



Climate-induced response of commercially important flatfish species during the 20th century

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ABSTRACT

The consequence of elevated ocean temperatures on commercial fish stocks is addressed using time series of commercial landings (1906–2004) and juvenile survey catch data (1904–2006) collected around Denmark. We analyze (i) whether warm-water sole (*Solea solea*) has increased relative to Boreal plaice (*Pleuronectes platessa*) and (ii) whether two related warm-water species (turbot, *Psetta maxima* and brill, *Scophthalmus rhombus*) show similar responses to increasing temperature or, alternatively, whether turbot (which has a broader juvenile diet) has been favored. Since the early 1980s, both sole and turbot have constituted an increasing part of the commercial landings and survey catches, as compared with plaice and brill, respectively. These changes in species composition were linked to sea surface temperatures, Northern Hemisphere temperature anomalies (NHA) and the North Atlantic Oscillation. NHA was closely related and explained 43% of the observed variation in sole survey catches relative to the plaice catches and almost 38% of the observed variation in the sole landings relative to the plaice landings. For the less common species, turbot and brill, none of the global change indicators explained more than 15% of the variation, although all showed a positive relationship. Survey catch per unit effort increased significantly for both sole and turbot around the early 1980s, whereas catch per unit

effort for plaice and brill remained constant. The results indicate that the abundance of warm-water species is likely to increase with increasing temperature but also that species with similar life histories might react differently according to degree of specialization.

Key words: Baltic Sea, descriptor, indicator, Kattegat, Marine Strategy Framework Directive, North Sea, regime shift

INTRODUCTION

Global warming has already affected many parts of the biosphere (Rosenzweig *et al.*, 2008) and will continue to do so with the anticipated increase in temperature (IPCC, 2007). This represents a challenge for science to provide predictions on issues such as changes to species distributions and biodiversity and consequences for worldwide food supply, including commercial fish catches. Compared with terrestrial environments, alterations in marine ecosystems have proven more difficult to predict (Brander, 2007; Lindegren *et al.*, 2010a; Ottersen *et al.*, 2010), even though changes in the seasonal timing and the rate at which climatic changes takes place are higher or similar to what is observed on land (Burrows *et al.*, 2011). One explanation for this prediction deficiency is that key processes regulating the population dynamic of marine organisms are often unpredictable in time and/or space (Bakun, 1996). Thus, disentangling one particular underlying causal mechanism, between for example a temperature increase and a change in population abundance, is difficult. However, an alternative way to deduce future changes is to learn from the past and identify trends and patterns in ecological time series. This has been done when analyzing spatial changes in species distribution (Attrill and Power, 2002; Mieszowska *et al.*, 2006; Rindorf and Lewy, 2006; van Hal *et al.*, 2010), depth distribution (Dulvy *et al.*, 2008), individual (Attrill and Power, 2002; Teal *et al.*, 2008) and population growth (O'Brien *et al.*, 2000; Attrill and Power, 2002). A problem that often emerges when relying on ecological time series is that the timespan covered is often short and therefore embodies a relatively narrow range of climate variability. Moreover,

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in those cases where a large number of years are covered, the consistency in sampling procedures such as gear setup and spatial coverage is often low. Combining several ecological time series that are complementary to each other can in some cases mitigate these problems. This may require the use of a common metric to compare among different time series.

In this study we rely on such common metrics, namely the proportion SP, which is the amount of sole relative to the sum of sole and plaice, and the proportion TB, which is the amount of turbot relative to the sum of turbot and brill. These proportions are calculated from two data sources: commercial landings (1905–2004), for which effort is unknown, and juvenile survey catches (67 yr during the period 1904–2006), for which effort is known although sampling gear has undergone minor modification. The rationale for using proportions as a common metric is that a proportion, when calculated using comparable species with similar habitat preference caught in a mixed fishery, is robust to changes in gear setup, effort and fishing pattern.

The use of SP is not new. Brander *et al.* (2003) found that SP increases with decreasing latitude and mean annual bottom temperature. The proposed rationale behind this result is that sole is a more southerly Lusitanian species compared with the Boreal plaice, which has its center of distribution in the North Sea (Fishbase, 2011). In the North Sea, sole has shown a southward shift in distribution during the last nine decades, a trend which is ascribed to both rising temperature and fishing pressure (Engelhard *et al.*, 2011). However, a more northward distribution of North Sea sole has been observed in recent years (Rijnsdorp, 2010). Whether SP can also be used to detect temporal changes within a limited geographical area as indicated by Brander (2009) is yet unresolved, and hence one objective of the present study.

TB is based upon two commercially valuable flatfish species (turbot and brill) that are ecologically similar in the sense that they can produce hybrids (e.g., Heap and Thorpe, 1987), use common nurseries (e.g., Haynes *et al.*, 2011) and are as adults predominantly piscivorous (Piet *et al.*, 1998). However, as juveniles their diets differ, such that turbot includes several food items in its diet as compared with brill, which almost exclusively preys on mysids (Beyst *et al.*, 1999; Haynes *et al.*, 2011; Vinagre *et al.*, 2011).

Thus, we hypothesize that the consequence of a temperature increase will be a rise in both TB and SP. The rise in TB will be a result of favorable conditions for the Lusitanian sole compared with the Boreal plaice, whereas the increase in TB will be a result of

turbot being better adapted than brill to cope with environmental changes because it has a more flexible diet.

MATERIAL AND METHODS

The study area is the transition zone between the North Sea and the Baltic Sea, which corresponds to the inner Danish waters and comprises the *International Council for the Exploration of the Sea* (ICES) subdivisions (SD) 21, 22 and 23 (Figs 1 and S1). Juvenile survey data consists of counts and individual length measures of all captured sole, plaice, turbot and brill taken between 1904 and 2006. The sampling is conducted using a young fish trawl which mainly targets age-0 and age-1 flatfish in the shallow nurseries. Only hauls at depths shallower than 4.5 m were included in the analyses. Data collected earlier than 1930 were retrieved from Johansen (1915) and Bruun (1927). Later data were accessible from in-house databases (see Johansen, 1908 and/or Støttrup *et al.*, 2002 for references on the sampling procedure and gear). In 1957 the trawl was modified when a tickle chain was attached as foot rope. All survey-caught individuals smaller than 20 cm were included in the proportion calculation, i.e., they were judged as being juveniles.

As a complement to juvenile data, commercial landings in weight of sole, plaice, turbot and brill in the inner Danish waters from 1905 to 2004 were collected from the official Danish landings statistics (Gislason, 2006).

As a common standardized metric for comparison, the proportion of sole relative to plaice (SP) was calculated as:

$$SP = \frac{\text{Sole}}{\text{Sole} + \text{Plaice}} \quad (1)$$

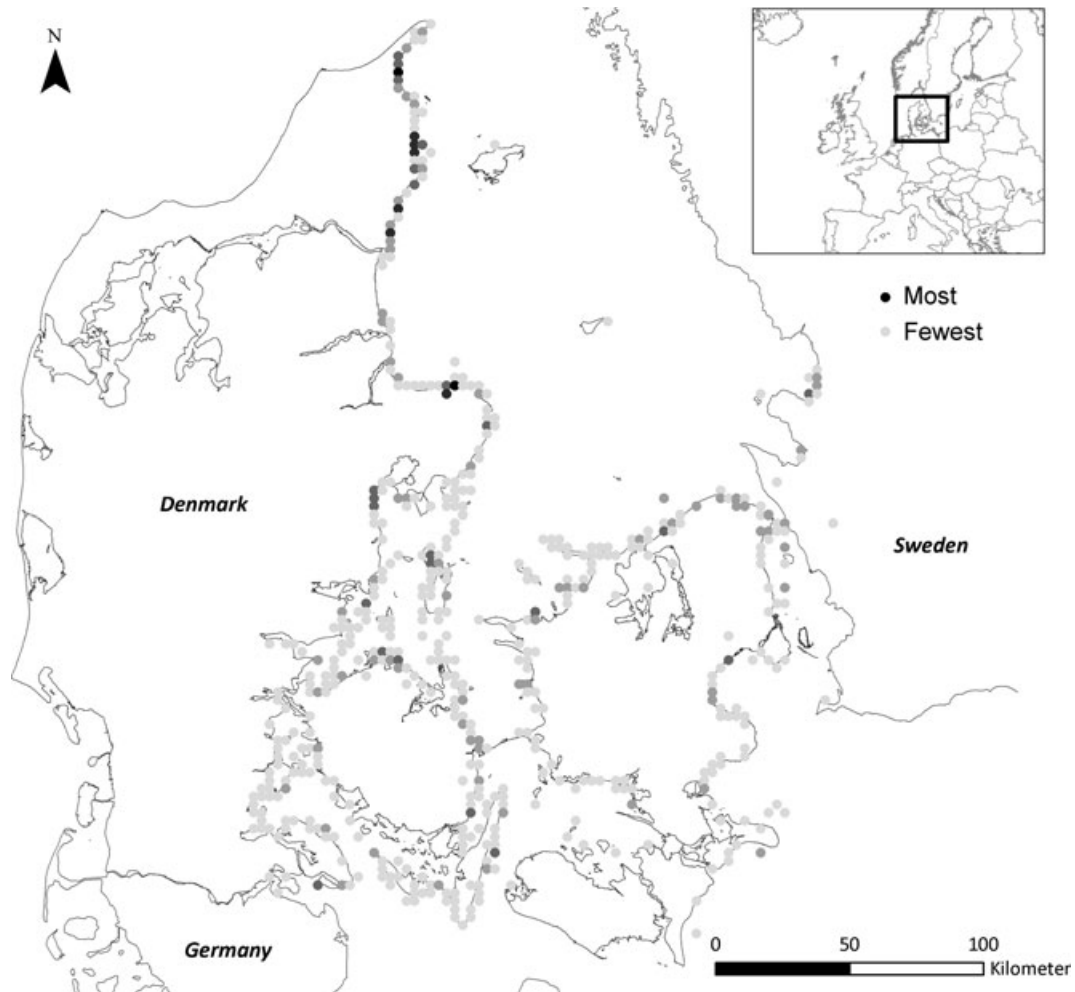
and as

$$TB = \frac{\text{Turbot}}{\text{Turbot} + \text{Brill}} \quad (2)$$

for TB. Both proportions were calculated based upon either annual Danish commercial landings in tons in the Kattegat/Belt Sea (SP_{lan} and TB_{lan}) or juvenile flatfish survey data provided in counts per 10-min hauls (SP_{juv} and TB_{juv}).

To estimate the ocean-atmospheric conditions in the area, both regional climate indices as well as local hydrographic variables were collected. Monthly Northern hemisphere temperature anomalies (NHA) were retrieved from the United States National Oceanic and Atmospheric Administration (NOAA, 2011) and the winter North Atlantic Oscillation

Figure 1. Geographical location of study area, indicating sampling and fishing regions. Dots are locations where young fish survey hauls were completed; the darker the dot, the more hauls taken at that location. All hauls after 1985 have exact GPS positions, whereas positions for earlier hauls were deduced from landmarks given in the ships' logbooks. The hatched area illustrates the inner Danish waters where commercial landings from ICES SD21, SD22 and SD23 were obtained.



(NAO) index from Hurrell (2010). Monthly sea surface temperatures (SST) covering the period from 1905 to 2007 were extracted from the ICES database (ICES, 2010) from the Marsden Square 215;3 (55°–60°N; 10°–15°E). To estimate the timing of juvenile flatfish migration from the deeper areas to the shallow nurseries, April temperatures measured between surface and 1 m depth were averaged and used as proxy for the temperature in the shallow and coastal areas (Fig. S2).

To detect significant breakpoints in time series of SP and TB, the sequential regime shift detection method (STARS) (Rodionov, 2004) was applied. The STARS algorithm is designed to detect statistically significant shifts in the mean level and the magnitude of fluctuations in time series by using modified two-sided Student's *t*-tests. STARS can detect shifts at

different time scales and magnitudes by varying the probability level of the tests and the cut-off length controlling the duration of regimes (Rodionov and Overland, 2005). In this study we applied a significance level of $P = 0.01$ and varied the cut-off length between 15, 20 and 25 yr in order to account for potential sensitivity of the STARS algorithm to window size. More information on the STARS method and EXCEL add-in software is available online at www.beringclimate.noaa.gov.

Finally, simple Gaussian linear regression models were used to test the relationship between the logit-transformed mean annual proportions and SST, NHA and NAO, respectively. The logit transformation and handling of 0 and 1 values were performed as suggested by Warton and Hui (2011). Adult landings were

lagged by 3 yr and juvenile survey catches by 1 yr to account for delays between impact of temperature during birth-year and the age when the fish were captured. These lag periods assume that our temperature and climate variables impact processes affecting survival during first year of life.

Because it is impossible to evaluate the extent to which changes in SP_{juv} reflect changing sole or plaice catches (and likewise for TB_{juv} if changes reflect changes in turbot or brill catches), catch per unit effort (CPUE) was calculated for all four species using juvenile survey data. CPUE was defined as the mean annual number caught (ind) per unit effort, with effort standardized to 10-min hauls. Only data collected from 1957 onwards were included, since the young fish trawl was modified that year with the mounting of a tickler chain. Prior to testing for significance, CPUE was \log_e+1 -transformed, a value referred to as $CPUE_{\log+1}$. Welch's t -test (unequal variance and unequal sample size) was used to test whether the $CPUE_{\log+1}$ value collected before the identified significant breakpoint differed from values collected after. Note that it was not possible to perform this analysis for the commercial landing records, as these data do not contain any information regarding effort.

RESULTS

SP and TB remained at a low level until the start of the 1980s, at which time an increase occurred (Figs 2

and 3). This pattern is evident regardless of whether SP or TB was based upon commercial landings or juvenile survey catches. The regime shift detection method (STARS) indicated a significant breakpoint in TB_{lan} during 1983/1984, independent of window size, whereas for SP_{lan} the exact timing of the breakpoint varied between 1985/1986 and 1987/1988. Unfortunately, a gap in the sampling from 1971 to 1985 prevents evaluation of breakpoints in the SP_{juv} or TB_{juv} time series.

Increasing SST, NAO or NHA was in all cases followed by increasing SP_{lan} , SP_{juv} , TB_{lan} and TB_{juv} (Figs 4 and 5). However, depending on which climate predictors are chosen as covariate, the explanatory strength of the correlation differed from non-significant to 42% of the variation (Table 1). In general, NHA as a covariate of SP produced the highest R^2 values, followed by SST, whereas NAO showed the lowest degree of correlation. For TB the R^2 values were in general much lower than for SP; the highest value was found using NHA as covariate.

Juvenile sole $CPUE_{\log+1}$ increased almost sixfold, from 0.24 ind haul⁻¹ prior to the early 1980s to 1.35 ind haul⁻¹ after the early 1980s (Table 2). In contrast, no significant difference in juvenile $CPUE_{\log+1}$ was observed for plaice between the periods prior to and after the significant breakpoint. Likewise, no significant change in $CPUE_{\log+1}$ was found for brill, whereas for turbot the increase observed was significant.

Figure 2. Temporal variations in temperature–climate indices and indicators of flatfish abundance of two flatfish species (sole *Solea solea* and plaice *Pleuronectes platessa*) in the Kattegat-Belt Sea region during the 20th and early 21st centuries. Solid lines are SP based upon landings (SP_{lan} ; blue) or juvenile (SP_{juv} ; red). Significant breakpoints (STARS; Rodionov, 2004) are shown by a blue vertical line. Joined green dots represent sea surface temperature (SST), grey bars Northern Hemisphere Anomalies (NHA) and the black dotted line North Atlantic Oscillation index (NAO).

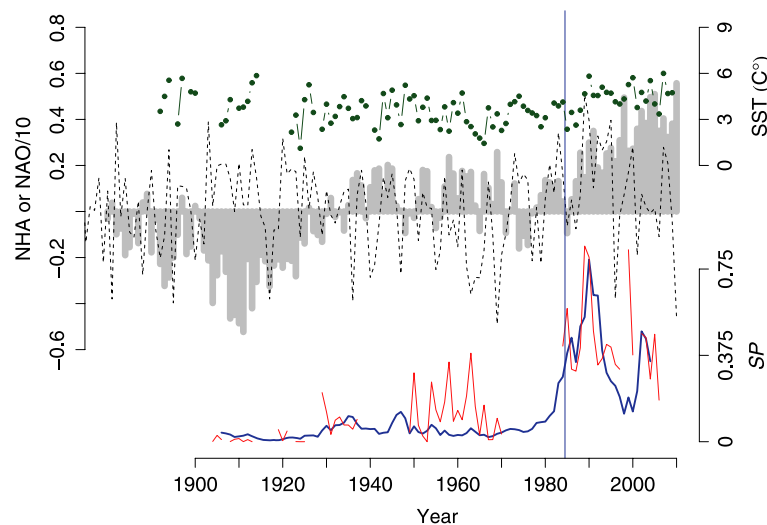


Figure 3. Same as Figure 2, but for turbot *Psetta maxima* and brill *Scophthalmus rhombus*.

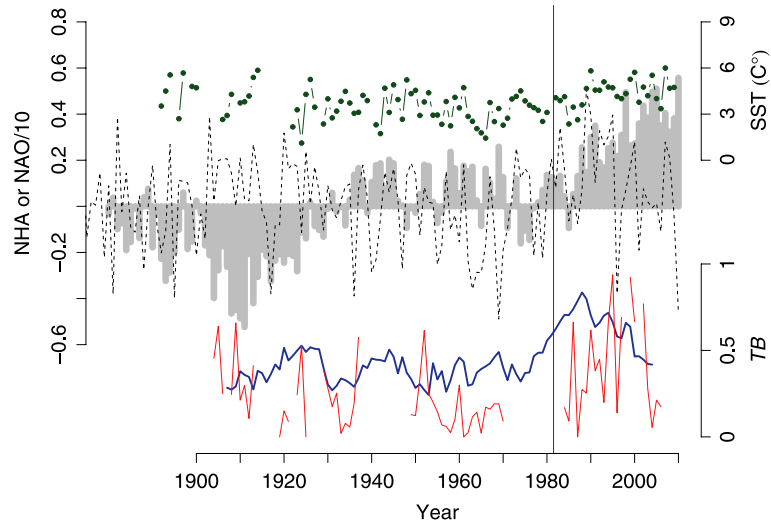
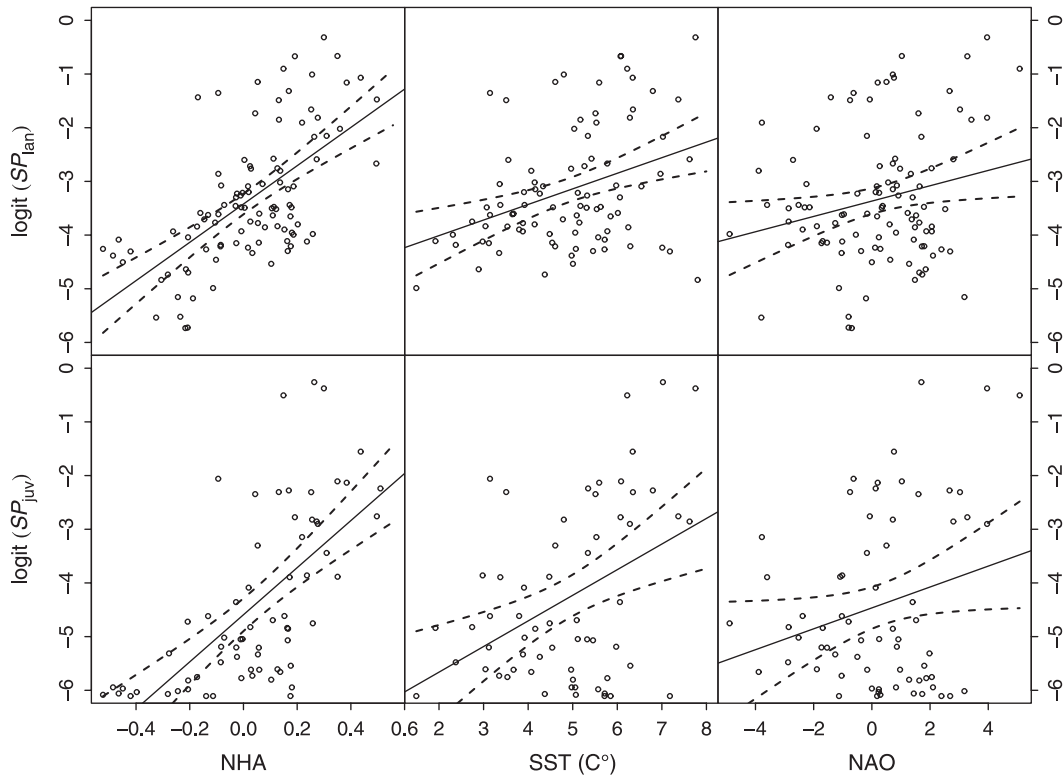


Figure 4. Logit-transformed SP_{lan} and SP_{juv} and the Northern Hemisphere Anomalies (NHA), sea surface temperature (SST) and North Atlantic Oscillation index (NAO). Solid black line shows the predicted relationship and dotted lines represent 95% confidence intervals.



DISCUSSION

Effort-independent metrics such as SP and TB have the advantage that time series can be analyzed even when effort is unknown or gear setup and efficiency

have changed over the years. In the present study, the method enabled the evaluation of historical commercial landings, revealing that a change in the flatfish community occurred in the early 1980s. This could not have been detected using juvenile survey data

Figure 5. Same as Figure 4, but logit-transformed TB_{lan} and TB_{juv} .

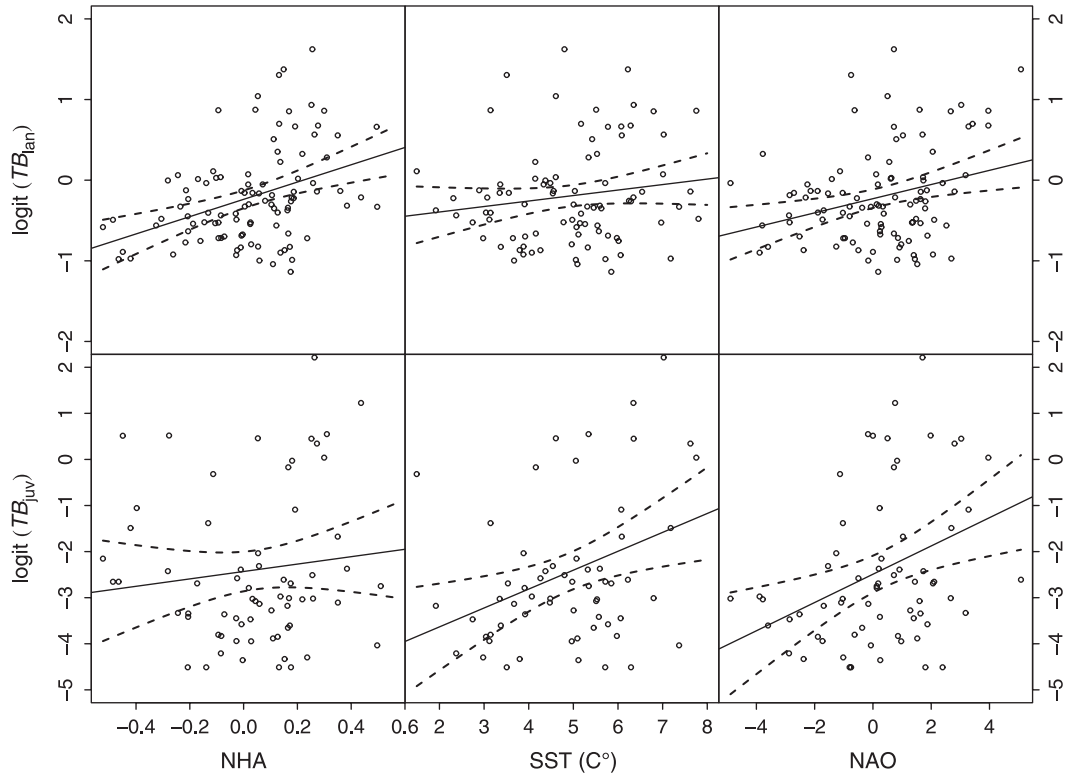


Table 1. R^2 values for the linear regression models with NHA, SST or NAO as covariate. Only significant are given, i.e., $P > 0.05$.

	NHA	SST	NAO
SP_{lan}	0.38	0.13	0.05
SP_{juv}	0.42	0.17	0.06
TB_{lan}	0.15	n.s.	0.08
TB_{juv}	n.s.	0.12	0.13

n.s., non-significant.

alone, since no survey took place in the period from 1972 to 1986. However, the disadvantage of using metrics such as SP and TB is that changes may arise from different trends in the numerator and denominator. Does the observed increase in SP reflect an increase in sole or a decrease in plaice? Likewise, does the observed increase in TB reflect an increase in turbot or a decrease in brill? These questions cannot be resolved based upon commercial landings alone, but here the juvenile survey catch data provide insight. No difference in the plaice catches was present, whereas the sole catches had increased significantly. That the increase in SP is a result of increasing sole and not decreasing plaice is further supported by the

Table 2. Mean $CPUE_{log+1}$ (ind haul⁻¹) for years prior to and post the identified significant breakpoint in the early 1980s. Welch's t -test statistics with degrees of freedom (d.f.) and significance level (P).

	Prior	Post	P	d.f.
Sole	0.24	1.35	<0.01	22.8
Plaice	2.32	2.63	n.s.	23.11
Turbot	0.04	0.12	<0.01	26.0
Brill	0.24	0.32	n.s.	33.9

n.s., non-significant.

observed stable to moderate increase in the Kattegat-Skagerrak plaice spawning stock biomass (SSB) during the period from the 1970s to 2000 (Cardinale *et al.*, 2009a). Similarly, an increase in juvenile turbot catches was identified, whereas no change in brill abundance was found. The increase in turbot is consistent with the trend observed in the adult population during the early 1980s (Cardinale *et al.*, 2009b). The degree to which an increase in sole and turbot is a consequence of habitat expansion of populations from neighboring areas or, alternatively, an increase in local population numbers, is an open question. However, for both sole and turbot no genetically distinct Kattegat

population has been identified (Nielsen *et al.*, 2004; Rolland *et al.*, 2007).

The onset of the observed increases in abundance of sole and turbot is in agreement with large-scale changes observed in neighboring ecosystems, for example the 1982–83 regime shift in the North Sea (Beaugrand *et al.*, 2003; Beaugrand, 2004) and the late 1980s regime shift in the Sound and Baltic Sea (Möllmann *et al.*, 2009; Lindegren *et al.*, 2010b). SP and TB increased with increasing SST, NHA and NAO using data from both commercial landings and survey catches, although the strength of the relationship differed. This underlines that identifying the major climatic indicator linking climate variability to a response in a given species or community is difficult. For instance, indices such as NHA and NAO will typically be suited for describing an overall climate trend but have a number of drawbacks when used as proxies for local hydrographic conditions (Stenseth *et al.*, 2003), whereas local SST measurement may suffer from a high degree of variability (noise). In addition, the overall positive relationships may be explained by a direct physiological effect (i.e., through increased metabolism), an indirect effect due to an extension of the period where juvenile flatfish can occupy nurseries, thereby achieving higher growth and increased survival (Gibson *et al.*, 2002; Ryer *et al.*, 2010), or a combination of both. The onset of the seasonal warming has changed during the last decades, such that it is approximately 10 days earlier than in 1960. Combined with a delayed fall, this results in a potential increased nursery growth period of 18 days (Burrows *et al.*, 2011). Such a prolonged period in the shallow nursery has a positive effect on a warm-water species like sole but not on plaice (Teal *et al.*, 2008). Thus the extended nursery period has the potential to cause an increase in SP, an increase which is possibly more drastic than if climate changes were simply a question of increased mean summer temperature.

The increasing temperatures did not seem to affect brill and turbot identically, even though the two species are similar in many respects. They both have the ability to produce hybrids (e.g., Heap and Thorpe, 1987), use the same nurseries (e.g., Haynes *et al.*, 2011) and both species are piscivorous as adults (Piet *et al.*, 1998). However, during the juvenile stage their diets differ. Turbot is more omnivorous than brill, and include smaller fish in their diet, whereas brill rely almost exclusively on a diet of mysids (Beyst *et al.*, 1999; Haynes *et al.*, 2011; Vinagre *et al.*, 2011). A broader diet might be an advantage during a changing environment, since increasing temperature during spring will instigate migration of both juvenile turbot

and brill into the nursery earlier than normal, potentially leaving brill with fewer suitable food items if the migration of mysids to the nurseries is not synchronized (mismatched).

Alternative explanations, such as interspecific competition, predation mortality and fishery-induced effects could also influence the composition of commercially important flatfish. Interspecific competition seems unlikely, even though all four species share the same nurseries, due to a limited dietary overlap of plaice and sole (Beyst *et al.*, 1999; Amara *et al.*, 2001) as well as turbot and brill (Beyst *et al.*, 1999; Haynes *et al.*, 2011; Vinagre *et al.*, 2011). The predation mortality on juvenile flatfish caused by cod (*Gadus morhua*) has likely decreased since the early 1980s, parallel to the decreasing cod stock (Cardinale and Svedäng, 2004). Yet, were SP and TB to increase due to decreased mortality, this would imply that sole was affected differently from plaice and turbot differently from brill. There appears to be no spatial segregation between the four species, as they share common nurseries, namely non-vegetated shallow beaches. That cod may have a preference for one of the species cannot be ruled out, but in general the predator/prey length relationship seems to be more important for the diet than the actual species preyed upon (Ellis and Gibson, 1995). The fishery is unlikely to have caused the observed changes in SP and TB, because sole and plaice are typically targeted in a mixed commercial fishery (Rijnsdorp *et al.*, 2006) and have a spatio-temporal overlap during adult life-stages (Maxwell *et al.*, 2009). Similarly, brill and turbot are also caught in a mixed fishery (Ulrich and Andersen, 2004).

CONCLUSION

We have demonstrated that metrics such as SP and TB can be used to assess climate-induced changes in species composition of commercially important flatfish. Moreover, the metrics are applicable for data sources where effort is unknown, and they are meaningful even within a relatively small geographic area. Finally, use of proportions is not restricted to assessment of the effect of climate changes; they could also be valuable as indicators of good environmental status, e.g., as requested in the European Union Marine Strategy Framework Directive (EC, 2008). Here the advantage of using effort-independent metrics is to be able to combine biological samples gathered over many years, by different countries and under shifting circumstances, into one single descriptor useful for management purposes.

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REFERENCES

- Amara, R., Laffargue, P., Dewarumez, J.M., Maryniak, C., Lagardere, F., Luczac, C. (2001) Feeding ecology and growth of 0-group flatfish (sole, dab and plaice) on a nursery ground (Southern Bight of the North Sea). *J. Fish Biol.* **58**:788–803.
- Attrill, A.J., Power, M. (2002) Climatic influence on a marine fish assemblage. *Nature* **417**:275–278.
- Bakun, A. (1996) Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. San Diego: University of California Sea Grant (in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California Sur, Mexico).
- Beaugrand, G. (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog. Oceanogr.* **60**:245–262.
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C. (2003) Plankton effect on cod recruitment in the North Sea. *Nature* **426**:661–664.
- Beyst, B., Cattrijsse, A., Mees, J. (1999) Feeding ecology of juvenile flatfishes of the surf zone of a sandy beach. *J. Fish Biol.* **55**:1171–1186.
- Brander, K.M. (2007) Global fish production and climate change. *Proc. Natl Acad. Sci. USA* **104**:19709–19714.
- Brander, K.M. (2009) Fisheries and climate. In: Encyclopedia of Ocean Sciences, 2nd edn. J.H. Steele, S.A. Thorpe & K.K. Turekian (eds) Waltham: Academic Press, pp. 483–490.
- Brander, K.M., Blom, G., Borges, M.F. *et al.* (2003) Changes in fish distribution in the eastern North Atlantic: are we seeing a coherent response to changing temperature?. *ICES Mar. Sci. Symp.* **219**:261–270.
- Bruun, A.F. (1927) Quantitative investigations of the 0-group and 1-group of the Plaice, Turbot, Brill and Sole in the Skagerrak, Kattegat and Belt Sea. *Meddelelser fra Kommissionen for Havundersøgelser. Series: Fiskeri*, No. **VIII**: 35 pp.
- Burrows, M.T., Schoeman, D.S., Buckley, L.B. *et al.* (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**:652–655.
- Cardinale, M., Svedäng, H. (2004) Modelling recruitment and abundance of Atlantic cod, *Gadus morhua*, in the eastern Skagerrak–Kattegat (North Sea): evidence of severe depletion due to a prolonged period of high fishing pressure. *Fish. Res.* **69**:263–282.
- Cardinale, M., Hagberg, J., Svedäng, H. *et al.* (2009a) Fishing through time: population dynamics of plaice (*Pleuronectes platessa*) in the Kattegat-Skagerrak over a century. *Popul. Ecol.* **52**:251–262.
- Cardinale, M., Linder, M., Bartolino, V., Maiorano, L., Casini, M. (2009b) Conservation value of historical data: reconstructing stock dynamics of turbot during the last century in the Kattegat-Skagerrak. *Mar. Ecol. Prog. Ser.* **386**:197–206.
- Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmuller, V., Dye, S.R., Skjoldal, H.R. (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J. Appl. Ecol.* **45**:1029–1039.
- EC (2008) Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of environmental policy (Marine Strategy Framework Directive). OJ L 164, 25.06.2008, pp. 19.
- Ellis, T., Gibson, R.N. (1995) Size-selective predation of 0-group flatfishes on a Scottish coastal nursery ground. *Mar. Ecol. Prog. Ser.* **127**:27–37.
- Engelhard, G.H., Pinnegar, J.K., Laurence, T.K., Rijnsdorp, A.D. (2011) Nine decades of North sea sole and plaice distribution. *ICES J. Mar. Sci.* **68**:1090–1104.
- Fishbase (2011) <http://www.fishbase.org> [accessed 21 September 2011].
- Gibson, R.N., Robb, L., Wennhage, H. and Burrows, M.T. (2002) Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. *Mar. Ecol. Prog. Ser.* **229**:233–244.
- Gislason, H. (2006) Havet som menneskets spisekammer. In: Havet. T. Fenchel (ed.) Copenhagen: Gyldendal. pp. 397–431. (In Danish)
- 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.
- Haynes, P.S., Brophy, D., De Raedemaeker, F., McGrath, D. (2011) The feeding ecology of 0 year-group turbot *Scophthalmus maximus* and brill *Scophthalmus rhombus* on Irish west coast nursery grounds. *J. Fish Biol.* **79**:1866–1882.
- Heap, S.P., Thorpe, J.P. (1987) A preliminary study of comparative growth rates in 0-group malpigmented and normally pigmented turbot, *Scophthalmus maximus* (L.), and turbot-brill hybrids, *S. maximus* × *S. rhombus* (L.), at two temperatures. *Aquaculture* **60**:251–264.
- Hurell, J. (2010) <http://www.cgd.ucar.edu/cas/jhurrell/indices.html> [accessed 22 March 2010].
- ICES (2010) <http://www.ices.dk/ocean/data/surface/surface.htm> [accessed 14 July 2010].
- IPCC (2007) Climate Change 2007: Synthesis Report (Fourth Assessment Report). Geneva: Intergovernmental Panel on Climate Change.
- Johansen, A.C. (1908) Contributions to the Biology of the Plaice, with Special Regard to the Danish Plaice-fishery. On the Variation in the Frequency of Young Plaice in the Danish waters in 1902–1907. *Meddelelser fra Kommissionen for Havundersøgelser. Serie: Fiskeri*, No. **III**: pp. 47.
- Johansen, A.C. (1915) Fünfter Bericht über die Pleuronectiden in der Ostsee. *Rapports et Proces-Verbaux des Reunions*, No. **XXII**: pp. 104. (In German)
- Lindgren, M., Möllmann, C., Nielsen, A., Brander, K.M., MacKenzie, B.R., Stenseth, N.C. (2010a) Ecological forecasting under climate change: the case of Baltic cod. *Proc. R. Soc. London Ser. B* **277**:2121–2130.

- Lindegren, M., Diekmann, R., Möllmann, C. (2010b) Regime shifts, resilience and recovery of a cod stock. *Mar. Ecol. Prog. Ser.* **402**:239–253.
- Maxwell, D.L., Stelzenmüller, V., Eastwood, P.D., Rogers, S.I. (2009) Modelling the spatial distribution of plaice (*Pleuronectes platessa*), sole (*Solea solea*) and thornback ray (*Raja clavata*) in UK waters for marine management and planning. *J. Sea Res.* **61**:258–267.
- Mieszowska, N., Kendall, M.A., Hawkins, S.J. et al. (2006) Changes in the range of some common rocky shore species in Britain – a response to climate change? *Hydrobiologia* **555**:241–251.
- Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., Axe, P. (2009) Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the central Baltic Sea. *Global Change Biol.* **15**:1377–1393.
- Nielsen, E.E., Nielsen, P.H., Meldrup, D., Hansen, M.M. (2004) Genetic population structure of turbot (*Scophthalmus maximus* L.) supports the presence of multiple hybrid zones for marine fishes in the transition zone between the Baltic Sea and the North Sea. *Mol. Ecol.* **13**:585–595.
- NOAA (2011) <http://www.ncdc.noaa.gov/cmb-faq/anomalies.php#anomalies> [accessed 21 January 2011].
- O'Brien, C.M., Fox, C.J., Planque, B., Casey, J. (2000) Fisheries: climate variability and North Sea cod. *Nature* **404**: 142.
- Ottersen, G., Kim, S., Huse, G., Polovina, J.J., Stenseth, N.C. (2010) Major pathways by which climate may force marine fish populations. *J. Mar. Syst.* **79**:343–360.
- Piet, G.J., Pfisterer, A.B., Rijnsdorp, A.D. (1998) On factors structuring the flatfish assemblage in the southern North Sea. *J. Sea Res.* **40**:143–152.
- Rijnsdorp, A.D. (2010) Sole. In: *Resolving Climatic Impacts on Fish Stocks*. A.D. Rijnsdorp, M.A. Peck, G.H. Engelhard, C. Möllmann & J.K. Pinnegar. *ICES Cooperative Research Report*, 301. pp. 193–198.
- Rijnsdorp, A.D., Daan, N., Dekker, W. (2006) Partial fishing mortality per fishing trip: a useful indicator of effective fishing effort in mixed demersal fisheries. *ICES J. Mar. Sci.* **63**:556–566.
- Rindorf, A., Lewy, P. (2006) Warm, windy winters drive cod north and homing of spawners keeps them there. *J. Appl. Ecol.* **43**:445–453.
- Rodionov, S. (2004) A sequential algorithm for testing climate regime shifts. *Geophys. Res. Lett.* **31**:L09204.
- Rodionov, S., Overland, J.E. (2005) Application of a sequential regime shift detection method to the Bering Sea ecosystem. *ICES J. Mar. Sci.* **62**:328–332.
- Rolland, J.L., Bonhomme, F., Lagardère, F., Hassan, M., Guinand, B. (2007) Population structure of the common sole (*Solea solea*) in the Northeastern Atlantic and the Mediterranean Sea: revisiting the divide with EPIC markers. *Mar. Biol.* **151**:327–341.
- Rosenzweig, C., Karoly, D., Vicarelli, M. et al. (2008) Attributing physical and biological impacts to anthropogenic climate change. *Nature* **453**:353–357.
- Ryer, C.H., Laurel, B.J., Stoner, A.W. (2010) Testing the shallow water refuge hypothesis in flatfish nurseries. *Mar. Ecol. Prog. Ser.* **415**:275–282.
- Stenseth, N.C., Ottersen, G., Hurrell, J.W. et al. (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc. R. Soc. Lond. B* **270**:2087–2096.
- Støttrup, J.G., Sparrevojn, C.R., Modin, J., Lehmann, K. (2002) The use of releases of reared fish to enhance natural populations: a case study on turbot *Psetta maxima* (Linné, 1758). *Fish. Res.* **59**:161–180.
- 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.
- Ulrich, C., Andersen, B.S. (2004) Dynamics of fisheries, and the flexibility of vessel activity in Denmark between 1989 and 2001. *ICES J. Mar. Sci.* **61**:308–322.
- Vinagre, C., Silva, A., Lara, M., Cabral, H.N. (2011) Diet and niche overlap of southern populations of brill *Scophthalmus rhombus* and turbot *Scophthalmus maximus*. *J. Fish Biol.* **79**:1383–1391.
- Warton, D.I., Hui, F.K.C. (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology* **92**:3–10.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1. Supplementary information on changes in survey coverage and the background for selecting sea surface temperature from April month.

Figure S1. Maps showing change in spatial coverage of young fish surveys.

Figure S2. R^2 values of linear regressions with different months as covariates to either SP or TB.