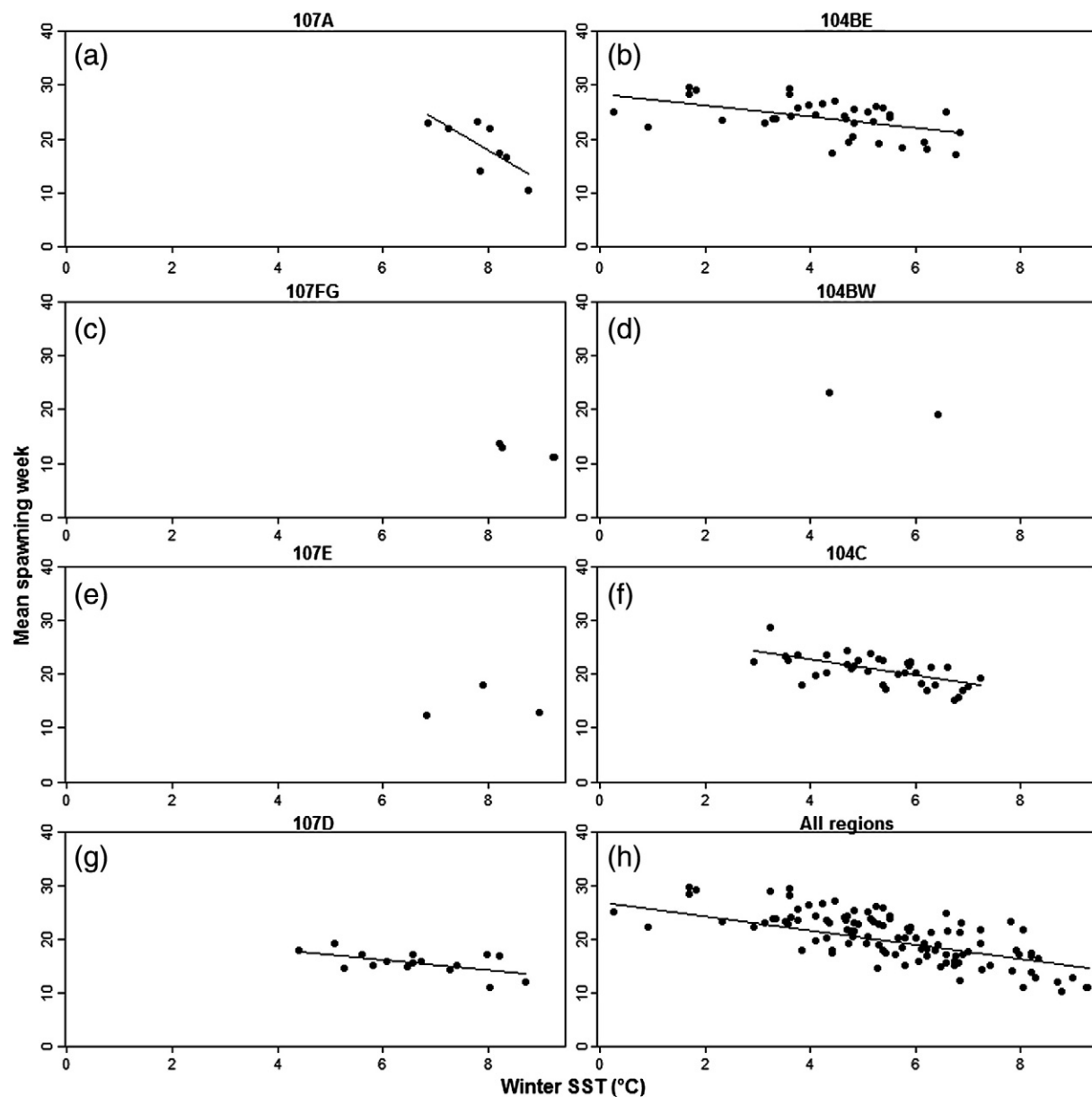
There was evidence that winter SST was closely associated with the timing of spawning and this came from both between- and within-stock variability (Fig. 4). Sole stocks inhabiting warmer waters (e.g. 107A, 107FG) generally showed earlier spawning than those inhabiting colder waters (notably 104BE). Furthermore, at least four out of seven stocks showed significant relationships between warmer winter SST and earlier spawning phenology (Fig. 4a, b, f, g). These were the stocks inhabiting the Irish Sea (107A,  $p = 0.036$ ), east-central North Sea (104BE,  $p = 0.0017$ ), southern North Sea (104C,  $p < 0.0001$ ), and eastern Channel (107D,  $p = 0.021$ ). Data were very limited for the other three substocks.

These relationships were confirmed by linear mixed-effects models on the effects of temperature on spawning week for all regions (Table 4), where the ‘best’ model based on the AIC (model 4) included the region and year as random effects and winter SST as fixed effect.

When fitted with maximum likelihood the sole spawning advanced substantially with temperature rises, by  $-1.35 \pm 0.19$  weeks for every  $1^\circ\text{C}$  rise in temperature (model 3). Regions varied significantly in their phenology (variance component = 3.5, model 4) indicating that they are acting as individual subpopulations. We can see from Table 4 that regions differ in their spawning times and temperatures impact on the peak spawning times of the sub-populations.

## 4. Discussion

We found that temperatures have risen across sole habitats in the North Sea, Irish Sea and English Channel whilst the spawning dates of sole have advanced in the last 40 years. Our study showed that the timing of spawning of sole is inversely correlated with the winter temperature. Therefore, we believe that in a warmer world sole populations will spawn earlier. Further temperature increases are expected due to climate change. In Western Europe, the frequency



**Fig. 4.** Relationships between winter SST and the timing of spawning in sole, shown separately for seven substocks (Fig. 4a–g) and for all substocks combined (Fig. 4h). Continuous lines indicate significant ( $p < 0.05$ ) relationships between winter SST and the mean spawning week, based on linear regressions for the individual substocks, and on linear mixed-effects models for all regions combined (with substock included as random effect).

of very cold winters is expected to decrease whilst the frequency of very hot summers is expected to increase (Hulme et al., 2002). Fish behaviours such as spawning patterns and growth rates have been seen to be changing in recent years. Increased temperatures are believed to have various effects on fish populations including effects on the phenology, growth and survival of juveniles and adults and reproductive traits. Research has found that species such as herring and

sole have had earlier maturation in response to both climate change and fishing pressures (Mollet et al., 2007; Vainikka et al., 2009).

We calculated the timing of the spawning season from the stages of gonad maturity as described in Bromley (2003). Teal et al. (2008) showed that the progression of gonad maturity is a reliable indicator of inter-annual variations in the timing of spawning. They showed a significant correlation between the end of spawning estimated from gonad maturity samples and the date of peak settlement of 0-group sole in coastal nursery grounds. A regression of our estimates with published estimates of the date of peak spawning from egg surveys (Fox et al., 2000; Rijnsdorp and Vingerhoed, 1994; van der Land, 1991) showed a significant linear relationship ( $p < 0.05$ ;  $n = 11$ ;  $r^2 = 0.78$ ) although our method overestimated the date of peak spawning determined in the egg surveys by 3.1 weeks. This discrepancy, however, does not affect the overall conclusion of this study that sole advanced spawning in relation to the increase in winter temperature.

**Table 4**

Summary of selected linear mixed-effects models examining the effects of winter SST, year, on spawning dates of sole.

Model	Random effect	Fixed effect	AIC, ML
Model 1	Region		730.3
Model 2	Region + year		691.1
Model 3	Region	Temperature	534.5
Model 4	Region + year	Temperature	519.3

No change in date of peak spawning was observed in three stocks. In one of the stocks (Bristol Channel, 107FG) this may be due to the more stable oceanic environments as in this area no significant increase in winter temperature was observed. In the other two stocks (104BW and 107E) our sample sizes on sole spawning were very limited.

Although shifts in the timing of spawning were here related here to winter (January–March) temperatures, it is probable that over a somewhat longer time window, temperatures may affect sole spawning phenology. Maturation rates, measured as the increase in leading oocyte size (Ramsay and Witthames, 1996), show this to be a progressive linear process lasting from August to the start of spawning, which can be from January to April depending on year and stock. Temperatures throughout this process are expected to influence oocyte growth. We validated whether winter sea temperatures averaged over different time windows (ranging from 1 to 5 months) yielded similar relationships to sole spawning phenology as did the winter (January–March) temperature. Very similar results were obtained (unpublished) supporting that winter temperatures as reported here are appropriate to capture the environmental variations relevant during the period preceding sole spawning.

Against a background of climate change, from 1970 to 2010 several other factors that might affect sole spawning phenology have changed. These include population density, growth and maturity at age, whilst fishing pressure has generally been high in all stocks examined, although somewhat decreased in recent years (ICES, 2011). In the North Sea, growth rates increased during the 1960s and 1970s coinciding with eutrophication and increasing bottom disturbance caused by beam trawling (de Veen, 1978; Millner and Whiting, 1996), but decreased in the 1990s (Millner et al., 1996). Growth rates have also increased in several sole stocks elsewhere during the 1970s–1990s (Millner et al., 1996). Temperature has a positive influence on the growth of age-0 sole (Teal et al., 2008), and faster juvenile growth will in turn lead to earlier ages at first spawning (Mollet et al., 2007). There is evidence that sole size and age at first spawning have decreased (Mollet et al., 2007) whilst timing of maturation may be delayed in smaller, relatively more abundant virgin fish in their first year of maturation (Ramsay and Witthames, 1996). However, if such an effect is real then it would lead to the reverse effect to rising temperature as observed here, i.e. delayed timing of spawning. Hence the phenological shifts reported here are less likely to be the indirect result of changes in the size-age composition of spawning fish, than of a more direct effect of winter temperatures on gonad maturation.

Whether the change in phenology coincides with a change in egg size and fecundity remains to be investigated. There is a clear seasonal pattern in egg size and fecundity both across and within sole populations (Rijnsdorp and Vingerhoed, 1994; Witthames et al., 1995). Egg size may have consequences for larval survival. There is a positive relationship between egg size and larval size, as well as between larval size and larval survival (Rijnsdorp and Vingerhoed, 1994). It is not known whether the seasonal patterns in egg size are due to phenotypic response to differences in the environment, or are genetically determined. Recent genetic studies have revealed that there the sole stocks considered in this study show local genetic differentiation (Maes et al., 2011).

The change in the phenology may have implications for the population dynamics, since recruitment is critically dependent on the match between the occurrence of the larvae and their food (Cushing, 1990; Platt et al., 2003). The timing of peaks in larval food abundance may not necessarily advance with warming temperatures; for example, in the south-eastern North Sea (Helgoland Roads time series), no shift in the peak of the phytoplankton has occurred since 1975 (Wiltshire et al., 2008), although there was evidence for earlier timing of the peak in copepod abundance. In some of the sole stocks, strong year-classes coincide with cold conditions in early spring although the causal

mechanism is still obscure (Rijnsdorp et al., 1992). Warmer conditions may also improve survival of juveniles. Earlier spawning will prolong the growing season of 0-group fish and may result in an increase in the body size during the 1st winter (Teal et al., 2008). Since winter survival is positively related with body size, 0-group survival may be enhanced under warmer winter conditions (Post and Parkinson, 2001). Cold winters result in extra winter mortality. High mortality has been observed in severe winters in the North Sea (Horwood and Millner, 1998; Woodhead, 1964).

Climate change is affecting fish populations in a variety of ways, and changes in productivity and distribution shifts have received much attention recently (Brander, 2007; Cheung et al., 2009; Dulvy et al., 2008; Engelhard et al., 2011; Perry et al., 2005; van Keeken et al., 2007). Changes in the phenology of fish populations as described here, and in some other studies (Jansen and Gislason, 2011; Sims et al., 2004; van der Land, 1991), are an additional, arguably more subtle effect of climate change. Phenological changes, nevertheless, require further research attention: not only because of the implications for such management measures as spawning fishery closures (Kraus et al., 2009), but also because it should not be taken for granted that all ecosystem components will show similar temporal shifts with climate change, with the possibility of mismatches between fish larval developmental stages and the peak prey abundances.

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## References

- Ainsworth, C.H., Samhour, J.F., Busch, D.S., Cheung, W.W.L., Dunne, J., Okey, T.A., 2011. Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. *ICES Journal of Marine Science* 68, 1217–1229.
- Bevington, P.R., 1969. *Data Reduction and Error Analysis*. McGraw Hill, New York.
- Brander, K.M., 2007. Global fish production and climate change. *Proceedings of the National Academy of Sciences of the United States of America* 104, 19709–19714.
- Bromley, P.J., 2000. Growth, sexual maturation and spawning in central North Sea plaice (*Pleuronectes platessa* L.) and the generation of maturity ogives from commercial catch data. *Journal of Sea Research* 44, 27–43.
- Bromley, P.J., 2003. The use of market sampling to generate maturity ogives and to investigate growth, sexual dimorphism and reproductive strategy in central and south-western North Sea sole (*Solea solea* L.). *ICES Journal of Marine Science* 60, 52–65.
- Carscadden, J., Nakashima, B.S., Frank, T., 1997. Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences* 54, 781–787.
- Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Pauly, D., 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* 10, 235–251.
- Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* 26, 249–293.
- Cuveliers, E.L., Larmuseau, M.H.D., Hellems, B., Verherstraeten, S.L.N.A., Volckaert, F.A.M., Maes, G.E., 2012. Multi-marker estimate of genetic connectivity of sole (*Solea solea*) in the North-East Atlantic Ocean. *Marine Biology* 159, 1239–1253.
- de Veen, J.F., 1978. Changes in North Sea sole stocks (*Solea solea* (L.)). *Rapp. P.-V. Réun. Conseil International pour l'Exploration de la mer* 172, 124–136.
- Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmüller, V., Dye, S.R., Skjoldal, H.R., 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* 45, 1029–1039.
- Engelhard, G.H., Pinnegar, J.K., Kell, L.T., Rijnsdorp, A.D., 2011. Nine decades of North Sea sole and plaice distribution. *ICES Journal of Marine Science* 68, 1090–1104.
- Fox, C.J., O'Brien, C.M., Dickey-Collas, M., Nash, R.D.M., 2000. Patterns in the spawning of cod (*Gadus morhua* L.), sole (*Solea solea* L.) and plaice (*Pleuronectes platessa* L.) in the Irish Sea as determined by generalized additive modelling. *Fisheries Oceanography* 9, 33–49.

- Genner, M.J., Halliday, N.C., Simpson, S.D., Southward, A.J., Hawkins, S.J., Sims, D.W., 2010. Temperature-driven phenological changes within a marine larval fish assemblage. *Journal of Plankton Research* 32, 699–708.
- Halliday, R.G., 1988. Use of seasonal spawning area closures in the management of haddock fisheries in the Northwest Atlantic. Northwest Atlantic Fisheries Organization Science Council Studies 12, 27–36.
- Horwood, J., 1993. The Bristol Channel Sole (*Solea solea* (L.)) – a fisheries case study. *Advances in Marine Biology* 29, 215–367.
- Horwood, J.W., Millner, R.S., 1998. Cold induced abnormal catches of sole. *Journal of the Marine Biological Association of the United Kingdom* 78, 345–347.
- Hulme, M., Jenkins, G.L., Lu, X., Turnpenny, J.R., Mitchell, T.D., Jones, R.G., Lowe, J., et al., 2002. Climate Change Scenarios for the United Kingdom: the UKCIP02 Scientific Report. Tyndall. Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich, UK. 120 pp.
- Hutchings, J.A., Myers, R.A., 1994. Timing of cod reproduction: interannual variability and the influence of temperature. *Marine Ecology Progress Series* 108, 21–31.
- ICES, 2011. Report of the working group on the assessment of Demersal stocks in the North Sea and Skagerrak (WGNSSK). ICES CM 2011/ACOM:13.
- Jansen, T., Gislason, H., 2011. Temperature affects the timing of spawning and migration of North Sea mackerel. *Continental Shelf Research* 31, 64–72.
- Kraus, G., Pelletier, D., Dubreuil, J., Möllmann, C., Hinrichsen, H.-H., Bastardie, F., Vermard, Y., Mahévas, S., 2009. A model-based evaluation of Marine Protected Areas: the example of eastern Baltic cod (*Gadus morhua callarias* L.). *ICES Journal of Marine Science* 66, 109–121.
- MacKenzie, B.R., Schiedek, D., 2007. Long-term sea surface temperature baselines—time series, spatial covariation and implications for biological processes. *Journal of Marine Science* 68, 405–420.
- Maes, G.E., Cuveliers, E.L., Diopere, E., Cariani, A., Geffen, A.J., Rijnsdorp, A.D., Volckaert, F.A.M., 2011. The power of integrating genetic and otolith analytical approaches into the management of exploited marine species. Abstract: 8th International Flatfish Symposium, 5–10 November 2011, IJmuiden, The Netherlands.
- Millner, R.S., Whiting, C.L., 1996. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. *ICES Journal of Marine Science* 53, 1185–1195.
- Millner, R., Flatman, S., Rijnsdorp, A.D., van Beek, F.A., De Clerck, R., Damm, U., Tetard, A., Forest, A., 1996. Comparison of long-term trends in growth of sole and plaice populations. *ICES Journal of Marine Science* 53, 1196–1198.
- Mollet, F.M., Kraak, S.B.M., Rijnsdorp, A.D., 2007. Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*. *Marine Ecology Progress Series* 351, 189–199.
- Ottersen, G., Hjermann, D.O., Stenseth, N.C., 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography* 15, 230–243.
- Pawson, M.G., Pickett, G.D., Witthames, P.R., 2000. The influence of temperature on the onset of first maturity in sea bass. *Journal of Fish Biology* 56, 319–327.
- Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. *Science* 308, 1912–1915.
- Planque, B., Frédou, T., 1999. Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 56, 2069–2077.
- Platt, T., Fuentes-Yaco, C., Frank, K.T., 2003. Spring algal bloom and larval fish survival. *Nature* 423, 398–399.
- Post, J.R., Parkinson, E.A., 2001. Energy allocation strategy in young fish: allometry and survival. *Ecology* 82, 1040–1051.
- Ramsay, K., Witthames, P.R., 1996. Using oocyte size to assess seasonal ovarian development in *Solea solea* (L.). *Journal of Sea Research* 36, 275–283.
- Rijnsdorp, A.D., Vingerhoed, B., 1994. The ecological significance of geographical and seasonal differences in egg size in sole *Solea solea* (L.). *Netherlands Journal of Sea Research* 32, 255–270.
- Rijnsdorp, A.D., Witthames, P.R., 2005. Ecology of Reproduction. In: Flatfishes: Biology and Exploitation. In: Gibson, R.N. (Ed.), Blackwell Science, Oxford, UK, pp. 68–93.
- Rijnsdorp, A.D., van Beek, F.A., Flatman, S., Miller, J.M., Riley, J.D., Giret, M., de Clerk, R., 1992. Recruitment of sole, *Solea solea* (L.), in the Northeast Atlantic. *Neth. Journal of Sea Research* 29, 173–192.
- 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 Journal of Marine Science* 66, 1570–1583.
- Rindorf, A., Lewy, P., 2006. Warm, windy winters drive cod north and homing of spawners keeps them there. *Journal of Applied Ecology* 43, 445–453.
- Roessig, J.M., Woodley, C.M., Cech, J.J., Hansen, L.J., 2005. Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries* 14, 251–275.
- Sims, D.W., Wearmouth, V.J., Genner, M.J., Southward, A.J., Hawkins, S.J., 2004. Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology* 73, 333–341.
- 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. *Marine Ecology Progress Series* 358, 219–230.
- Vainikka, A., Mollet, F., Casini, M., Gårdmark, A., 2009. Spatial variation in growth, condition and maturation reaction norms of the Baltic herring *Clupea harengus membras*. *Marine Ecology Progress Series* 383, 285–294.
- van Aken, H.M., 2008. Variability of the water temperature in the western Wadden Sea on tidal to centennial time scales. *Journal of Sea Research* 60, 227–234.
- van der Land, M.A., 1991. Distribution of flatfish eggs in the 1989 egg surveys in the southeastern North Sea, and mortality of plaice and sole eggs. *Netherlands Journal of Sea Research* 27, 277–286.
- 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. *Journal of Sea Research* 57, 187–197.
- Whitehead, P.J.P., Bauchot, M.L., Hureau, J.C., Nielsen, J., Tortonese, E., 1986. Fishes of the North-Eastern Atlantic and the Mediterranean. United Nations Educational Scientific and Cultural Organisation, Paris.
- Wiltshire, K.H., Malzahn, A.M., Wirtz, K., Greve, W., Janisch, S., Mangelsdorf, P., Manly, B.F.J., Boersma, M., 2008. Resilience of North Sea phytoplankton spring bloom dynamics: an analysis of long-term data at Helgoland Roads. *Limnology and Oceanography* 53, 1294–1302.
- Witthames, P.R., Greer Walker, M., Dinis, M.T., Whiting, C.L., 1995. The geographical variation in the potential annual fecundity of Dover sole *Solea solea* (L.) from European shelf waters during 1991. *Netherlands Journal of Sea Research* 34, 45–58.
- Woodhead, P.M.J., 1964. The death of North Sea fish during the winter of 1962/63, particularly with reference to the sole, *Solea vulgaris*. *Helgolander Wissenschaftliche Meeresuntersuchungen* 10, 283–300.