Vol. 480: 199–203, 2013
doi: 10.3354/meps10314

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 22

THEME SECTION

Harvested fish stocks in a changing environment

Editors: J. M. Durant, N. C. Stenseth

Marine Ecology Progress Series Vol. 480, pages 199–287

CONTENTS

INTRODUCTION

Impact of climate and fisheries on sub-Arctic stocks

Joël M. Durant[1,*], Geir Ottersen[1,2], Nils C. Stenseth[1,3]

[1]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo,
PO Box 1066 Blindern, 0316 Oslo, Norway
[2]Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway
[3]Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway

ABSTRACT: Understanding the drivers (internal and external) that determine the productivity of marine ecosystems is challenging. For example, the correct estimate of recruitment is essential to estimate fish stock abundance. In this Theme Section, 5 papers explore the effect of fishing and climate on population structure across sub-Arctic ecosystems. The studies focus on how temperature- and fishing-induced changes in spatial and demographic population structure affect recruitment and population growth rate. The results suggest common patterns, but also highlight differences in the relative importance of fishing and climate among the populations and ecosystems examined.

KEY WORDS: Climate · Non-stationarity · Spatial distribution · Recruitment · Population growth · Sub-Arctic

---

[*]Email: joel.durant@bio.uio.no

Introduction

There is growing awareness among fisheries scientists that climate variability and fisheries influence the state and functioning of marine ecosystems. Importantly, the effects of climate and exploitation interact, such that climate alterations may cause failure in a fishery management scheme, while fisheries may disrupt the ability of a population to withstand, or adjust to, climate change (Planque et al. 2010). Accordingly, marine ecosystems under intense exploitation may evolve towards stronger bottom-up control and greater sensitivity to climate forcing (Perry et al. 2010). Because climate change occurs slowly, its effects are not likely to have immediate ecosystem impacts, but will gradually become evident by affecting the interactions between fishing and environmental variability.

To explore this topic — with a focus on comparative analyses of sub-Arctic seas — two international workshops were hosted by the Centre for Ecology and Evolutionary Synthesis (CEES) of the University of Oslo in November 2009 and March 2011. The workshops brought together scientists from 5 countries (Canada, France, Norway, Russia and the USA) with expertise in theoretical ecology, animal behaviour, fish ecology, fisheries oceanography and ecosystem modelling. This Theme Section is composed of 5 papers that resulted from the workshops and the surrounding discussions.

There is no *a priori* reason to assume that fish populations, let alone ecosystems, display a linear response to the joint pressure from climate and exploitation. Thus, the methods employed to study such effects should be able to deal with non-additive and non-linear patterns. Moreover, the relationship between recruitment, spawning stock biomass and temperature frequently varies over time, so temporal non-stationarity should also generally be taken into consideration when analysing fish stock data. Besides temporal non-stationarity, spatial non-stationarity may also affect population dynamics. For instance, the non-uniform fishing pressure on population sub-units may lead to a reduction in the capacity of populations to withstand climate variability and change. In addition, since small, pelagic forage fish often prey on the egg and juvenile stages of their larger fish predators, selective fishing of either the top predators or the pelagic forage fish component of the system may lead to a role-reversal and destabilize the ecosystem (Bakun 2010, Fauchald 2010).

This Theme Section provides substantial insights into how environmental variability and fisheries affect population dynamics of harvested marine fish stocks. Each paper addresses one of 5 key points, as detailed in the following sections.

(1) Temporal shifts in and temperature effects on recruitment dynamics

Density-independent environmental factors are assumed to be of primary importance in regulating the size of fish populations, accounting for most of the variability in pre-juvenile survival (Houde 2008). On the other hand, density-dependent survival in the juvenile phase is also considered to be a key factor and is embodied in many age structured fisheries assessment models where regulation is effected through a stock–recruitment relationship (Hilborn & Walters 1992). Thus, disentangling the effects of climate variability and internal population dynamics on recruitment remains a challenge.

In the first paper in this Theme Section, Ottersen et al. (2013) tested, by means of statistical modelling, 7 hypotheses relating variation in sea temperature, spawning stock biomass, and mean age in the spawning stock to temporal patterns in recruitment dynamics of 38 commercially harvested North Atlantic fish stocks. Their results highlight the need to be careful not to over-interpret purely linear environment–recruitment associations (like correlations), since the underlying relations may be non-linear and variable over time. The reason for established correlations to break down when new data are added may be non-stationarity, i.e. recruitment dynamics undergoing temporal shifts. Ottersen et al. (2013) found that non-stationarities in recruitment dynamics are quite frequent and often abrupt. The most frequent alteration in the non-stationary linear models occurred in the intercept in recruitment success, suggesting a change in pre-recruit mortality over time (observed for 14 stocks).

(2) Erosion of population spatial structure

All animal populations are spatially structured as a result of the physical environment and of behavioural and biological processes occurring within and between different populations. Changes in the spatial structure of marine populations can be a prelude to further changes in abundance and can affect the resilience of a population to human and environmental perturbations. There is evidence that large variations in species abundance over time are typically accompanied by equally dramatic and large-scale changes in spatial distribution patterns, not only for marine fishes but for animal populations in general (e.g. Gaston et al. 2000, Bacheler et al. 2009). Moreover, changing spatial patterns can subject individuals to a set of new environmental constraints and interspecific interactions, and can have consequences at the community level.

Ciannelli et al. (2013, this Theme Section) underscore the importance of examining the spatial ecology of fish populations to (1) understand the underlying mechanisms that can lead to rapid alterations in population abundance and community interactions, (2) provide indicators of stock health, and (3) characterize the consequences of changing spatial patterns on the population susceptibility to human exploitation and environmental variability. In their review, Ciannelli et al. (2013) have shown how populations can be spatially structured, regardless of their genetic and demographic connections, and that the erosion of such spatial structure has negative consequences at the population and community levels.

(3) Predicting fish recruitment

Prediction of year-class strength is a critical challenge for fisheries managers. Spawning stock biomass (SSB) may be a useful predictor of future recruitment at extreme high or low values, but there is enormous variability in the relationship between SSB and recruitment strength at intermediate values of SSB. This lack of relationship indicates that other, environmental, variables are likely to play an important role in determining the production of recruits. In particular, the survival of egg and larval stages are vulnerable to any number of catastrophic impacts from the environment, whereas the survival of juveniles may be more predictable.

Stige et al. (2013, this Theme Section) examined the usefulness of juvenile relative to larval abundance in predicting recruitment. They analysed data on 5 marine fish stocks covering 4 species and 3 Arctic ecosystems. They found that abundance indices of later life stages do not always provide better estimates than those based on earlier life stages, and suggest that this unexpected result was due to the poor quality of the time series collected for older life stages. Stige et al. (2013) showed that the inclusion of environmental indices often improved the accuracy of 'honest' predictions of recruitment, i.e. predictions based upon data not used when fitting the recruitment models. Stige et al. (2013) finally stressed that even with complex marine systems, the environment–recruitment correlations were found to be unstable, and the available time-series were short, consideration of environmental information may still improve recruitment predictions.

(4) Predator–prey interaction

Unlike most terrestrial ecosystems, marine systems may allow for role-reversal between prey and predators. Small, pelagic forage fish are often themselves predators of, and competitors with, the egg and juvenile stages of their larger fish predators. In fact, prey species may flourish as a result of decreased predation pressure when predatory fish have been fished down (e.g. Frank et al. 2011). Subsequently, they may prevent the recovery of the predator, e.g. by preying on the predator's eggs and larvae (Bakun & Weeks 2006, Bakun 2010). Thus a large population of forage fish may reduce the recruitment of predators to the extent that the system switches to an alternate prey-dominated state. Consequently, selective human harvesting of either the predators or the forage fish may cause ecosystem shifts by 'pushing' the system between the respective states (Bakun 2010, Fauchald 2010).

Hjermann et al. (2013, this Theme Section) scrutinized the potential predator–prey reversal scenario for the North Sea suggested by Fauchald (2010) by conducting a spatially resolved analysis based upon 40 yr of cod and herring *Clupea harengus* data. They found that the mechanisms for the changes in cod and herring abundance vary spatially throughout the North Sea. For instance, the largest decline in cod recruitment occurred along the coasts of the Netherlands, Germany and Denmark, where herring abundance and water temperature have increased more than in other parts of the North Sea. In this area, the cod and herring were oppositely affected by the observed increase in sea surface temperatures (the cod negatively, the herring positively), and herring abundance had an additional negative effect on cod recruitment. Thus, for parts of the southern North Sea, the findings of Hjermann et al. (2013) are consistent with the hypothesis of alternative stable states, while for other parts there is no evidence that such mechanisms operate.

(5) Population growth rate across heterogeneous environments

Population growth is affected by several factors such as climate, species interactions, and harvesting pressure, with the latter making marine populations more sensitive to climate forcing (Hsieh et al. 2010). Age-truncated or juvenescent populations are a worldwide consequence of high and often size-selective mortality from commercial fishing, typically targeting the older and larger individuals (Law 2000). Juvenation may increase a populations' ability to directly respond to environmental fluctuations (Rouyer et al. 2011), emphasizing the importance of the interaction between fisheries, environment, and recruitment and population growth that produces complex synergic effects on the population dynamics of marine species.

Durant et al. (2013, this Theme Section) explored how external forcing (climate and fishing) and recruitment modulate the population dynamics of fish within different environments. They calculated the realized yearly population growth rate of 7 gadoid stocks across different ecosystems. By comparing the corresponding sensitivity of population growth to recruitment change across the 7 stocks, Durant et al. (2013) showed that reduction in generation time triggered an increase in the relative contribution of recruitment to population growth, while the increase of fishing mortality—suggested to truncate the age structure of the stocks—had a weaker effect. The findings of Durant et al. (2013) emphasise how the elasticity of the population growth to recruitment change can be affected by a long-term change in age structure of the population, maybe due to fishing (e.g. Rouyer et al. 2011, but see Ottersen et al. 2013), but also directly by the ongoing fishing intensity.

Conclusions

The key message of this Theme Section is the importance of the interplay between environment and stock (size and structure) in shaping recruitment of sub-Arctic marine fish stocks. The 5 papers highlight different aspects of this theme and draw attention to the value of monitoring temporal and spatial patterns, as well as environmental forcing. In this Theme Section, we have demonstrated that:

(1) Recruitment estimates may be improved by taking into account environmental information and non-stationarity. Ottersen et al. (2013) showed that temperature may affect the stock-recruitment relation and that the effect can change through time, also abruptly. The situation is further complicated by the temperature–recruitment relation also displaying spatial differences within the same sea (Hjermann et al. 2013). Still, Stige et al. (2013) showed that environmental information can aid the prediction of recruitment. Furthermore, while much of the year class strength is determined during egg and larval stages, this pattern may be overshadowed by density-dependent mortality factors operating at later life stages (Stige et al. 2013). Later measures, closer to recruitment, should thus be the better recruitment predictors. However, Stige et al. (2013) did not find such a consistent improvement, perhaps due to the shortness of the available time series.

(2) Age-structure may be important for understanding the dynamics of harvested populations. Durant et al. (2013) showed that the contribution of recruitment to population growth was affected by environmental conditions and by the age-structure of the population. However, contrary to what was expected, Ottersen et al. (2013) found little or no general decrease in mean age in the spawning stock. Still, results shown at our second workshop demonstrate remarkable decreases in the number of reproductive age groups in 6 NW Atlantic cod stocks, in the most extreme case from 12 to 4 groups (K. Frank, pers. comm.). The lack of clear patterns may result from the different species having evolved a variety of life history strategies, including life expectancies and age of maturity, and thus cannot be expected to respond in the same way to intensive fishing.

(3) Spatial ecology is important to understand the underlying mechanisms that drive fish population dynamics. Ciannelli et al. (2013) showed that spatial structure of a population can be modified by both climate and fishing, with consequences at the population and community levels. Ciannelli et al. (2013) advocated that the preservation of a population's spatial structure should be an explicit management goal, especially since spatial structures in marine populations are easier to monitor and characterize than demographic and genetic structures. Many commercially exploited stocks are surveyed multiple times in a year and over different life history stages. Therefore, there is already a large body of available information that can be integrated in management scenarios and that is less difficult or expensive to obtain than other data on population structures. However, the 'poor' data stocks (i.e. those stocks that are irregularly monitored or those not monitored at all because they are not commercially important) represent a challenge; these stocks will need to be monitored in order to reach the sustainable management objectives.

Acknowledgements. We thank the participants of the Tropharct workshops for their contributions, and the Research Council of Norway (RCN) for funding through the project MICO (Match/Mismatch and Ecosystem; no. 186310). G.O. and J.M.D. thank RCN for funding their contribution to this paper through the ADMAR (Adaptive management of living marine resources by integrating different data sources and key ecological processes, number 200497/130). We thank Mette Skern-Mauritzen, Lorenzo Ciannelli, Leif Chr. Stige and George Hunt for their comments on an early version of this paper.

LITERATURE CITED

➤ Bacheler NM, Bailey KM, Ciannelli L, Bartolino V, Chan KS (2009) Density-dependent, landscape, and climate effects on spawning distribution of walleye pollock *Theragra chalcogramma*. Mar Ecol Prog Ser 391:1–12

➤ Bakun A (2010) Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: conceptual templates and schematic constructs. J Mar Syst 79:361–373

➤ Bakun A, Weeks SJ (2006) Adverse feedback sequences in exploited marine systems: Are deliberate interruptive actions warranted? Fish Fish 7:316–333

Ciannelli L, Fisher JAD, Skern-Mauritzen M, Hunsicker ME, Hidalgo M, Frank KT, Bailey KM (2013) Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. Mar Ecol Prog Ser 480:227–243

Durant JM, Hidalgo M, Rouyer T, Hjermann DØ and others (2013) Population growth across heterogeneous environments: effects of harvesting and age structure. Mar Ecol Prog Ser 480:277–287

➤ Fauchald P (2010) Predator–prey reversal: a possible mechanism for ecosystem hysteresis in the North Sea? Ecology 91:2191–2197

➤ Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. Science 308:1621–1623

Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH (2000) Abundance–occupancy relationships. J Appl Ecol 37 (Suppl 1):39–59

Hilborn R, Walters CJ (1992) Quantitative fisheries stock assessment. Chapman & Hall, New York, NY

Hjermann DØ, Fisher JAD, Rouyer T, Frank KT, Stenseth NC (2013) Spatial analysis of North Sea cod recruitment: concurrent effects of changes in spawning stock biomass, temperature and herring abundance. Mar Ecol Prog Ser 480:263–275

➤ Houde ED (2008) Emerging from Hjort's Shadow. J Northwest Atl Fish Sci 41:53–70

➤ Hsieh CH, Yamauchi A, Nakazawa T, Wang WF (2010) Fishing effects on age and spatial structures undermine population stability of fishes. Aquat Sci 72:165–178

➤ Law R (2000) Fishing, selection, and phenotypic evolution. ICES J Mar Sci 57:659–668

Ottersen G, Stige LC, Durant JM, Chan KS, Rouyer TA, Drinkwater KF, Stenseth NC (2013) Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. Mar Ecol Prog Ser 480:205–225

➤ Perry RI, Cury P, Brander K, Jennings S, Möllmann C, Planque B (2010) Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. J Mar Syst 79:427–435

➤ Planque B, Fromentin JM, Cury P, Drinkwater KF, Jennings S, Perry RI, Kifani S (2010) How does fishing alter marine populations and ecosystems sensitivity to climate? J Mar Syst 79:403–417

➤ Rouyer T, Ottersen G, Durant JM, Hidalgo M and others (2011) Shifting dynamic forces in fish stock fluctuations triggered by age truncation? Glob Change Biol 17: 3046–3057

Stige LC, Hunsicker ME, Bailey KM, Yaragina NA, Hunt GL Jr (2013) Predicting fish recruitment from juvenile abundance and environmental indices. Mar Ecol Prog Ser 480: 245–261

Vol. 480: 205–225, 2013
doi: 10.3354/meps10249

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 22

Contribution to the Theme Section 'Harvested fish stocks in a changing environment'

Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature

Geir Ottersen[1,2,*], Leif Christian Stige[2], Joël M. Durant[2], Kung-Sik Chan[3], Tristan A. Rouyer[2,6], Kenneth F. Drinkwater[4], Nils Chr. Stenseth[2,5]

[1]Institute of Marine Research, Gaustadalléen 21, 0349 Oslo, Norway
[2]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway
[3]Department of Statistics and Actuarial Science, University of Iowa, Iowa City, Iowa 52242, USA
[4]Institute of Marine Research, PB 1870 Nordnes, 5817 Bergen, Norway
[5]Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway
[6]*Present address:* IFREMER, UMR EME 212, Sète, France

ABSTRACT: Effects of variation in spawning stock and sea temperature on long-term temporal patterns in recruitment dynamics of 38 commercially harvested fish stocks in the northern North Atlantic were studied. Different statistical models were explored within a Ricker stock-recruitment framework. This includes, in order of complexity, adding a linear temperature term, a nonlinear (smooth) temperature effect, and non-stationarities (trends in intercept or in temperature effect) and finally allowing for a stepwise change (a threshold). The different models were compared in a uniform approach using Akaike's information criterion corrected for small sample size as the model selection criterion. The relationship between recruitment, spawning stock biomass and temperature varied over time. The most frequent alteration in the non-stationary linear models was, for 14 stocks, in the intercept in recruitment success, suggesting a change in pre-recruit mortality over time. Threshold models performed better than the best linear or nonlinear stationary models for 27 of the stocks, suggesting that abrupt changes (maybe even regime shifts) are common. For half of the stocks studied, the temperature effect was statistically significant when added to the model of the relationship between recruitment success and spawning stock biomass. This includes all 6 of the herring stocks studied, with a positive effect for cold-water stocks and negative effect for stocks in the more temperate southern areas. For the 4 plaice stocks analysed, all located towards the centre of the overall distribution range of plaice, a tendency toward recruitment being favoured by lower temperatures was found.

KEY WORDS: Recruitment · Spawning stock biomass · Temperature · North Atlantic · Statistical modelling · Non-stationarity · Climate

INTRODUCTION

The quest toward understanding what regulates the variability in recruitment of commercially exploited fish stocks, i.e. the abundance of a cohort surviving to establish a new year-class, has been a 'search for the Holy Grail' in fisheries science since at least the early 20th century (Hjort 1914). Unfortunately, the answer still seems to be as elusive as the Grail itself, and despite progress, forecasting recruitment remains a formidable challenge (Houde 2008). Intuitively, there should be a quantitative relation-

---

*Email: geir.ottersen@imr.no

ship between the mature population and the recruits, i.e. stock-recruitment curves. However, although strong recruitment does tend to co-occur with high spawner abundance (Myers & Barrowman 1996), the stock-recruitment relationship is frequently weak (Hilborn & Walters 1992, Koslow 1992). There are several possible reasons for this seemingly weak link: (1) the influence of environmental variability (both interannual and long-term variation) on recruitment may make it difficult to identify stock-recruitment relationships, (2) not all stocks may have exhibited variation in stock size large enough to see a significant influence on recruitment, (3) there is uncertainty in the recruitment estimates (from e.g. virtual population analysis [VPA]), and (4) there are insufficient data. Still, a general denial of meaningful stock-recruitment relationships would have rather alarming consequences for the science of fish population dynamics (Iles 1994).

Density-dependent survival in the juvenile phase is generally believed to be of key importance in regulating the size of fish populations (Rothschild 1986, Vincenzi et al. 2012). Under this assumption, the emphasis is on quantifying the form of the density-dependence, which in turn determines the shape of the stock-recruitment relationship. This view is embodied in many age-structured fisheries assessment models in which regulation is effected through a stock-recruitment relationship (Hilborn & Walters 1992). Further, it implies that recruitment may depend on the size of the parental stock in a nonlinear manner.

In contrast, density-independent environmental factors are also assumed to be of primary importance, accounting for most of the variability in pre-juvenile survival (Houde 2008). Paleo-record studies on fish abundance variability prior to the onset of extensive fishing indicate the importance of environmental factors for population regulation (Emeis et al. 2010, Finney et al. 2010). Actually, the importance of the environment for fluctuations in fish stocks was already acknowledged as early as the 1870s (Kendall & Duker 1998). Since then, recruitment has been correlated with temperature in numerous studies on single stocks and fewer covering many stocks (examples of the latter are in Planque & Fredou 1999, Fox et al. 2000, and Brunel & Boucher 2007). Unfortunately, many such correlations tend to weaken or disappear when retested with extended data series (Myers 1998). Thus, unequivocal identification of the relative importance of density-dependent versus density-independent factors underlying recruitment variations remains an enigma (Frank & Leggett 1994).

Disentangling the effects of climate variability and internal population dynamics on recruitment by means of statistical data analysis is no easy task. For instance, indirect, interacting and nonlinear effects of environmental factors could lead to non-stationary behaviour of linear and additive models (e.g. Stige et al. 2006). Moreover, the inter-annual variability in temperature (or any other environmental variable) experienced by a single fish stock is often quite small (Brander 2000). These problems may be reduced by using long time series on many stocks in a comparative analysis, which should widen the thermal range and increase the number of degrees of freedom. The comparative analysis may be either a joint analysis, in which the results of identical analyses of individual stocks are compared, or a pooled analysis, in which the data are pooled and then analysed together (Brander 2000). Such studies can help to determine what is fundamental and what is specific to particular ecosystems for certain species (Drinkwater et al. 2010).

In the present paper, a comparative, joint approach is employed in statistically modelling temporal changes in recruitment dynamics in 38 commercially harvested fish stocks in the northern North Atlantic region, with a focus on the European side (see Table 1). We focus in particular on the possible non-stationarity in the long-term relationship between recruitment, spawning stock biomass (SSB) and temperature and on the effect of the population structure (SSB and body mass weighted mean age in the spawning stock [MA]) on the stock-recruitment relationship. Specifically, we examine the validity of the hypotheses given below. In each case, the formulation of the hypothesis is followed by a brief description of why we address this particular issue.

H1: recruitment success varies among years in response to temperature

Theory suggests that the environment (e.g. temperature) may modify the quantitative relationship between the mature population and the recruits, i.e. recruitment success (ln[R/SSB], where R is the number of recruits), and the stock-recruitment curves (Cushing & Horwood 1994, Johansen 2007). While temperature-recruitment studies are numerous, far fewer have analysed the joint effects of temperature and stock size on recruitment. Exceptions include work on Baltic cod *Gadus morhua* and sprat *Sprattus sprattus* (Köster et al. 2003), red mullet *Mullus barba-*

tus in the Strait of Sicily (Levi et al. 2003), and North Sea cod (Olsen et al. 2011). Moreover, if effects of interannual differences in temperature are not accounted for, apparent nonstationarity in the stock-recruitment relationship may result.

H2: the relationship between recruitment, SSB, and temperature is not constant over time

This implies that the recruitment dynamics is non-stationary, either with a gradual alteration or a more abrupt temporal shift, with different dynamics before and after this shift. Such shifts may be part of broader ecological regime shifts, which have been defined as 'large, abrupt, persistent changes in the structure and function of a system' (Biggs et al. 2009). Marine ecological regime shifts have been described in numerous earlier publications, including Francis & Hare (1994) regarding the Northeast Pacific and Beaugrand (2004) regarding the North Sea.

Myers (1998) re-examined previously published environment-recruitment correlations with prolonged data series and found that the proportion of published correlations that could be verified upon retest was low. The original findings could be merely statistical artefacts, but real changes in underlying regulating processes may have taken place, altering the observed relationships. Indeed, long-term changes in the ecosystem, for example in response to climate change or harvesting, could lead to changes in the relative roles of the different abiotic and biotic factors that influence juvenile fish survival and thus the relationships studied here. For example, increased abundance of predators on juveniles could lead to diminished importance of abiotic factors (Bailey 2000).

For stocks that displayed a statistically significant temporal shift in recruitment dynamics, we examined possible causes for these shifts, formulated as Hypotheses H3, H4, and H5.

H3: recruitment per SSB decreases with decreasing MA

High exploitation levels of many marine fish populations usually result in a disproportional loss of the largest (and thus oldest) individuals. Consequently, a juvenated, age-truncated spawning stock has been suggested as a potential problem for long-lived fish (Law 1991, Berkeley et al. 2004, Planque et al. 2010).

The concern about stock juvenation largely stems from its potential impairment of recruitment success (e.g. Ponomarenko 1973, Beamish et al. 2006). Especially for cod, there is a considerable literature, which collectively indicates that the proportion of larger (and thus older) fish present in a population may contribute considerably toward determining the number of eggs, larvae, and subsequently successful recruits. Larger females tend to produce more eggs per gram of body weight (Marteinsdottir & Thorarinsson 1998) and also to produce eggs that have a wider range of vertical distribution, thus causing broader horizontal dispersion (Kjesbu et al. 1992). Further, the size of cod eggs and larvae generally increases with maternal size (Chambers & Waiwood 1996, Trippel et al. 1997), also increasing viability, as both field studies (Meekan & Fortier 1996) and theory (Houde 1987) suggest a tendency toward increased survival among faster-growing larvae.

H4: recruitment per SSB decreases with long-term reduction in SSB

While the Ricker model predicts that recruitment per SSB is higher at low SSB because of reduced intraspecific competition, we hypothesize that a long-term reduction in SSB has the opposite effect. Although this may seem counterintuitive, several mechanisms could cause such an outcome. First, in the ocean, it is common for prey fishes to eat the eggs and larvae of the predators that prey on them. When a dominant predator population declines due to an external impact, such as fishing or climatic variation, it is logical that its favoured prey, if not equally impacted, should increase in abundance. Thus, an observed reduction in SSB (of, e.g., cod) may have resulted in a lessened predation pressure on fishes that prey on cod eggs and larvae. This again should cause increased predation on early life stages of cod and thus decreased survival until recruitment (prey to predator feedback loop; Bakun 2010). Depensatory effects can then delay or prevent stock rebuilding (Walters & Kitchell 2001), resulting in a prolonged period of reduced SSB.

Secondly, a long-term reduction in SSB may be associated with loss of spatial and genetic structure in the populations, for example through the loss of geographically separated subunits of the stocks. The eggs and larvae of such 'unstructured' stocks are likely to experience more uniform environmental conditions compared to the eggs and larvae from more 'pristine' stocks (Ciannelli et al. 2013, this vol-

Table 1. Species, stock identification, location, number of data points where all necessary (population and temperature) data are available, and results from linear non-stationary and stationary models (see 'Materials and methods', Eqs. 2–5). Temp.: sign (+ or −) of the temperature effect in Eq. (2) with corresponding statistical significance. Effect: form of temperature effect in best model as evaluated by the corrected Akaike's information criterion (AIC_C) with corresponding statistical significance. Year: sign and statistical significance of the year effect in Eq. (4). A year effect indicates a change in the intercept. Year.temp: sign and statistical significance of the Temp × Year effect in Eq. (5). Significant year.temp effect indicates a temporal trend in the temperature effect. dAIC_C: difference in AIC_C between the best non-stationary linear and stationary model. Species: cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, herring *Clupea harengus*, plaice *Pleuronectes platessa*, saithe *Pollachius virens*, sole *Solea solea*, whiting *Merlangius merlangus*. $^{*}p < 0.05$, $^{**}p < 0.01$ (*F*-tests on nested models with and without variable)

Species and stock	Location	N	Temp.	Effect	Year	Year.temp	dAIC_C
Cod 3NO[a]	Southern Grand Bank	49	+	None	−**	+**	−25.6
Cod 3Pn4RS[b]	Northern Gulf of St. Lawrence	33	+	None	−*	+	−1.0
Cod 4TVn[c]	Southern Gulf of St. Lawrence	36	+	None	−**	+	−6.0
Cod 4X[d]	Western Scotian Shelf	28	−	None	−*	−	−4.0
Cod 5Zjm[e]	Eastern Georges Bank	31	+	None	−	−	0.8
Cod Baltic 22-24	Western Baltic Sea	39	−	Nonlinear**	−**	−	−0.9
Cod Baltic 25-32	Baltic Sea proper	41	+	None	−	+**	−9.0
Cod Faroe Plateau	Faroe Plateau	46	−**	Linear**	−	−	−1.6
Cod Iceland	Icelandic waters	54	−*	Linear*	−	+	−1.1
Cod North Sea	North Sea	45	−**	Linear**	+	+	2.4
Cod Northeast Arctic	Barents Sea	83	+	None	+*	+	−2.7
Cod VIa	West of Scotland	29	−	None	−	+	−1.7
Cod VIIa	Irish Sea	40	−**	Linear**	−	−	−1.8
Cod VIIek	Western English Channel and SW of Ireland	36	−	Nonlinear	+**	+	−11.8
Haddock Arctic	Barents Sea	56	+**	Linear**	+	+	1.9
Haddock Faroe Plateau	Faroese waters	52	−	None	−*	−	−4.5
Haddock Iceland	Icelandic waters	29	+**	Nonlinear**	+	−	0.8
Haddock North Sea	North Sea	46	−	Nonlinear**	−*	−*	−1.1
Haddock VIa	West of Scotland	29	−	None	−	−	1.1
Herring Baltic 25-32	Baltic Sea proper	34	+**	Linear**	−	+	1.2
Herring Baltic 30	Bothnian Sea (Baltic)	35	+*	Linear*	+*	−	−3.5
Herring Baltic Riga Bay	Riga Bay (Baltic)	31	+**	Linear**	−	−	1.6
Herring North Sea	North Sea	49	−**	Linear**	+	−	−1.2
Herring Norweg. SS	Norwegian and Barents Sea (Norwegian spring-spawning)	86	+**	Nonlinear**	−	−	−1.6
Herring VIa	West of Scotland	51	−**	Nonlinear**	−	−	2.7
Plaice North Sea	North Sea	51	−**	Nonlinear**	+**	−	0.0
Plaice VIIa	Irish Sea	42	−**	Linear**	−**	+	−9.7
Plaice VIId	Eastern English Channel	28	−	Nonlinear*	+	+	5.7
Plaice VIIe	Western English Channel	31	− **	Nonlinear**	+	+	2.7
Saithe Faroe	Faroese waters	45	+*	Linear*	+	−	−0.7
Saithe Iceland	Icelandic waters	34	+	None	−	+	1.3
Saithe 3a46	North Sea and west of Scotland	39	+	None	−*	−	−2.1
Saithe Northeast Arctic	Barents Sea	46	+*	Nonlinear*	+	+	−0.6
Sole North Sea	North Sea	51	−	None	+	+	1.9
Sole VIIa	Irish Sea	35	+	None	−**	−*	−10.0
Sole VIIe	Western English Channel	38	+**	Nonlinear*	+	+	1.6
Sole VIIfg	Celtic Sea	36	+	Linear	−	−	1.4
Whiting VIIek	Western English Channel and SW of Ireland	26	−	Linear	+	−	2.6

[a]Shelton et al. (2006), Power et al. (2010), K. Frank, BIO, Halifax, Canada, pers. comm.; [b]Fréchet et al. (2009); [c]Swain et al. (2007), K. Frank, BIO, Halifax, Canada, pers. comm.; [d]Brander (2005b), K. Frank, BIO, Halifax, Canada, pers. comm.; [e]Wang et al. (2009), K. Frank, BIO, Halifax, Canada, pers. comm.

ume). As a consequence of reduced opportunities for 'bet-hedging' (Hsieh et al. 2010), a stock in this state may be hit harder during years with unfavourable environmental conditions, with lower egg and larval survival and subsequently reduced recruitment. In contrast, stock state may be less important in years with environmental conditions favourable for high egg and larval survival, when a sufficient number in any case survive through these stages, and recruitment may be more limited by compensatory density dependence in juvenile survival.

H5: recruitment per SSB changes with long-term changes in temperature

Long-term change in temperature is here taken as a proxy for a change in climate regime, with a potentially different ecological effect than short-term fluctuations. Ecosystem regime shifts (as briefly described under H3 above) are often linked to climate but can also be driven by anthropogenic forcing, such as heavy fishing or pollution (Bakun 2004). Examples of shifts in climate regime that have had pronounced ecological impact on the study area of the present paper include the warming of the northern North Atlantic Ocean during the 1920s and 1930s (Drinkwater 2006) and the ecosystem regime shift in the North Sea during 1982 to 1988, which are related to pronounced changes in large-scale hydro-meteorological forcing (Beaugrand 2004).

Finally, for the stocks that displayed a statistically significant temporal shift in recruitment dynamics and an effect of temperature in at least one of the 2 periods, we examined how the strength of the temperature effect changed between the periods. Specifically, we explored how this change corresponded to the changes in respective body mass-weighted mean age of the spawning stock (MA) and SSB, as formulated in Hypotheses H6 and H7.

H6: the temperature-recruitment relationship strengthens with decreasing MA

Juvenation of the parent stock has caused concern since this could potentially affect recruitment by making it more susceptible to environmental fluctuations (e.g. Ponomarenko 1973, Beamish et al. 2006). H6 was examined for Northeast Arctic cod by Ottersen et al. (2006). They found statistical substantiation for the climate–recruitment link strengthening with reduced age of spawners and suggested this may be a more general mechanism. The idea has been supported by several recent reviews, e.g. Brander (2010), Hsieh et al. (2010), and Planque et al. (2010). Here, we wish to examine if there is general evidence for this suggestion or if it is restricted to particular groups of fish, for instance naturally long-lived stocks.

H7: the temperature-recruitment relationship strengthens with decreasing SSB

It has been proposed that the relationship between the environment (e.g. temperature) and recruitment may be affected by the size of the parent stock. For example, Brander (2005a) examined all cod stocks on the European Shelf south of 62° N and found that environmental variability (in this case the North Atlantic Oscillation [NAO]) only has a noteworthy effect on recruitment when the spawning stock is low.

If we assume that a low SSB is connected with a generally decreased stock size, one possible mechanism is the decrease of density dependent regulation. Density dependent processes are expected to stabilise recruitment variations (e.g. Vincenzi et al. 2012). Lighter density dependent control may hence lead to stronger influence of density independent processes, and a result of that may be an increased link between recruitment and temperature.

Further, at low population size, a stock may lose spatial and/or genetic diversity through selection of certain population sub-units within metapopulations, which may reduce the buffering capacity of the population in response to environmental fluctuations (Hsieh et al. 2010, Planque et al. 2010, Ciannelli et al. 2013).

MATERIALS AND METHODS

Fish population data

For each of the fish stocks studied, the geographical area, the length of the period with available time series for all of the SSB, number of recruits (R), and MA are given in Table 1, while the actual years covered for each stock are found in Table 2. The time series of recruitment and SSB of the 38 stocks analysed are shown in Fig. 1. For 33 northeast Atlantic stocks, the population data were extracted from the latest reports made available by the relevant working groups at the International Council for the Exploration of the Sea (ICES, www.ices.dk). For 5 Northwest Atlantic cod stocks, the population data were extracted from the most recent available papers and reports or through personal communication (for references, see Table 1).

Fish population values were used as estimated in previously published results, mainly from VPA which is based upon commercial catch statistics; recent years are typically tuned by scientific surveys, often by means of extended survivor analysis (XSA; Shepherd 1999). We are aware of potential problems with the use of VPA, especially for recruitment estimates. These problems include the assumptions of constant natural mortality and

Table 2. Characteristics of stocks with a statistically significant temporal shift in recruitment dynamics (see 'Materials and methods', Eq. 6). Period: period from year of spawning to last year of data. Shift: if the best model (lowest corrected Akaike's information criterion [AIC_C]) for the stock includes a threshold, separating the time-series into 2 periods, the first year of the second 'regime' is given. Asterisk indicates statistical significance of threshold. dInt: change in Intercept ($\ln[R/\text{SSB}]$) from Regime 1 to Regime 2, with standard error in parentheses and statistical significance. R: no. of recruits; SSB: spawning stock biomass. T1: coefficient for temperature effect in first regime with standard error and statistical significance (if term selected in model with lowest AIC_C). T2: temperature effect in second regime. T1+2: common temperature effect for whole period (nl: nonlinear). dAIC_C: difference in AIC_C between best threshold and best stationary model. These values are directly comparable to the corresponding values in Table 1 (for non-stationary linear models). *$p < 0.05$, **$p < 0.01$

Species and stock	Period	Shift	dInt	T1	T2	T1+2	dAIC_C
Cod 3NO	1959–2007	1983**	−2.01 (0.27)**		0.42 (0.18)*		−33.9
Cod 3Pn4RS	1974–2006	1984**	−1.03 (0.22)**				−14
Cod 4TVn	1971–2006	1985**	−0.62 (0.16)**				−9.2
Cod 4X	1980–2007	1995	−0.66 (0.24)*				−2.9
Cod 5Zjm	1978–2008	1991	−1.5 (0.48)**				−4.9
Cod Baltic 22-24	1970–2008					nl**	1.1
Cod Baltic 25-32	1966–2006	1986**	−0.8 (0.16)**	−0.52 (0.24)*	0.26 (0.16)		−17.9
Cod Faroe Plateau	1961–2006	1983*	−0.55 (0.17)**			−1.05 (0.29)**	−6
Cod Iceland	1955–2008	1986	−0.35 (0.1)**				−3.2
Cod North Sea	1963–2007	1984	−0.85 (0.35)*			−0.71 (0.17)**	−1.6
Cod Northeast Arctic	1921–2003	1947**	0.58 (0.15)**		0.26 (0.16)		−11.6
Cod VIa	1978–2006						1.6
Cod VIIa	1968–2007	1992	−0.83 (0.33)*			−0.89 (0.24)**	−2
Cod VIIek	1971–2006	1982**	1.55 (0.36)**	−2.76 (0.95)**	−0.81 (0.32)*		−9.7
Haddock arctic	1950–2005	1970	−0.24 (0.28)		1.23 (0.33)**		−1.6
Haddock Faroe Plateau	1957–2008	1977*	−0.95 (0.26)**				−8.3
Haddock Iceland	1979–2007					nl*	0.9
Haddock North Sea	1963–2008					nl**	2.2
Haddock VIa	1978–2006						0.7
Herring Baltic 25-32	1974–2007	1985	−0.58 (0.18)**			0.18 (0.08)*	−5.2
Herring Baltic 30	1973–2007	1984	0.92 (0.31)**			0.6 (0.18)**	−4.4
Herring Baltic Riga Bay	1977–2007					0.55 (0.13)**	2.3
Herring North Sea	1960–2008	1980*	0.55 (0.15)**			−0.73 (0.14)**	−8
Herring Norweg. SS	1921–2006	1951	−0.99 (0.31)**			0.77 (0.25)**	−5.8
Herring VIa	1957–2007					nl**	1
Plaice North Sea	1957–2007	1972*	0.59 (0.14)**			−0.38 (0.12)**	−3.7
Plaice VIIa	1964–2005	1988**	−0.57 (0.08)**				−22.7
Plaice VIId	1980–2007					nl*	3.8
Plaice VIIe	1976–2006	1994	0.6 (0.25)*			−0.96 (0.25)**	−0.8
Saithe Faroe	1961–2005	1980	0.44 (0.19)*			0.59 (0.27)*	−0.8
Saithe Iceland	1974–2007	1987	−0.51 (0.19)*		0.59 (0.33)		−2.4
Saithe 3a46	1967–2005	1984	−0.61 (0.23)*	0.74 (0.36)*			−1.1
Saithe Northeast Arctic	1960–2005	1988*	0.6 (0.14)**				−8.8
Sole North Sea	1957–2007						1
Sole VIIa	1970–2004	1990**	−1.18 (0.3)**	0.85 (0.36)*			−12.9
Sole VIIe	1969–2006					nl*	2.1
Sole VIIfg	1971–2006					0.25 (0.13)	2.6
Whiting VIIek	1982–2007	1990	0.59 (0.27)*			−0.81 (0.27)**	−0.2

catchability over time and the effects of aging errors. However, the quality of the data used in the present paper is the best available for the stocks studied and the relatively long period covered and, since the North Atlantic is a data-rich area, is likely better than for stocks from most other areas.

MA was calculated for each stock and year separately as the spawner biomass-weighted average across all age classes:

$$\text{MA}_t = \frac{\sum_{a=a_{\min}}^{a=a_{\max}} a\, M_{a,t}\, N_{a,t}\, W_{a,t}}{\sum_{a=a_{\min}}^{a=a_{\max}} M_{a,t}\, N_{a,t}\, W_{a,t}}$$

where $a_{\min}$ and $a_{\max}$ are the ages of the youngest and the oldest of the spawners in year t, respectively, and $M_{a,t}$, $N_{a,t}$, and $W_{a,t}$ are the proportion of mature fish, the number of fish, and the mean weight of fish, respectively, at age a and time t.

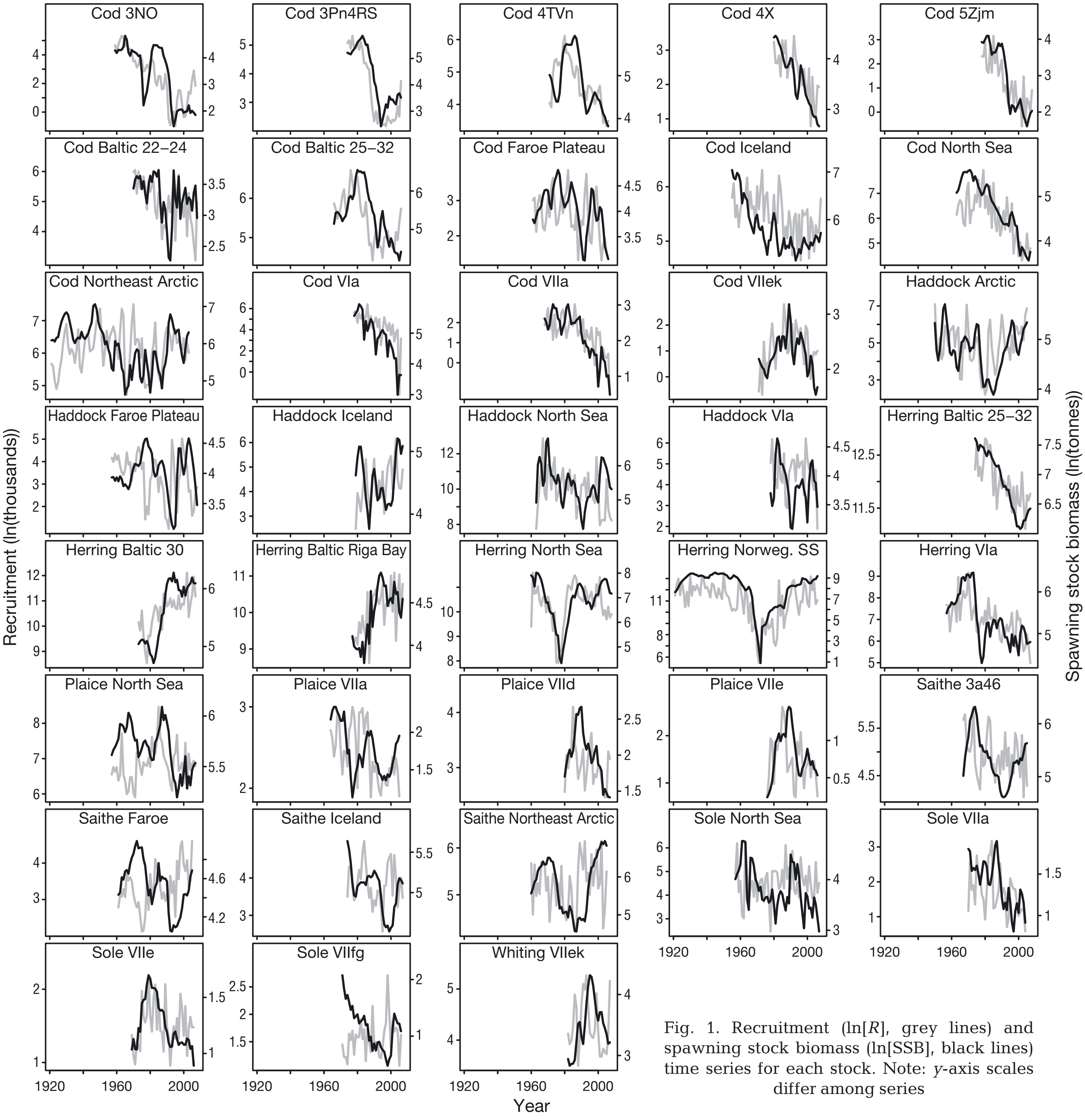

Fig. 1. Recruitment (ln[*R*], grey lines) and spawning stock biomass (ln[SSB], black lines) time series for each stock. Note: *y*-axis scales differ among series

Time series of MA for each of the stocks are presented in the form of 15 yr moving averages centred on the mean year. The averaging was done to smooth over the variation caused by the influence of particularly strong cohorts. This is for visualisation purposes only; the smoothed values were not used in any calculations.

Temperature data

We compiled area-specific sea temperature data series (T) based on several sources, according to availability. For the 4 Barents Sea stocks (cod, haddock *Melanogrammus aeglefinus*, herring *Clupea harengus*, and saithe *Pollachius virens*; Table 1), temperature data were obtained from the Kola meridian transect (33° 30′ E, 70° 30′ to 72° 30′ N). The monthly values made available to us were calculated by averaging temperatures horizontally along the transect and vertically from 0 to 200 m water depth (Bochkov 1982, Tereshchenko 1996), with recent data kindly made available by PINRO, Murmansk (www.pinro.ru). Yearly winter values were calculated by averaging over the months of December to March as in Ottersen et al. (2006).

For each of the remaining NE Atlantic stocks, time series of sea surface temperature (SST) were averaged annually and over the statistical areas defined by ICES to correspond to the distribution area of the respective stock. Data were extracted from the extended reconstructed SST (NOAA_ERSST_V3) data set based on the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) SST data and provided by the NOAA/OAR/ESRL PSD, Boulder, CO, USA, at www.esrl.noaa.gov/psd/data/gridded/data.coads.2deg.html (accessed 12 August 2011). These data are available from 1880 to 2009 with 2° × 2° grid resolution.

For NW Atlantic cod stocks, temperature values were allocated as follows:

- 3NO: ICOADS SST values (i.e. source as above)
- 3Pn4RS and 4TVn: annual temperature averages at 150 m depth for the Gulf of St. Lawrence from www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/climat/stlawrence/depth-profondeur-eng.htm (Galbraith et al. 2009)
- 4X and 5Zjn: annual averages of monthly SST values from www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/climat/sst-tsm/costal-cotieres-eng.asp?id=Halifax (missing values replaced by the long-term monthly mean for 1926 to 2009 before averaging).

Statistical analyses

Stability of temperature-recruitment correlations

As an initial, visual inspection of how the strength of temperature-recruitment correlations changed with time, we conducted a moving-windows correlation analysis applying a 15 yr time window. That is, we sliced the time-range into overlapping time-slots of 15 yr and for each time-slot computed the correlation between the temperature in the spawning year and the natural logarithm of the number of recruits lagged so that the year corresponds to the spawning year. The resulting series of correlation coefficients were plotted against the mid-year of the time-slots. As for MA, the averaging was done for visualisation purposes only; the smoothed values were not used in any calculations.

Recruitment models

We then fitted statistical recruitment models to each time series. We first considered stationary models with no effect of temperature, a linear effect of temperature, or a nonlinear effect of temperature on recruitment success. The nonlinear model was included because a nonlinear effect of temperature could hypothetically lead to apparent non-stationarity in the linear effect if the mean temperature changed over time. We then considered non-stationary model formulations, in which the recruitment success or the effect of temperature changed over time, either gradually (linearly) or stepwise. The different models were compared in a uniform approach, using Akaike's information criterion (Akaike 1974) corrected for small sample size ($\mathrm{AIC_C}$; Hurvich & Tsai 1989) as the model selection criterion.

Baseline recruitment model

The recruitment dynamics were analysed using regression models with the natural logarithm of the ratio between the number of recruits (R_{t+a}) and spawning stock biomass (SSB_t) as the response variable. The subscript a is the recruitment age (which varied among stocks), such that R_{t+a} represents the recruitment back-lagged to the spawning year. According to the Ricker model (Ricker 1954), this log-ratio is a linear function of SSB_t:

$$\ln(R_{t+a} / \mathrm{SSB}_t) = \mathrm{a} + \mathrm{b}\,\mathrm{SSB}_t + \varepsilon_t \quad (1)$$

This linear regression formulation of the Ricker model was fitted by maximum likelihood methods assuming normally distributed errors (ε_t).

As a simple test of the suitability of applying Ricker-type models, we examined plots of $\ln(R_{t+a}/\mathrm{SSB}_t)$ against SSB (Appendix 1). A linear relationship, as implied by Eq. (1), seemed to fit the data relatively well; there were no obvious systematic deviations that might, for example, have indicated Allee effects (disproportionally low recruitment success at very low SSB). Additional modelling, analysing log-recruitment as a smooth function of SSB, showed that the main results reported in the present paper were not strongly sensitive to the choice of a particular stock-recruitment model (results not shown).

Linear temperature-effect model

To introduce temperature effects on the stock-recruitment relationship and thus allow for exploration of H1, we extended Ricker's model (Eq. 1) by separating the density-independent effect into a global intercept and a linear temperature-dependent effect (T_t, scaled to zero mean) on pre-recruit survival:

$$\ln(R_{t+a} / \mathrm{SSB}_t) = \mathrm{a} + \mathrm{b}\,\mathrm{SSB}_t + \mathrm{c}\,T_t + \varepsilon_t \qquad (2)$$

Note that if SSB_t scales with the egg production, $\ln(R_{t+a}/\mathrm{SSB}_t)$ is a linear function of the instantaneous pre-recruit survival rate (i.e. $1 - M$ in $N_t = N_0 e^{-Mt}$, where N_t is cohort size at time t). Linear terms in the right-hand side of the equation therefore represent linear effects on survival rate.

Nonlinear temperature effects

To explore if temperature had nonlinear effects on pre-recruit survival, we compared Model 2 to a model with a smooth temperature effect:

$$\ln(R_{t+a} / \mathrm{SSB}_t) = \mathrm{a} + \mathrm{b}\,\mathrm{SSB}_t + f(T_t) + \varepsilon_t \qquad (3)$$

Here, $f(T_t)$ is a natural cubic spline function with maximally 2 degrees of freedom (3 knots). Model 3 is a generalized additive model (GAM) and was fitted by maximum-likelihood methods using the mgcv package (Wood 2006) in the R program development environment (R Development Core Team 2010). The AICc values of Models 1, 2 and 3 were compared, and the model formulation that provided the lowest $\mathrm{AIC_C}$ value was selected as the most parsimonious stationary model.

Non-stationarity in recruitment dynamics: testing for gradual changes

To examine if the relationship between spawning stock biomass, recruitment, and temperature changed over time (i.e. that the recruitment model was non-stationary, H2), we first considered 2 linear extensions of Model 2:

$$\ln(R_{t+a} / \mathrm{SSB}_t) = \mathrm{a} + \mathrm{b}\,\mathrm{SSB}_t + \mathrm{c}\,T_t + \mathrm{d}\,yr_t + \varepsilon_t \qquad (4)$$

$$\ln(R_{t+a} / \mathrm{SSB}_t) = \mathrm{a} + \mathrm{b}\,\mathrm{SSB}_t + \mathrm{c}\,T_t + \mathrm{d}\,yr_t + \mathrm{e}\,yr_t T_t + \varepsilon_t \qquad (5)$$

With Model 4, we tested for a linear effect of year (yr), that is, for a trend in the intercept; with Model 5 we tested for an interaction effect between year and temperature, that is, for a trend in the effect of temperature. When searching for the most parsimonious non-stationary linear model, we also calculated the $\mathrm{AIC_C}$ of a reduced version of Model 4, with the temperature term omitted.

Stepwise shifts in recruitment dynamics

The subsequent analysis focused on non-stationary models testing for a stepwise change in the recruitment dynamics. That is, instead of assuming linear changes in the intercept or temperature effect as in Models 4 and 5, the intercept and potentially the coefficient for the temperature effect were assumed to change abruptly at some time-point for each stock.

When a statistically significant shift in recruitment dynamics was detected, we followed up by assessing which other variables changed for that stock, to evaluate the hypotheses H3 to H7.

We considered the following threshold models:

$$\ln(R_{t+a} / \mathrm{SSB}_t) = \mathrm{a}_0 I_{A,t} + \mathrm{a}_1 I_{B,t} + \mathrm{b}\,\mathrm{SSB}_t + \varepsilon_t \qquad (6a)$$

$$\ln(R_{t+a} / \mathrm{SSB}_t) = \mathrm{a}_0 I_{A,t} + \mathrm{a}_1 I_{B,t} + \mathrm{b}\,\mathrm{SSB}_t + \mathrm{c}\,T_t + \varepsilon_t \qquad (6b)$$

$$\ln(R_{t+a} / \mathrm{SSB}_t) = \mathrm{a}_0 I_{A,t} + \mathrm{a}_1 I_{B,t} + \mathrm{b}\,\mathrm{SSB}_t + \mathrm{c}_0 T_t I_{A,t} + \varepsilon_t \qquad (6c)$$

$$\ln(R_{t+a} / \mathrm{SSB}_t) = \mathrm{a}_0 I_{A,t} + \mathrm{a}_1 I_{B,t} + \mathrm{b}\,\mathrm{SSB}_t + \mathrm{c}_1 T_t I_{B,t} + \varepsilon_t \qquad (6d)$$

$$\ln(R_{t+a} / \mathrm{SSB}_t) = \mathrm{a}_0 I_{A,t} + \mathrm{a}_1 I_{B,t} + \mathrm{b}\,\mathrm{SSB}_t + \mathrm{c}_0 T_t I_{A,t} + \mathrm{c}_1 T_t I_{B,t} + \varepsilon_t \qquad (6e)$$

Here, I_A and I_B are indicator variables separating the time-series into 2 periods, A and B, with $I_{A,t} = 1$ and $I_{B,t} = 0$ for Period A, while $I_{A,t} = 0$ and $I_{B,t} = 1$ for Period B. For any given threshold year separating Period A from Period B, Models 6a to 6e are linear and were estimated by maximum-likelihood methods assuming normally distributed errors. The optimal threshold year for any given stock and model formulation was found by comparing the $\mathrm{AIC_C}$ of alternative threshold years and selecting the threshold providing the lowest $\mathrm{AIC_C}$.

Model 6a (Eq. 6a) modifies the Ricker model (Eq. 1) in that the intercept is different between 2 time periods. Model 6b is similar to Model 6a but includes a temperature effect. In Model 6c, temperature only has an effect in the first period (Period A), and in Model 6d, only in the second period (Period B). In Model 6e, temperature has an effect in both periods, but the strength (and possibly sign) of the temperature effect differs between the periods. Note that

Model 6e is the most general model and that Models 1, 2 and 6a to 6e can be seen as special cases (with $a_0 = a_1$, $c_0 = c_1$, $c_0 = 0$ and/or $c_1 = 0$). The optimal threshold model formulation was found by comparing the AIC_C of Models 6a to 6e.

If the AIC_C of the best threshold model (Models 6a to 6e) was lower than that of the best stationary model (Models 1 to 3), we then went on to calculate the statistical significance of the threshold. The statistical significance of the threshold was calculated for the full model (Eq. 6e) using a permutation test as described by Liu et al. (2011). To calculate the AIC_C of threshold models, the threshold value was arbitrarily counted as 1 parameter.

Testing hypotheses for temporal shifts in recruitment dynamics

For each of the stocks with an identified shift in recruitment dynamics, we calculated the change from Period A to B in the intercept and in the effect of temperature on recruitment success. To evaluate the hypotheses relating to the temporal shifts in recruitment dynamics, we conducted statistical tests regarding whether these changes were associated with changes in MA, SSB, and temperature, tested individually (Table 3). Specifically, we fitted linear regression models with stock as the sampling unit, the change in the intercept or the change in temperature effect as the response variable, and the change in MA, SSB, and temperature as predictor variables.

Table 3. Test of hypotheses exploring if a shift in recruitment dynamics (non-stationarity) is explainable through changes in mean age in the spawning stock (MA), spawning stock biomass (SSB) or temperature. Change in intercept: $a_1 - a_0$ in Eq. (6). Change in temperature effect: change in the estimated effect of temperature on recruitment success, $c_1 - c_0$ in Eq. (6)

Hypothesis	Prediction
H3	Change in intercept correlates positively to the concurrent change in MA
H4	Change in intercept correlates positively to the concurrent change in SSB
H5	Change in intercept correlates to the concurrent change in mean temperature
H6	Change in absolute value of temperature effect correlates negatively to the concurrent change in MA
H7	Change in absolute value of temperature effect correlates negatively to the concurrent change in SSB

RESULTS

Effect of temperature on recruitment success (H1)

To address the impact of temperature on the stock-recruitment relationship, (1) linear temperature terms were added to simple Ricker models of the relationship between recruitment success (ln[*R*/SSB]) and SSB. Of the 38 stocks, 18 showed temperature effects statistically significant at the 5% level, with 9 negative and 9 positive (Table 1). (2) GAMs were used. Adding possibly nonlinear (smooth) terms of temperature to the Ricker models within the GAM framework led to the identification of statistically significant temperature effects for an additional 3 stocks (Table 1).

The most interesting result at the species level is for herring. All 6 herring stocks displayed significant temperature effects. The cold-water stocks (Norwegian spring-spawning and the 3 from the Baltic) showed a positive response to higher temperatures, while the North Sea and West of Scotland stocks responded negatively (Table 1). Note that none of the 5 NW Atlantic cod stocks studied displayed a statistically significant temperature effect.

Temporal development of temperature-recruitment correlations (H2)

For each stock, the temporal development of the temperature-recruitment correlations was inspected by calculating moving 15 yr window correlations. The correlations between temperature and recruitment have for many stocks changed considerably over time (Fig. 2). For example, for the populations of cod, herring, haddock and saithe in the Barents Sea region, there were increasingly strong positive correlations from around the 1960s onwards, which weakened in the 1990s to 2000s. In contrast, in the North Sea there is a pattern of increasingly negative correlations for several stocks.

Temporal development of MA and possible link to temperature-recruitment correlations (background for H3 and H6)

No general pattern was found. For some stocks, notably the Northeast Arctic and Icelandic cod, plaice *Pleuronectes platessa* in the North Sea, and sole *Solea solea* in the North Sea, Celtic Sea

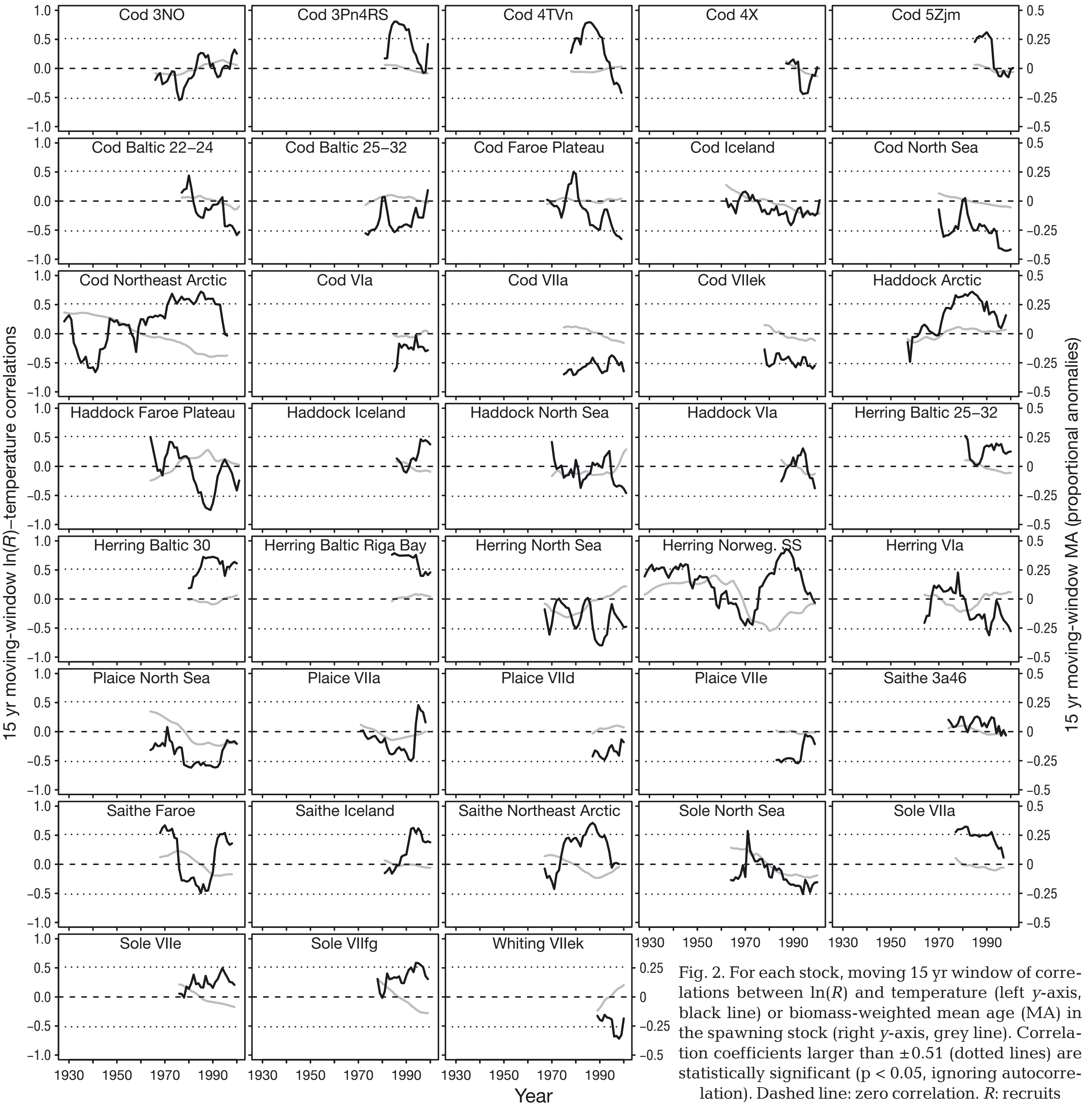

Fig. 2. For each stock, moving 15 yr window of correlations between $\ln(R)$ and temperature (left *y*-axis, black line) or biomass-weighted mean age (MA) in the spawning stock (right *y*-axis, grey line). Correlation coefficients larger than ±0.51 (dotted lines) are statistically significant ($p < 0.05$, ignoring autocorrelation). Dashed line: zero correlation. *R*: recruits

(VIIfg), and Western English Channel (VIIe), there was a clear decrease in MA (Fig. 2). In contrast, other stocks showed very little change in MA, e.g. Icelandic saithe, Faeroe Plateau and Baltic cod, and herring in the Baltic and Gulf of Riga. Further, some stocks displayed an increase in MA, either over the full period (Southern Grand Banks [3NO] cod) or the recent decades (Norwegian spring-spawning, North Sea, and West of Scotland herring; Fig. 2).

Further, for some stocks, such as the Northeast Arctic cod, the Norwegian spring-spawning herring, and the Northeast Arctic saithe, a general reduction in MA was accompanied by an increase in the temperature-recruitment correlation. The pattern is far from universal, however. For example, reduced MA did not coincide with increased temperature-recruitment correlations of the Arctic haddock or the Faroe Islands cod stocks (Fig. 2).

Detecting temporal shifts in recruitment dynamics (H2)

When comparing stationary (Eqs. 1–3) and non-stationary linear (Eqs. 4 & 5) models of recruitment dynamics, we found that 14 stocks showed statistically significant ($p < 0.05$) linear changes in the intercept over time, and 4 stocks statistically significant linear changes in the effect of temperature (Table 1). These stocks largely coincided with the 13 stocks showing statistically significant stepwise changes (Eq. 6), as confirmed by a statistically significant ($p < 0.05$) threshold in recruitment dynamics (Table 2). For an additional 14 stocks, threshold models provided lower (approximate) AICc compared to the best linear or nonlinear stationary models (Eqs. 1–3), but the threshold was not statistically significant. For 12 of the 13 stocks with a statistically significant threshold, the AICc was also lower for the threshold models (Table 2) compared to the non-stationary linear models (Table 1). Note that these p-values do not account for multiple testing and that we expect that ~2 stocks would show statistically significant results at $p < 0.05$ just by chance. If we use a more conservative critical value of 0.01, we expect that ~0.4 stocks would show statistically significant results just by chance. Eight stocks showed shifts in recruitment dynamics that were statistically significant at $p < 0.01$ (Table 2). Among the 13 stocks with a significant threshold ($p < 0.05$), all showed significant changes in the intercept; 5 of these also showed changes in the effect of temperature.

Examining possible causes of temporal shifts in recruitment dynamics (H3, H4, and H5)

All further analyses focused on the 13 stocks with a temporal (threshold) shift in recruitment dynamics (as shown in Fig. 3 and Table 2). Fig. 4 shows the change from the first to the second period in the intercept for each stock in response to the change in SSB, MA, and temperature. We see a clear positive effect of SSB and a negative effect of MA (both $p < 0.01$ when added into 1 regression model) that together explain 77% of the variation among stocks. Stocks that declined in SSB from the first to the second period produced less recruits after the shift than expected from a Ricker model fitted to the whole time series, while stocks that increased in SSB showed an increase in recruitment success. To further investigate the possible causal relationship between the changes in recruitment success and SSB, we tested what changed first. By fitting threshold models for a stepwise change in SSB over time for each of the 13 stocks, we found that the change in recruitment success generally preceded the change in spawning stock biomass. Specifically, for 10 stocks, the major change in SSB occurred 5 to 21 yr after the estimated shifts in recruitment dynamics. The changes in recruitment success were not statistically significantly linked to concurrent changes in sea temperature (Fig. 4).

Examining the temperature-recruitment relationship (H6 and H7)

The next step was to explore how the strength of the temperature effect changed between the periods for the 8 stocks with a temporal shift in recruitment dynamics and a statistically significant effect of temperature in at least 1 of the 2 periods (Table 2, Fig. 3). Specifically, we explored how this change corresponded to the changes in SSB and MA. We *a priori* predicted that lower SSB and lower MA would lead to stronger recruitment-temperature correlation (in terms of the absolute value). However, the changes in the strength of the temperature effect were not statistically significantly linked to either the changes in SSB or MA (Fig. 5). The results did not change qualitatively if we included in the analysis stocks with weaker statistical support for the threshold dynamics (lower AIC_C than stationary models but non-significant threshold; points outlined in grey in Figs. 4 & 5).

DISCUSSION

The discussion of our results in the context of earlier related work is focused around and structured according to the hypotheses formulated in the 'Introduction'.

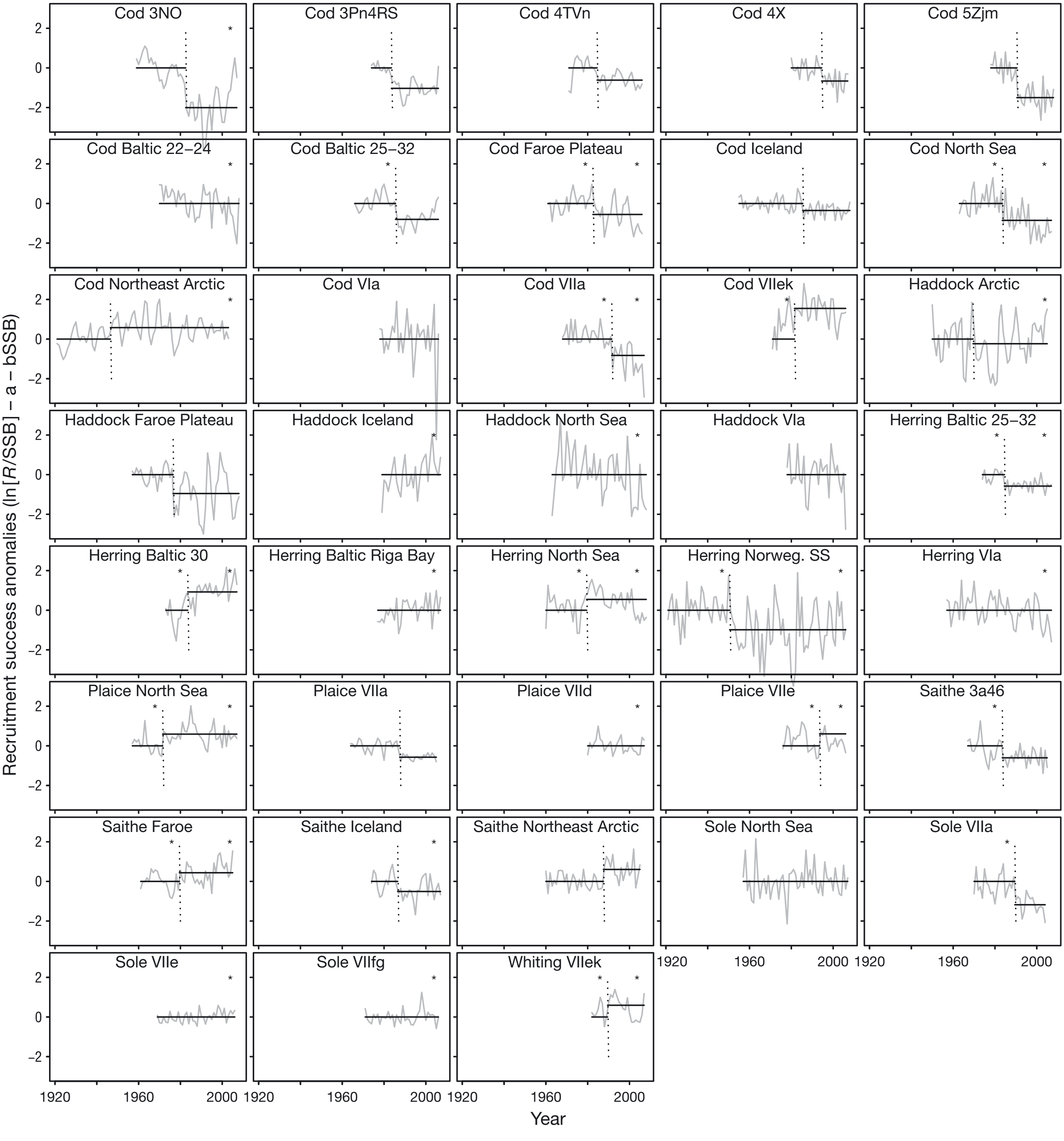

Fig. 3. Temporal shifts in recruitment dynamics. Grey lines show time series of recruitment success anomalies (= ln[*R*/SSB] – a – b SSB, where a and b are regression coefficients from Ricker-based models potentially also including effects of climate and recruitment shifts, *R* is number of recruits, and SSB is spawning stock biomass). Horizontal lines show how predicted recruitment success at a given SSB and mean temperature changes over time. Vertical dotted lines: shifts in recruitment dynamics. Asterisks indicate that the selected model included an effect of temperature for the given period

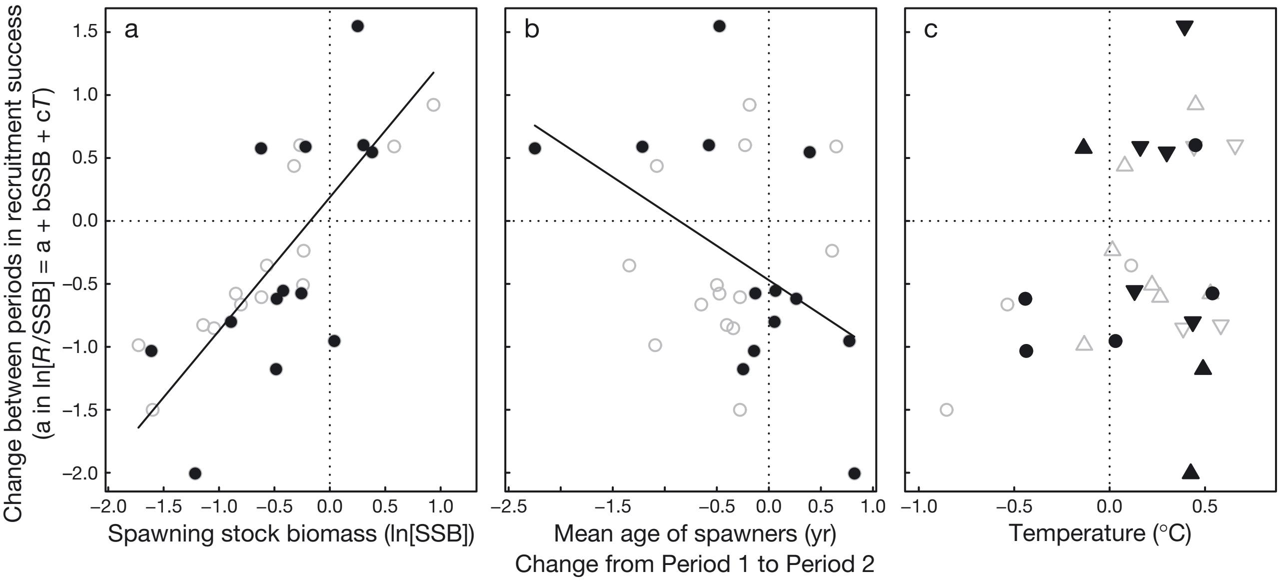

Fig. 4. Temporal change in predicted recruitment success for 27 stocks with an estimated shift in recruitment dynamics in response to the concurrent changes in factors potentially linked to these shifts. Filled, black symbols: shift in recruitment dynamics statistically significant ($p < 0.05$, N = 13 stocks). Open, grey symbols: shift not statistically significant, but threshold-model has lower AIC_C (N = 14). The *y*-variable is the change in the predicted number of recruits (*R*) per biomass of spawners (ln[*R*/SSB]) at a given spawning stock biomass (SSB) and temperature from the first to the second period (= difference between horizontal lines in Fig. 3). The *x*-variables are the concurrent changes between the periods in (a) spawning stock biomass, (b) mean age of the spawners, and (c) temperature. Lines: regression lines for across-stock comparison of the change in recruitment success in response to the change in SSB and MA combined (both $p < 0.01$, $R^2 = 0.77$, n = 13 stocks with statistically significant shifts). Symbols in (c) represent sign of average estimated temperature effect for the 2 periods for each stock (upward-pointing triangles: positive; downward-pointing: negative; circles: none)

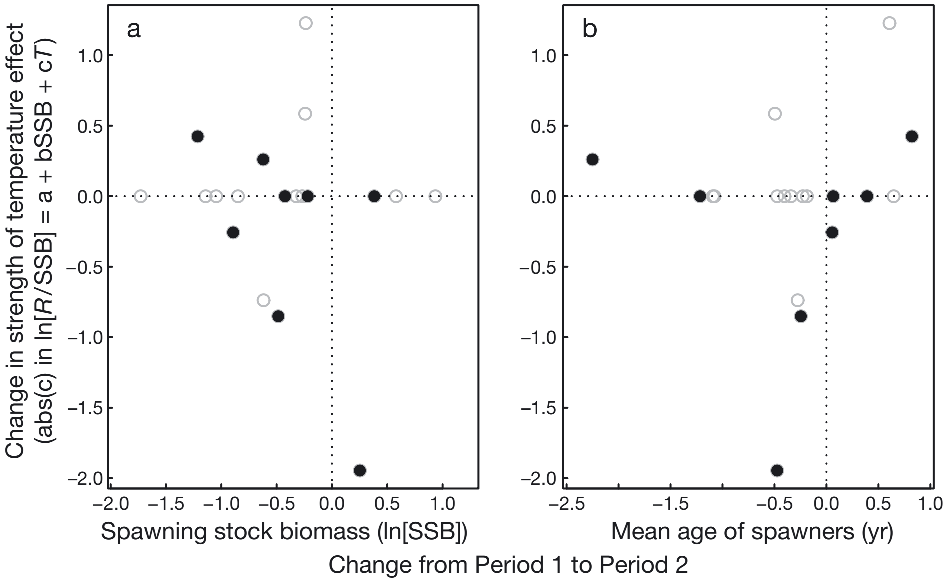

Fig. 5. Temporal change in strength of the temperature effect on recruitment success as a function of the concurrent changes in (a) spawning stock biomass (SSB) and (b) mean age. The *y*-variable is the change in the absolute value of the estimated temperature effect for each of 8 stocks with a significant shift in recruitment dynamics and a statistically significant effect of temperature in at least 1 of the 2 periods (Fig. 3). Open, grey symbols: shift not statistically significant, but threshold-model has lower AIC_C (N = 12). *R*: number of recruits

The stock-recruitment relationship is enhanced by including a temperature term (H1)

Our results support earlier work in that temperature is an important factor for some of the stocks and provide suggestive evidence for several general patterns (Table 1). For instance, the effect of temperature on recruitment was positive for cold-water herring stocks and negative for stocks in the more temperate southern areas. It is likely no coincidence that we found a temperature signal for this species as small pelagic fish, like herring, are well-known to respond to climate fluctuations (Checkley et al. 2009).

That the sign of the relationship can vary between stocks of the same species is also as expected, and it is intuitively sensible that populations that inhabit the coldest water within a species' temperature range tend to show increasing recruitment with increasing temperatures, whereas those inhabiting the warmest waters show decreasing recruitment with increasing temperatures. This pattern has earlier been shown to apply to the main Atlantic cod stocks (Planque & Fredou 1999) but to our knowledge not for herring.

For plaice, only 4 stocks from around the British Isles were analysed. For all of these stocks, located towards the centre of the overall distribution range of plaice, a tendency toward recruitment being favoured by lower temperatures was found. (Table 1). This is consistent with what has earlier been documented by Fox et al. (2000), who further pointed to temperature during the first months of the year being of particular importance by affecting predation pressure on the planktonic stages of plaice and subsequently their recruitment. There are unfortunately not sufficient data to examine the temperature effects on the populations of this species with a more southern distribution (e.g. Bay of Biscay and around the Iberian peninsula).

Our results for cod were less clear (Table 1). A negative temperature effect was, as expected from the above, found for the North Sea and Irish Sea stocks. However, no statistically significant effect was found for any of the Northwest Atlantic stocks. This may partly be explained by these time series being relatively short, but there may have been other changes in these stocks which overshadow the temperature impact and which we are not able to capture. It is more surprising that no statistically significant effect was detected for the Barents Sea cod. Several earlier papers have pointed to temperature being a particularly important driver for the recruitment to this most northerly cod stock (e.g. Sætersdal & Loeng 1987, Ottersen & Stenseth 2001), and Myers (1998) singled out this as one of the few stocks where the temperature-recruitment relationship was stable over time. Nevertheless, Fig. 2 shows clearly, as was demonstrated by Ottersen (2008), that the correlation is non-stationary, negative in some periods, positive in others, and with an increasing trend from around 1940 to 1990 followed by a distinct drop-off. This was supported by our statistical analysis, showing a significant shift in recruitment dynamics around 1947, with higher recruitment from 1947 onward compared to 1921 to 1946. Further recruitment was positively (although not statistically significantly) related to temperature only from 1947 onward.

To sum up, of the 21 stocks for which adding a smooth temperature term statistically significantly improved the Ricker model, linear temperature effects were favoured in terms of AIC_C for 11 stocks and nonlinear effects for 10 stocks (Table 1). The frequent occurrence of non-linearity is of importance since many studies, including earlier work by the present first author, examined linear or possibly log-linear environment-relationships only, typically through correlation or linear regression (Loeng et al. 1995, Ottersen et al. 2002). Moreover, such nonlinear effects can lead to changes in the linear relationship between temperature and recruitment.

The relationship between recruitment, spawning stock biomass, and temperature is not constant over time (H2)

As expected, but now further documented by systematic analyses, H2 is valid. The most frequent change in the non-stationary linear models was, for 14 stocks, in the intercept in recruitment success, suggesting a change in pre-recruit mortality over time. Furthermore, a statistically significant threshold in recruitment dynamics (Eq. 6) was found for 13 stocks; for an additional 14 stocks (making 27 of the total of 38 stocks), threshold models performed better than the best linear or nonlinear stationary models (Eqs. 1–3) in terms of AIC_C, but the threshold was not statistically significant. The good performance of threshold models, while not providing evidence for ecological regime shifts, does suggest that abrupt changes frequently take place. While no overall geographic pattern was found, some neighbouring stocks showed similar patterns. Most noteworthy is the statistically significant shift in 3 NW Atlantic cod stocks in 1983 to 1985, in all cases with a clear threshold (Table 2).

Changes in the relationship between temperature and recruitment were shown by the moving-window correlations (Fig. 2) and quantified by the non-stationary modelling. These analyses revealed significant linear changes in the effect of temperature for only 4 stocks (Table 1) and stepwise changes for 8 stocks (Table 2). In most cases with a change in recruitment dynamics, the best model had a common temperature effect for the whole period (Tables 1 & 2).

There are several reasons why the temperature-recruitment links examined might change over time. First, temperature effects may for some stocks be marginal compared to those of other environmental factors. We were, for instance, unable to detect a statistically significant temperature-recruitment relationship for cod in the Baltic Sea for the whole period studied (Table 1). For this brackish sea, there is substantial literature indicating that reproduction of cod is heavily dependent on the right salinity and oxygen conditions (e.g. Köster et al. 2005, Hinrichsen et al. 2011). If the correlation between salinity, oxygen, and temperature changes over time, this could then lead to a changed temperature-recruitment relationship. In our study, we found that temperature contributed to predict cod recruitment in the Baltic Sea proper prior to 1987, while from 1987 onward, the recruitment was drastically reduced and unlinked to temperature. This shift coincided with large-scale changes in both abiotic and biotic conditions in the Baltic Sea between 1988 and 1993, including reductions in salinity and oxygen and increased abundance of sprat *Sprattus sprattus*, predators on cod eggs (Möllmann et al. 2009).

Second, the effect of temperature may depend on ecosystem state. Temperature may affect fish stocks through complex pathways in the foodweb, where several direct and indirect mechanisms come into play. The importance to recruitment of the different mechanisms may change over time, as a mortality factor operating at an early life stage may or may not be overshadowed by mortality factors operating at later life stages. Mueter et al. (2007) emphasized that recruitment can be affected by predation; therefore, 'environmental' effects on productivity include changes in abundance of important predators, regardless of whether these were caused by environmental variability, fishing, or other factors. For instance, Stige et al. (2013, this volume) found changing relevance of different environmental factors (including sea temperature and abundance of cod age 3 to 6 yr) for predicting recruitment of the Northeast Arctic cod and the Northeast Arctic haddock in the Barents Sea. Further, variability in cannibalism (e.g. driven by changes in the availability of preferred prey, which again may be connected to temperature) may affect natural mortality of juveniles. Consequently, the net effect of temperature changes may be different, even opposite, according to the status of main prey, competitor, or predator populations. This has recently been examined in several Northeast Atlantic ecosystems, notably the Baltic (Cardinale et al. 2009, Lindegren et al. 2010), the Barents Sea (Svendsen et al. 2007, Stige et al. 2010), and the North Sea (Kempf et al. 2010).

Third, the effects of large-scale climate dynamics, as represented by e.g. the NAO, on fish recruitment may change at multi-decadal time scales for at least 3 different reasons (Stige et al. 2006): (1) Changes in demographic factors may affect the sensitivity of cod recruitment to climate fluctuations. (2) Changes may be related to long-term alterations in how the biotic or abiotic environment affects the way interannual variability in a given environmental factor affects cod recruitment. (3) The effect of NAO fluctuations on local environmental variables may change with time. This again implies that the lack of persistency of environment-recruitment correlations (Drinkwater & Myers 1987, Myers 1998) may reflect true biological or physical changes, rather than being mere statistical artefacts.

However, there is indeed a risk of such statistical artefacts. The breakdown of a correlation or explanatory power of a model may be a consequence of failure to capture the essential explanatory variables. This is not unlikely, as the statistical modelling is complicated by the explanatory variables not being statistically independent, the uncertainty in the data, and the limited number of years for which data are available for any given stock.

In the following, relating to stocks that were found to display a statistically significant temporal shift in recruitment dynamics, we discuss possible causes for these shifts, formulated as hypotheses H3, H4, and H5.

Recruitment per SSB decreases with decreasing MA (H3)

The concept that juvenation of the spawning stock is unfavourable is well established (Ponomarenko 1973, Berkeley et al. 2004, Planque et al. 2010), and there exists substantial support for this being biologically plausible (Kjesbu et al. 1996, Marteinsdottir & Thorarinsson 1998). Contrary to this, our results do not support H3 but indicate reduction in recruitment success from Period 1 to 2 for stocks with an increase in MA, and vice-versa (Fig. 4).

The result above is weakened by a marked reduction in MA being the case only for a minority of the stocks studied (Fig. 2); only a few showed a decrease of the MA of >1 yr of age from Period 1 to 2 (Fig. 4). This could also partly be due to most of the time series being rather short and hence to the fact that fisheries-induced juvenation is likely to have already occurred prior to the beginning of our time series.

It is hard to give a biologically sound explanation for our results. However, the number of populations and species for which the validity of H3 has actually been studied is fairly limited, and the results are mixed. Morgan et al. (2007) explored the effect of age composition on recruitment in 3 Atlantic cod populations and 1 of American plaice *Hippoglossoides platessoides*. No consistent relationship between age composition of the spawning stock and recruitment was found, and they concluded that further research is needed to explore how common the effect of age composition on recruitment actually is (Morgan et al. 2007). Similarly, Ottersen (2008) found no clear link between age structure and recruitment for the Northeast Arctic cod stock, despite a clear reduction in MA with time. It was suggested that strong recruitment compensation, i.e. increased juvenile survival rate due to reduced pre-recruitment competition, may be the reason for this stock seemingly being quite robust regarding spawner juvenation (Ottersen 2008). Actually, this stock, with its pronounced reduction in MA, is an outlier in our analysis and contributes in particular to the negative relationship between MA and change in recruitment success (Fig. 4).

Until recently, H3 had not been examined across stocks. Brunel (2010) investigated how common such effects are by applying meta-analysis to 39 NE Atlantic fish stocks. He tested relationships between age structure (spawner mean age, age diversity, and proportion of recruit spawners) and recruitment. Although statistically significant effects were found for some stocks, and indeed for some species overall, meta-analyses combining the stock-level tests revealed that none of the effects were statistically significant across all stocks. Thus, neither Brunel (2010) nor we find convincing support for H3 being generally applicable.

Recruitment per SSB decreases with long-term reduction in SSB (H4)

Our results seem to give support for H4. Stocks that declined in SSB from the first to the second period produced less recruits after the shift than expected from a Ricker model fitted to the whole time series, while stocks that increased in SSB showed an increase in recruitment (Fig. 4). This may suggest that long-term changes in SSB were associated with changes in pre-recruit mortality.

However, additional analysis showed that the change in pre-recruit survival generally preceded the change in stock size, suggesting that the low stock size was a result of the high mortality rather than the opposite. Consequently, the 2 mechanisms suggested in the 'Introduction' (prey to predator feedback loop and loss of spatial and genetic structure) do not seem to be the underlying cause of the findings. Instead, these results suggest that long-term changes in stock size often are driven by long-term changes in pre-recruit mortality. The literature suggests numerous biotic and abiotic factors that potentially may cause such long-term changes in pre-recruit mortality (see Houde 2008 and references therein).

Recruitment per SSB changes with long-term changes in temperature (H5)

Our results did not show support for H5 (Fig. 4). This is somewhat unexpected and seems to contradict earlier work by e.g. Mueter et al. (2007), who pointed out that climate may induce persistent change in recruitment dynamics. Our results, in contrast, indicate that climate generally is not the main driver behind the long-term (as opposed to inter-annual) changes in juvenile survival or that the temperature measurements fail to capture the key climate changes. Either alternative is possible; in most ecosystems there has been high fishing pressure, which, probably in combination with climate drivers, has caused major changes in fish stock abundance (Planque et al. 2010), both for the species analysed and their predators and prey. Further, temperature effects may for some stocks be marginal compared to those of other environmental factors, such as food availability or predation pressure, which may or may not be linked to temperature.

The following relates to stocks that were found to display a statistically significant temporal shift in recruitment dynamics and an effect of temperature in at least 1 of the 2 periods. We discuss how the strength of the temperature effect changed between the periods and how this change corresponded to the changes in MA and SSB, respectively, as formulated in hypotheses H6 and H7.

The temperature-recruitment relationship strengthens with decreasing MA (H6)

It has been suggested that recruitment to a fish stock is more susceptible to environmental fluctuations when the spawning stock age composition has been skewed toward younger ages, i.e. H6. However, in our multi-stock analysis, the changes in the strength of the temperature effect did not scale statistically significantly with the changes in body mass-weighted mean age of spawners (Fig. 5). This is comparable to the only other study we are aware of that deals with more than 1 or a few stocks (Brunel 2010). Brunel (2010), in his meta-analysis of 39 NE Atlantic fish stocks, also tested relationships between age structure (body mass weighted spawner mean age, age diversity, and proportion of recruit spawners) and recruitment sensitivity to temperature. Meta-analyses combining the stock-level tests revealed that the spawner mean-age influence on recruitment sensitivity to temperature was not statistically significant across all stocks.

The temperature-recruitment relationship strengthens with decreasing SSB (H7)

In our analyses, the changes in strength of the temperature effect on recruitment success did not show any statistically significant link to changes in SSB (Fig. 5). This is in concordance with the results of Stige et al. (2006), who studied 22 cod stocks and did not find strong evidence for density dependent climate effects, i.e. for an interaction between the climate (as represented by the NAO) effect and cod SSB. In contrast, in a study of the 6 main cod stocks in European waters south of 62° N, Brander (2005a) concluded that the NAO only has a notable effect on recruitment when the SSB is low.

CONCLUSIONS

The relationship between recruitment, spawning stock biomass, and temperature varied over time. The most frequent alteration in the non-stationary linear models was, for 14 stocks, in the intercept in recruitment success, suggesting a change in pre-recruit mortality over time.

Changes in pre-recruit mortality were associated with long-term changes in spawning stock biomass. However, the change in pre-recruit survival generally preceded the change in stock size, suggesting that long-term changes in stock size often are driven by long-term changes in pre-recruit mortality.

A statistically significant threshold in recruitment dynamics was found for 13 stocks; for an additional 14 stocks, threshold models performed better than the best linear or nonlinear stationary models, but the threshold was not statistically significant. The good performance of the threshold models, while not providing evidence for ecological regime shifts, does suggest that abrupt changes are common.

For half of the stocks, the temperature effect was statistically significant when added to the model of the relationship between recruitment success and spawning stock biomass. This includes all the 6 herring stocks studied, with a positive effect for cold-water stocks and negative for stocks in the more temperate southern areas. For plaice, only 4 stocks from around the British Isles were analysed. For all of these stocks, located towards the centre of the overall distribution range of plaice, a tendency toward recruitment being favoured by lower temperatures was found.

Acknowledgements. We are grateful to Prof. C. Möllmann, Dr. M. Lindegren, and 3 anonymous reviewers for constructive, valuable comments to earlier versions of this paper. We thank The Research Council of Norway (RCN) for funding the workshop Tropharct through the MICO project (number 186310, Match/Mismatch and Ecosystem). G.O. and J.M.D. thank RCN for partly funding their contributions to the paper through ADMAR (Adaptive management of living marine resources by integrating different data sources and key ecological processes, number 200497/130), a collaborative project between IMR, Bergen, and CEES, University of Oslo. This work is conducted in association with the IMBER regional program ESSAS (Ecosystem Studies of Sub-Arctic Seas).

LITERATURE CITED

Akaike H (1974) A new look at the statistical model identification. IEEE Transactions on Automatic Control 19: 716–723

➤ Bailey KM (2000) Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. Mar Ecol Prog Ser 198:215–224

Bakun A (2004) Regime shifts. In: Robinson AR, Brink K (eds) The sea, Vol 13. Harvard University Press, Cambridge, MA

➤ Bakun A (2010) Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: conceptual templates and schematic constructs. J Mar Syst 79:361–373

➤ Beamish RJ, McFarlane GA, Benson A (2006) Longevity overfishing. Prog Oceanogr 68:289–302

➤ Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog Oceanogr 60:245–262

Berkeley S, Hixon MA, Larson RJ, Love MS (2004) Fisheries sustainability via protection of age structure and spatial distributions of fish populations. Fisheries 29:23–32

Biggs R, Carpenter SR, Brock WA (2009) Turning back from the brink: detecting an impending regime shift in time to avert it. Proc Natl Acad Sci USA 106:826–831

Bochkov YA (1982) Water temperature in the 0-200 m layer in the Kola-Meridian in the Barents Sea, 1900-1981. Sb Nauchn Trud PINRO 46:113–122 (in Russian)

Brander K (2000) Effects of environmental variability on growth and recruitment in cod (*Gadus morhua*) using a comparative approach. Oceanol Acta 23:485–496

Brander K (2005a) Cod recruitment is strongly affected by climate when stock biomass is low. ICES J Mar Sci 62: 339–343

Brander K (2005b) Spawning and life history information for North Atlantic cod stocks. ICES Coop Res Rep 274. ICES, Copenhagen

Brander K (2010) Cod *Gadus morhua* and climate change: processes, productivity and prediction. J Fish Biol 77: 1899–1911

Brunel T (2010) Age-structure-dependent recruitment: a meta-analysis applied to Northeast Atlantic fish stocks. ICES J Mar Sci 67:1921–1930

Brunel T, Boucher J (2007) Long-term trends in fish recruitment in the north-east Atlantic related to climate change. Fish Oceanogr 16:336–349

Cardinale M, Möllmann C, Bartolino V, Casini M and others (2009) Effect of environmental variability and spawner characteristics on the recruitment of Baltic herring *Clupea harengus* populations. Mar Ecol Prog Ser 388: 221–234

Chambers RC, Waiwood KG (1996) Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua.* Can J Fish Aquat Sci 53:1986–2003

Checkley D, Alheit J, Oozeki Y, Roy C (eds) (2009) Climate change and small pelagic fish. Cambridge University Press, Cambridge

Ciannelli L, Fisher JAD, Skern-Mauritzen M, Hunsicker ME, Hidalgo M, Frank KT, Bailey KM (2013) Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes. Mar Ecol Prog Ser 480:227–243

Cushing DH, Horwood JW (1994) The growth and death of fish larvae. J Plankton Res 17:783–800

Drinkwater KF (2006) The regime shift of the 1920s and 1930s in the North Atlantic. Prog Oceanogr 68:134–151

Drinkwater KF, Myers RA (1987) Testing predictions of marine fish and shellfish landings from environmental variables. Can J Fish Aquat Sci 44:1568–1573

Drinkwater KF, Beaugrand G, Kaeriyama M, Kim S and others (2010) On the processes linking climate to ecosystem changes. J Mar Syst 79:374–388

Emeis KC, Finney BP, Ganeshram R, Gutierrez D, Poulsen B, Struck U (2010) Impacts of past climate variability on marine ecosystems: lessons from sediment records. J Mar Syst 79:333–342

Finney BP, Alheit J, Emeis KC, Field DB, Gutierrez D, Struck U (2010) Paleoecological studies on variability in marine fish populations: a long-term perspective on the impacts of climatic change on marine ecosystems. J Mar Syst 79: 316–326

Fox CJ, Planque BP, Darby CD (2000) Synchrony in the recruitment time-series of plaice (*Pleuronectes platessa* L) around the United Kingdom and the influence of sea temperature. J Sea Res 44:159–168

Francis RC, Hare SR (1994) Decadal scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. Fish Oceanogr 3:279–291

Frank KT, Leggett WC (1994) Fisheries ecology in the context of ecological and evolutionary theory. Annu Rev Ecol Syst 25:401–422

Fréchet A, Gauthier J, Schwab P, Lambert Y and others (2009) The status of cod in the Northern Gulf of St. Lawrence (3Pn, 4RS) in 2008. Can Sci Advis Sec Res Doc 2009/090. Department of Fisheries and Oceans, Ottawa

Galbraith PS, Pettipas RG, Chassé J, Gilbert D and others (2009) Physical oceanographic conditions in the Gulf of St. Lawrence in 2008. Can Sci Advis Sec Res Doc 2009/014. Department of Fisheries and Oceans, Ottawa

Hilborn R, Walters CJ (1992) Quantitative fisheries stock assessment. Chapman & Hall, New York, NY

Hinrichsen HH, Huwer B, Makarchouk A, Petereit C, Schaber M, Voss R (2011) Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (*Gadus morhua*). ICES J Mar Sci 68:2019–2028

Hjort J (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp P-V Reùn Cons Int Explor Mer 20:1–228

Houde E (1987) Fish early life dynamics and recruitment variability. Am Fish Soc Symp 2:17–29

Houde ED (2008) Emerging from Hjort's shadow. J Northwest Atl Fish Sci 41:53–70

Hsieh CH, Yamauchi A, Nakazawa T, Wang WF (2010) Fishing effects on age and spatial structures undermine population stability of fishes. Aquat Sci 72:165–178

Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. Biometrika 76:297–307

Iles TC (1994) A review of stock recruitment relationships with reference to flatfish populations. Neth J Sea Res 32: 399–420

Johansen R (2007) A model for the interaction between gadoid larvae and their nauplii prey. Math Biosci 208: 177–192

Kempf A, Dingsør GE, Huse G, Vinther M, Floeter J, Temming A (2010) The importance of predator–prey overlap: predicting North Sea cod recovery with a multispecies assessment model. ICES J Mar Sci 67:1989–1997

Kendall AWJ, Duker GJ (1998) The development of recruitment fisheries oceanography in the United States. Fish Oceanogr 7:69–88

Kjesbu OS, Kryvi H, Sundby S, Solemdal P (1992) Buoyancy variations in eggs of Atlantic cod (*Gadus morhua* L.) in relation to chorion thickness and egg size: theory and observations. J Fish Biol 41:581–599

Kjesbu OS, Solemdal P, Bratland P, Fonn M (1996) Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 53:610–620

Koslow J (1992) Fecundity and the stock–recruitment relationship. Can J Fish Aquat Sci 49:210–217

Köster FW, Hinrichsen HH, Schnack D, St John MA and others (2003) Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock–recruitment relationships. Sci Mar 67:129–154

Köster FW, Möllmann C, Hinrichsen HH, Wieland K and others (2005) Baltic cod recruitment — the impact of climate variability on key processes. ICES J Mar Sci 62: 1408–1425

Law R (1991) Fishing in evolutionary waters. New Sci 1758: 35–37

Levi D, Andreoli MG, Bonanno A, Fiorentino F and others (2003) Embedding sea surface temperature anomalies into the stock recruitment relationship of red mullet (*Mullus barbatus* L. 1758) in the Strait of Sicily. Sci Mar 67:259–268

Lindegren M, Möllmann C, Nielsen A, Brander K, MacKenzie BR, Stenseth NC (2010) Ecological forecasting under climate change: the case of Baltic cod. Proc Biol Sci 277: 2121–2130

Liu H, Ciannelli L, Decker MB, Ladd C, Chan KS (2011) Nonparametric threshold model of zero-inflated spatio-temporal data with application to shifts in jellyfish distribution. J Agric Biol Environ Stat 16:185–201

Loeng H, Bjørke H, Ottersen G (1995) Larval fish growth in the Barents Sea. In: Beamish RJ (ed) Climate change and northern fish populations. Can Spec Publ Fish Aquat Sci 121:691–698

Marteinsdottir G, Thorarinsson K (1998) Improving the stock–recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. Can J Fish Aquat Sci 55:1372–1377

Meekan MG, Fortier L (1996) Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. Mar Ecol Prog Ser 137:25–37

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. Glob Change Biol 15:1377–1393

Morgan MJ, Shelton PA, Brattey J (2007) Age composition of the spawning stock does not always influence recruitment. J Northwest Atl Fish Sci 38:1–12

Mueter FJ, Boldt JL, Megrey BA, Peterman RM (2007) Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts. Can J Fish Aquat Sci 64:911–927

Myers RA (1998) When do environment–recruitment correlations work? Rev Fish Biol Fish 8:285–305

Myers RA, Barrowman NJ (1996) Is fish recruitment related to spawner abundance? Fish Bull 94:707–724

Olsen EM, Ottersen G, Llope M, Chan KS, Beaugrand G, Stenseth NC (2011) Spawning stock and recruitment in North Sea cod shaped by food and climate. Proc Biol Sci 278:504–510

Ottersen G (2008) Pronounced long-term juvenation in the spawning stock of Arcto-Norwegian cod (*Gadus morhua*) and possible consequences for recruitment. Can J Fish Aquat Sci 65:523–534

Ottersen G, Stenseth NC (2001) Atlantic climate governs oceanographic and ecological variability in the Barents Sea. Limnol Oceanogr 46:1774–1780

Ottersen G, Helle K, Bogstad B (2002) Do abiotic mechanisms determine interannual variability in length-at-age of juvenile Arcto-Norwegian cod? Can J Fish Aquat Sci 59:57–65

Ottersen G, Hjermann D, Stenseth NC (2006) Changes in spawning stock structure strengthens the link between climate and recruitment in a heavily fished cod stock. Fish Oceanogr 15:230–243

Planque B, Fredou T (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 56:2069–2077

Planque B, Fromentin JM, Cury P, Drinkwater KF, Jennings S, Perry RI, Kifani S (2010) How does fishing alter marine populations and ecosystems sensitivity to climate? J Mar Syst 79:403–417

Ponomarenko VP (1973) On a probable relation between age composition of spawning stock and abundance of the year classes of cod in the Barents Sea. Rapp P-V Reun Cons Int Explor Mer 164:69–72

Power D, Morgan J, Murphy EF, Brattey J, Healey B (2010) An assessment of the cod stock in NAFO Divisions 3NO. In: SCR Doc 2010/42. Northwest Atlantic Fisheries Organization

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ricker WE (1954) Stock and recruitment. J Fish Res Board Can 11:559–623

Rothschild BI (1986) Dynamics of marine fish populations. Harvard University Press, Cambridge, MA

Sætersdal G, Loeng H (1987) Ecological adaption of reproduction in Northeast Arctic cod. Fish Res 5:253–270

Shelton PA, Sinclair AF, Chouinard GA, Mohn R, Duplisea DE (2006) Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 63:235–238

Shepherd J (1999) Extended survivors analysis: an improved method for the analysis of catch-at-age data and abundance indices. ICES J Mar Sci 56:584–591

Stige LC, Ottersen G, Brander K, Chan KS, Stenseth NC (2006) Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. Mar Ecol Prog Ser 325:227–241

Stige LC, Ottersen G, Dalpadado P, Chan KS and others (2010) Direct and indirect climate forcing in a multi-species marine system. Proc Biol Sci 277:3411–3420

Stige LC, Hunsicker ME, Bailey KM, Yaragina NA, Hunt GL Jr (2013) Predicting fish recruitment from juvenile abundance and environmental indices. Mar Ecol Prog Ser 480:245–261

Svendsen E, Skogen M, Budgell P, Huse G and others (2007) An ecosystem modeling approach to predicting cod recruitment. Deep-Sea Res II 54:2810–2821

Swain DP, Currie LG, Chouinard GA, Poirier GA, Savoie L, Hurlbut T, Daigle D (2007) Assessment of the southern Gulf of St. Lawrence cod stock, March 2007. CSAS Res Doc 2007/033. Department of Fisheries and Oceans, Ottawa

Tereshchenko VV (1996) Seasonal and year-to-year variations of temperature and salinity along the Kola meridian transect. ICES CM C:11, p 24

Trippel EA, Kjesbu OS, Solemdal P (1997) Effects of adult age and size structure on reproductive output in marine fishes. In: Chambers RC, Trippel EA (eds) Early life history and recruitment in fish populations. Chapman & Hall, London

Vincenzi S, Satterthwaite WH, Mangel M (2012) Spatial and temporal scale of density-dependent body growth and its implications for recruitment, population dynamics and management of stream-dwelling salmonid populations. Rev Fish Biol Fish 22:813–825

Walters C, Kitchell JF (2001) Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Can J Fish Aquat Sci 58:39–50

Wang Y, O'Brien L, Clark K, Gavaris S, Hatt B (2009) Assessment of Eastern Georges Bank Atlantic cod for 2009. In: Ref Doc 2009/01. Transboundary Resource Assessment Committee, Fisheries and Oceans Canada, St. Andrews, NB

Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC Press, Boca Raton, FL

Appendix 1

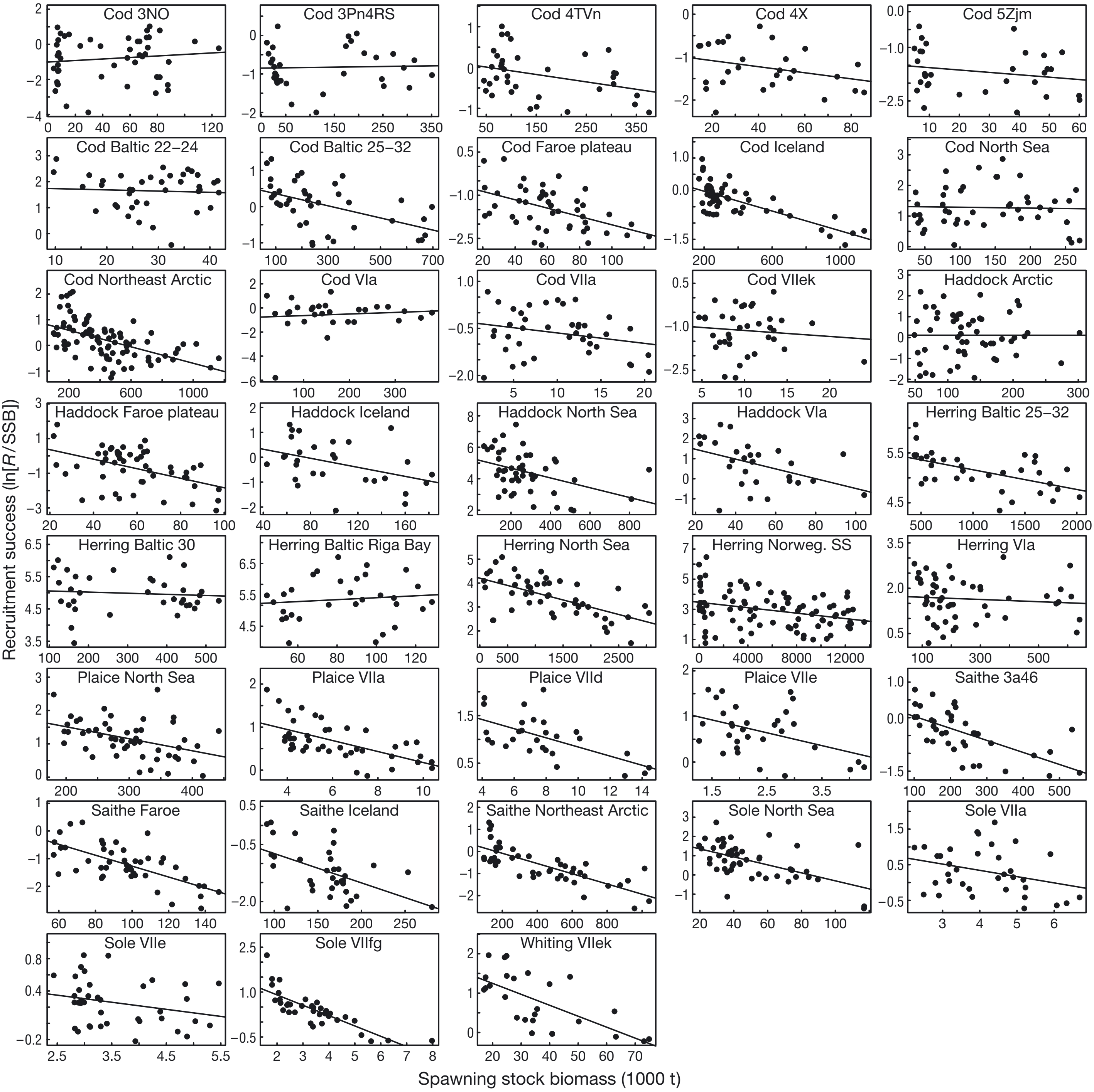

Fig. A1. Recruitment success as a function of spawning stock biomass (SSB) for 38 North Atlantic fish stocks. Recruitment success is measured as the natural logarithm of the fraction of the number of recruits (R, 1000s) on SSB (t). According to Ricker's spawner-recruit model (Ricker 1954), this log-fraction declines as a linear function of SSB, where stronger negative slope means stronger compensatory density dependence

Submitted: April 30, 2012; Accepted: January 7, 2013

Proofs received from author(s): March 22, 2013

Vol. 480: 227–243, 2013
doi: 10.3354/meps10067

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 22

Contribution to the Theme Section 'Harvested fish stocks in a changing environment'

Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review

Lorenzo Ciannelli[1,*], Jonathan A. D. Fisher[2], Mette Skern-Mauritzen[3], Mary E. Hunsicker[1], Manuel Hidalgo[4], Kenneth T. Frank[5], Kevin M. Bailey[6]

[1]College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, Oregon 97331, USA
[2]Centre for Fisheries Ecosystems Research, Fisheries and Marine Institute of Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1C 5R3, Canada
[3]Marine Mammal Research Group, Institute of Marine Research, Bergen, Norway
[4]Instituto Español de Oceanografía, Centre Ocenogràfic de les Balears, Moll de Ponent s/n, Palma 07015, Spain
[5]Department of Fisheries and Oceans, Bedford Institute of Oceanography, Ocean Science Division, Dartmouth, Nova Scotia B2Y 4A2, Canada
[6]National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center, Seattle, Washington 98115, USA

ABSTRACT: In marine populations, spatial structure arises over a wide range of scales and forms hierarchical aggregations. Changing spatial structure can alter the demographic and life history trait variation within populations and subject individuals to both novel environmental conditions and interspecific interactions. Thus, changes in the spatial structure of marine populations can be a prelude to further changes in abundance and can affect the resilience and recovery potential of populations following anthropogenic and environmental perturbations. These observations underscore the importance of studying the spatial ecology of marine fish populations in order to (1) understand the underlying mechanisms that can lead to rapid alterations in population abundance and community interactions, (2) provide indicators of stock health, and (3) characterize the consequences of changing spatial patterns on population susceptibility to exploitation and environmental variability. Here, we synthesize the interacting factors that influence the formation, maintenance and erosion of spatial structure in marine fish populations and identify the further consequences of such erosion at the population and community levels. We emphasize human driven changes of population spatial structure for 3 levels of population genetic aggregation that are common in fisheries management scenarios, namely sympatric populations, metapopulations and panmictic populations. Case studies are presented for each level of aggregation. Throughout our review, we both summarize the factors that link spatial and temporal dynamics in marine populations and highlight the management and conservation implications of such linkages.

KEY WORDS: Spatial structure · Spatial ecology · Population dynamics · Fisheries

BACKGROUND AND OBJECTIVES

All terrestrial and marine populations are, to varying degrees, spatially structured over a broad and hierarchical range of spatio-temporal scales (Goodwin & Fahrig 1998) that span from small schools to demes in a metapopulation complex. Regardless of its scale, the spatial structure of a population is a key component of the population's ecology (Dunning et al. 1992). However, in fisheries science, rarely have results from spatial ecology been connected back to population abundance (Cadrin & Secor 2009) nor

---

*Email: lciannel@coas.oregonstate.edu

have patterns of spatial variability been considered in revising boundaries of management units (Link et al. 2011). Yet there is increasing evidence that changes in marine fish species abundance over time are typically accompanied by equally dramatic and large-scale changes in spatial distribution patterns (Atkinson et al. 1997, Watanabe et al. 1997, McFarlane et al. 2002, Fisher & Frank 2004, Bacheler et al. 2009), a characteristic that is similarly reflected in animal populations in general (Gaston et al. 2000). Moreover, changes in spatial patterns can subject individuals to a new set of environmental forcing and interspecies interactions and therefore can influence dynamics at the community level (Frank et al. 2007). These observations generate 2 simple but, as yet, unanswered questions. First, is a change of population spatial structure a mere manifestation of removing individuals, or is it also a prelude to further changes in population abundance? Addressing this question is a general ecology problem and involves an understanding of whether and how the spatial and temporal dynamics of populations are linked to each other. Second, if a change in population spatial structure precedes changes in population abundance, is the spatial structure of fish populations that are commercially harvested an attribute that is worth monitoring and preserving? The second question is an applied ecology problem, and it requires an understanding of whether indices of population spatial distribution can effectively supplement existing indices of population status.

In the present review article, we address both of these questions by examining the factors affecting the formation, maintenance and erosion of spatial structure in marine fish populations and the consequences of erosion at the population and community levels. Given the fundamental and applied nature of the topic, the paper is organized in 4 main sections: 'Theories', 'Consequences', 'Evidence' and 'Conservation'. In the 'Theories' section, we describe the processes thought to generate, maintain and disrupt population spatial structure across various levels of ecological and genetic aggregation. Because there is already a growing body of literature that deals with natural variations of spatial distribution of fish populations (see e.g. Ciannelli et al. 2008, Planque et al. 2011), in the present review, we streamline the description of natural variations to emphasize changes that are driven by exploitation. This is not to say that environmental changes do not matter; in fact, as we explain in our manuscript, these 2 sources of variability may interact. In the second section, 'Consequences', we review the potential impacts of changing spatial structure (human- or environmentally driven) on population and community dynamics. In the third section, 'Evidence', we present case studies from marine fishes that expand the main principles of the previous 2 sections. In the last section, 'Conservation', we link our findings with ongoing efforts to conserve harvested marine fish populations.

As a starting point, Berryman (2002) defined a population as a group of conspecific individuals inhabiting a region within which the dynamics are mostly controlled by birth and death processes. In our review, we expand on Berryman's (2002) definition to include 3 common and complex aggregation levels encountered in applied management situations: (1) sympatric discrete populations (e.g. Iles & Sinclair 1982), (2) spatially complex populations, e.g. metapopulations (Smedbol et al. 2002) and source–sink populations (Pulliam 1988), and (3) panmictic populations (Table 1). In nature, these 3 levels of aggregations are present as a continuum rather than categorical groupings (Thomas & Kunin 1999), and different

Table 1. Types of populations based on their genetic and demographic characteristics. B: per capita birth rate, D: per capita death rate, E: per capita emigration rate, I: per capita immigration rate. For each population type, we review a case study (see 'Evidence') listed in the last column

Type	Definition	Demography	Genetic	Case study
Sympatric discrete populations	Reproductively and genetically isolated populations, which may occupy overlapping habitats, at least during one phase of their life cycles	$B+D \gg E+I$	Structured	Alaska walleye pollock *Theragra chalcogramma*
Spatially complex populations (metapopulation, source–sink)	Locally breeding subpopulations (deme) which may be genetically connected via dispersal	$B+D \geq E+I$	Homogenous and weakly structured	Eastern Scotian Shelf cod *Gadus morhua*
Panmictic population	Interbreeding individuals that are heterogeneously distributed over space	$B+D \ll E+I$	Homogeneous	Norwegian spring spawning herring *Clupea harengus*

levels of aggregations can co-exist. For example, a panmictic or metapopulation complex can comprise components of a larger sympatric complex. However, it is important to realize that regardless of their level of aggregation, heterogeneous spatial distributions of populations occur because of the underlying spatial variability in the physical and biological environment (Brown et al. 1995), intra- and inter-specific interactions, and individual behavioral responses (Planque et al. 2011). The nonrandom spatial patterns of marine populations give rise to what we here define as the spatial structure. Another aspect of a population's spatial distribution that changes in relation to abundance is the habitat extent or occupancy (MacCall 1990). In the present review, we consider changes of both spatial structure and spatial occupancy because they are both influenced by exploitation. In doing so, we make 2 assumptions. First, the spatial structure of a population can be quantified by the deviation of the population spatial distribution from a fully random pattern, and its occupancy can be quantified by the spatial extent. Second, a population that has experienced erosion of spatial structure and occupancy has shrunk its geographical range and/or become more homogeneous over space.

THEORIES

Mechanisms that generate and maintain population spatial structure

The spatial structure of populations results from a tension between dispersal and isolation forces (e.g. Iles & Sinclair 1982, Kokko & Lopez-Sepulcre 2006) and from differences in demographic rates across the species' range (Dunning et al. 1992). However, the degree of spatial structuring in populations, the mechanisms that generate structure and the consequences of its erosion will vary among life history strategies and over scales (Goodwin & Fahrig 1998). In marine environments, for example, we can expect that short-lived species inhabiting pelagic habitats exhibit more variability in spatial structure than longer-lived demersal or benthic species because of their short life cycle, earlier maturation, and association with more ephemeral environmental features. Likewise, we can expect that pelagic species may recover their spatial structure faster compared to long-lived demersal or benthic species, provided that the environmental conditions are favorable for such recovery.

With regard to scales, spatial structure gives rise to hierarchical levels of aggregation (Fauchald et al. 2000). In our review, we consider scales that separate ecological and genetic levels of population aggregation (Table 1). Sympatric but distinct populations are indicative of deep reproductive and genetic isolation among individuals belonging to different groups, which may take thousands of years to develop but which can be destroyed by minimal genetic exchange within just a few generations. Movement of reproductive individuals is therefore negligible between genetically distinguished populations and has minimal impact on the dynamics of each population, which are controlled mostly by internal birth and death processes. Such isolation is surprisingly common and increasingly revealed within marine species using molecular genetic techniques (Hauser & Carvalho 2008). The lack of genetic separation does not necessarily preclude the existence of a sympatric complex. Many factors can blur the genetic signature of demographically isolated populations, such as markers used for examining the separation, population sizes, and the isolation time (Palumbi 2003, Hutchings et al. 2007, Knutsen et al. 2011). In contrast to this pattern of isolation, a metapopulation is defined by the presence of several locally breeding subpopulations linked to each other by individual dispersal and each having equal potential for independent extinction and re-colonization (Smedbol et al. 2002). In a metapopulation, the internal dynamics of each composing subunit (deme) are still dominant compared to the dynamics caused by individual dispersal, but the level of dispersal is such that the genetic signature among the composing demes is blurred (McQuinn 1997). Instances in which dispersal among the composing units of a spatially complex population have demographic consequences on other units are termed source−sink populations (Pulliam 1988). Finally, in panmictic spatially structured populations, movement of individuals prevents both local extinction and genetic structuring and therefore has a dominant impact on the local dynamics. It is important to note that spatial structure arises at any aggregation level but for different reasons. One could therefore consider spatial structure an aggregation-free property of populations.

There are 2 facets of spatial distributions that can be modified by human and environmental forcing, namely the population's occupancy and the level of spatial heterogeneity within that range. Landscape and hydrographic features that constrain individual dispersal and reproduction bound the geographic range of a population (Levin 1992). For example, the geographic range of sympatric populations or metapopulations is maintained by the mechanisms that generate reproductively or demographically isolated groups of individuals. These mechanisms include imprinting (Cury 1994), local retention of early life stages (Jones et al. 1999, Ciannelli et al. 2010), social interactions during migratory phases (Corten 2001), or habitat- and geographic-specific mating behavior (Rowe & Hutchings 2003). Within the geographic range of a population, small-scale environmental forcing and individual behavior play dominant roles in determining the spatial structure. These variables may be considered as 'activating factors', promoting variability within the species' global or population's regional geographic range. For example, the spatial structure within a panmictic population is maintained by the underlying heterogeneity of the physical and biological environments (e.g. currents, patches of food or local prey depletion) and by behavioral interactions among the individuals of the same species (e.g. schooling and intra-specific competition) and other species (e.g. feeding aggregations and predation). Likewise, the spatial structure of a metapopulation or a sympatric complex of populations is maintained by the variation of demographic rates across the species range.

Factors affecting the spatial structure of marine populations can also be characterized based on whether they are density-independent or density-dependent. Generally, the response of individuals to density-dependent variables defines the population abundance-distribution relationship, while the effect of density-independent variables shapes the population's ecological niche (Brown et al. 1995). The Fretwell & Lucas (1969) ideal free distribution (IFD) and the subsequent depiction of a basin model of marine fish distributions based on IFD (MacCall 1990) quantify the potential outcomes of these density-dependent spatial dynamics. Density-dependent spatial dynamics can promote expansion (or contraction) when the population reaches high (or low) levels of abundance, assuming that individuals settle on habitat patches in proportion to the local resources available, such that the habitat suitability or the individuals' fitness is equalized over the species spatial domain (Fretwell & Lucas 1969). Within the area of distribution of a single panmictic population, spatial structure is also maintained through a preservation of the population age structure, as individuals of different ages/sizes and sexes are typically distributed differently over space due to stage-/age-specific requirements and size-related migration capabilities (e.g. Nøttestad et al. 1999, Holst et al. 2004, Fauchald et al. 2006). It follows that the spatial structure of a panmictic population can change in relation to cohort dominance; for instance, in pelagic fishes, where numerically dominant cohorts aggregate in certain areas, the sudden appearance of a large cohort can result in equally sudden changes of the population spatial structure (Huse et al. 2010).

Alternatively, or in addition to density-dependent dynamics, individuals are distributed over space following environmental preferences to optimize the use of spatially heterogeneous resources. Often, however, changes in population abundance, age structure, and occupancy also co-occur with large-scale changes in environmental variables, such as water temperature (Swain 1999). In such circumstances, it becomes harder to disentangle the sources of variability in population distribution or the degree to which a change of environmental conditions facilitate or curtail a change of occupancy. Such a level of understanding is paramount for defining population management units (Link et al. 2011). As in other systems (Borregaard & Rahbek 2010), identifying the cause–effect relationship between abundance and spatial distribution in exploited marine fishes remains a fundamental challenge (Shepherd & Litvak 2004).

The concept of source–sink populations (Pulliam 1988) is also relevant in the context of understanding and preserving spatial structure because the presence of different demographic rates across space violates the assumptions of many fishery stock assessment models. This has led to calls for inclusion of spatially varying demographic rates (Cadrin & Secor 2009). Furthermore, declining spatial structure of source–sink populations may compromise the connectivity among demes, with implications for recovery dynamics (Lawton 1993). Spatial variation in demographic rates underlines the argument for the quantification and preservation of structure to maintain biocomplexity and insure against catastrophic losses at higher levels of ecological organization (Hilborn et al. 2003).

Mechanisms that erode population spatial structures and occupancy

Erosion or reduction of population spatial structure can arise due to human-induced and natural events or by a combination of both factors. Over short spatial and temporal scales, individuals respond to the natural variability of the forcing factors that affect their distribution. Individuals will react by moving to new habitats, feeding on different prey, and generally exploiting any available niche. This set of mechanisms acts parallel to those that are linked to exploitation, which causes local depletions (Bartolino et al. 2012), reduced spatial occupancy (Atkinson et al. 1997), and alteration of the population demographic and genetic structures (Brander et al. 2010). Both environmentally and human driven changes of population spatial structure and occupancy can be abrupt (e.g. regime shift and rapid transitions of population spatial distributions) and deleterious (e.g. invasive species, establishments of new trophic interactions, and age truncation). There are also synergies between the 2 drivers, e.g. a population that is heavily harvested is more likely to undergo further changes of its spatial structure in relation to environmental changes (Hsieh et al. 2010).

Depletion, induced by exploitation, can indeed contribute to the loss of spatial structure, especially when isolation forces historically prevailed over dispersal (Hauser & Carvalho 2008). For example, exploitation that concentrates on spawning seasons and habitats has the potential to eliminate a single stock or a deme within a sympatric population system or a metapopulation complex, ultimately eroding the spatial structure. Similarly, localized depletion can dig a 'hole' within the geographic extent of a panmictic population, especially when migrants cannot refill that vacuum of space at the same rate at which individuals are being removed and/or when the habitat has been compromised (Bartolino et al. 2012). It is primarily the overharvesting of local populations/aggregations (i.e. sub-units; often those closest to port suffer first) that erodes population structure. Harvest practices that are not concentrated in space and time (although they generally are; this property is what makes industrial fishing efficient) can also reduce population abundance, causing a spatial contraction. Spatial contractions are associated with fishery-induced stock declines (MacCall 1990, Atkinson et al. 1997, Walters & Martell 2004). Similarly, if harvest is changing the demographic structure of a population, it can have consequences by changing spatial distributions and migration pathways and by causing a mismatch between early life stages and favorable environmental conditions. In general, multistock fishing is prone to declines of less productive stocks and those that are most vulnerable to sequential exploitation, i.e. the stocks in proximity to fishing ports are often overfished and then fishers move on to the next (Walters & Martell 2004). The common outcome of these and other scenarios is the unintended overfishing of local populations and diminished spatial variability within marine populations.

Climate forcing can also contribute to the loss of population spatial structure. For example, climate change can alter dispersal pathways during early life stages (Bailey et al. 2008, Duffy-Anderson et al. 2012) and influence survival over different locations (Ciannelli et al. 2007a). Changing oceanographic conditions can inhibit population exchange and the survival of eggs and larvae by affecting their transport and retention in favorable areas (Bailey et al. 2008). Shifts in the distribution and phenology of fish and their prey can have a substantial effect on recruitment and production (Brander 2010). Also, populations or life stages that have specific habitat requirements may be severely affected by loss of favorable habitat due to changes in ocean conditions, including increasing temperatures, depleted oxygen and ocean acidification (Fabry et al. 2008, Voss et al. 2011). Such changes also reduce suitable spawning habitats and thus population reproductive success (Eby et al. 2005, Köster et al. 2005). As with the effects of fisheries, the causes of climate impacts may or may not be strictly related to space; if climatic variability results in large-scale changes in the abundance/demographic structure, it will also cause changes in spatial distributions. There are many examples of changes in species spatial distributions that are attributed to large-scale changes in oceanographic conditions (Perry et al. 2005, Mueter & Litzow 2008, Nye et al. 2009). These trajectories are likely to continue as climate change persists (Cheung et al. 2010).

CONSEQUENCES

The outcome of the processes that affect a population's spatial structure and its occupancy is based on traits that, to some extent, are adaptive and therefore increase the individual fitness (e.g. Fretwell & Lucas 1969, MacCall 1990, Kokko & Lopez-Sepulcre 2006). Eroding such structure interferes with how individuals interact with each other, with other species, and with the environment. This interference is likely to have consequences at the population and community levels and has in fact accompanied the collapse of many commercial stocks. Likewise, changes of trophic control in many marine ecosystems have been caused by changes of species abundance and distributions (e.g. Frank et al. 2007, Litzow & Ciannelli 2007). In the following sections, for each of the 3 aggregations levels outlined in Table 1, we provide greater details on how erosion of spatial structure affects population and community interactions.

Over larger spatial scales, the consequences of a loss in spatial structure can be particularly relevant for management and conservation purposes. Spatial structure is especially manifested during the spawning season, when reproductive individuals aggregate on spawning grounds. Iles & Sinclair's (1982) seminal work using Atlantic herring populations indicated that populations exist as a combination of many sub-stocks. The number of sub-stocks and abundance of each sub-stock is proportional to the number and size of geographic areas that allow retention during the early life stages. Thus, the variability of spatial abundance during spawning (or very early life stages) reflects the genetic structure of the population. Each subpopulation or deme can be adapted to the local environmental conditions, which may result in a heterogeneous spatial pattern in the life history traits (e.g. different somatic growth, maturing schedules, or reproduction phenology).

Since Iles & Sinclair's (1982) work, numerous studies have revealed that genetic differentiation of many marine fishes is more complex and may occur at much smaller scales than once thought, raising concern about the mismatch between genetic population structure and current fisheries management units (Reiss et al. 2009). Fishing-induced depletion of subpopulations or demes will trigger a decrease in the genetic and phenotypic diversity, with consequences on the variety of ways in which populations can counteract environmental or human-induced variability. Evidence has been observed in different populations of anadromous fish, such as Alaskan salmon, in which the maintenance of life history diversity has been demonstrated to have clear implications for global dynamics and biomass trajectories (e.g. Schindler et al. 2010). Under conditions of locally adapted populations, abundance recovery after a local extinction may take a long time and probably a lot longer than the time estimated by models that do not take into account the spatial and genetic structure of the populations (Hutchings 2000, Heath et al. 2008, Murawski 2010). These consequences highlight the relevance of maintaining the 'biocomplexity' of exploited populations. That is, preserving different sub-populations or demes ensures high life history diversity and yields more temporal stability because of the independent but complementary dynamics (Hilborn et al. 2003, Olsen et al. 2008) (Fig. 1).

In the context of metapopulations, a consequence of loss of spatial structure is a reduction of the 'rescue effects', or reduced source–sink dynamics, due to the reduced dispersal of individuals from one deme to another (Gonzalez et al. 1998) (Fig. 1). Specifically, when local abundance is reduced, the ensuing migration of individuals will also be curtailed. This can have consequences for re-colonization, thus altering the metapopulation dynamics and making the metapopulation more likely to experience wide fluctuations and potential extinction. Thus, subunits within a metapopulation may feel the effect of depletion occurring elsewhere in the metapopulation complex. Habitat fragmentation also reduces the exchange of individuals among demes (Betts et al. 2006). This is particularly relevant for benthic or demersal species,

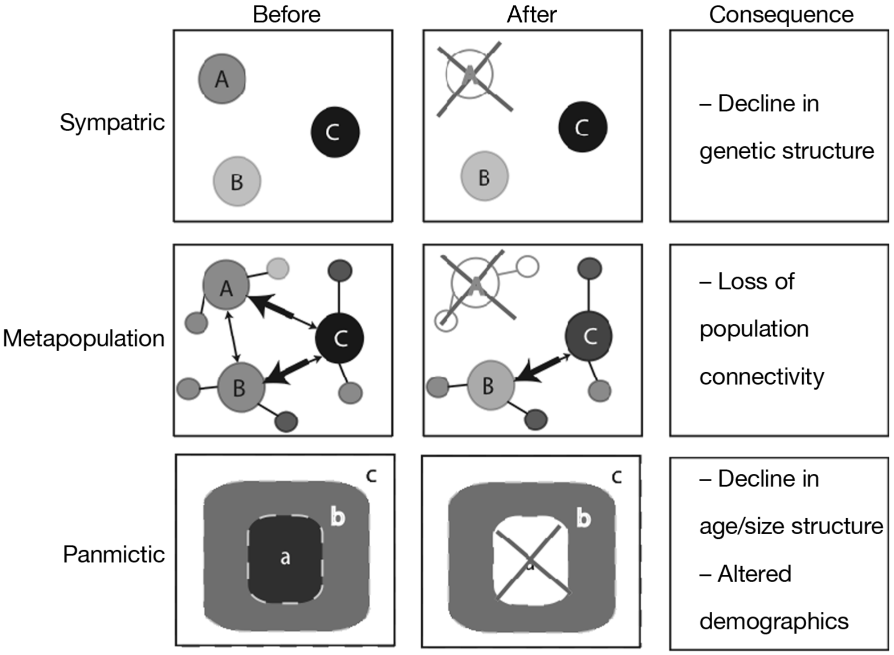

Fig. 1. Schematic representations of declines in 3 types of spatially structured populations and their consequences. A, B and C in the sympatric and metapopulation panels represent subpopulations and demes, respectively; a, b, and c in the panmictic population represent areas of different local abundance. In each panel, shading represents relative abundance across space, and the weights of arrows among metapopulations indicates relative sub-population connectivity. Examples of these 3 types of population structural decline are described in 'Theories'

which may move along corridors with specific characteristics (e.g. sediment size and infaunal assemblages). The process of colonization/recolonization may also depend on population thresholds being reached in a locale before the population expands outwards, perhaps being driven by density dependence, in search of new habitats (Ciannelli et al. 2012). This is similar to MacCall's (1990) geographic basin model, where a spillover occurs into initially less favorable habitats when the preferred habitat is occupied. There are several examples of such population behaviors, although abundance and geographic range may co-vary for a number of reasons (Shepherd & Litvak 2004), and fishing on aggregations may erode the detection of preferred habitats (Shackell et al. 2005).

Another consequence reported for stocks which have experienced spatial erosion is a greater sensitivity to further spatial changes. For example, analyzing a long-term data set on larval distribution from the southern California region, Hsieh et al. (2008) showed that stocks that were more sensitive to environmentally driven changes in spatial distribution during the larval phase were also commercially harvested. One explanation offered by the authors was that a reduction of the stock biomass caused erosion of spatial structure in the form of lower spatial heterogeneity, potentially because of local depletion of subunits within a population. In turn, a stock with eroded spatial structure is more likely to show changes of its distribution simply because of reduced heterogeneity of spatial responses to environmental variation. Ultimately, the strong dependence of a stock on a single or few geographic locations may imperil the viability of the stock in the face of further harvest under environmental change.

We have a better appreciation of the consequences of loss of the spatial structure of sympatric discrete populations or demes within a metapopulation (e.g. McQuinn 1997, Hsieh et al. 2010, Perry et al. 2010) than we have for loss of structure within a panmictic population. However, there are several mechanisms by which an erosion of spatial structure can affect panmictic populations and community dynamics. For example, the sudden loss of local density hotspots may create a spatial mismatch between predator and prey species, where predators consistently exploit such areas for food. This in turn will affect predator–prey temporal dynamics and, where these food web links are important, impact the surrounding assemblages. Furthermore, spatial contractions with reduced abundance can also change the spatial overlap with predators (Kempf et al. 2008, Hunsicker et al. 2010, Zador et al. 2011). With the selective removal of older individuals from the population or from certain locations, the remaining individuals may also lose the ability to 'learn' established migratory pathways (e.g. Corten 2001) or may be led to unsuitable habitats. For example, if repeat spawning at a site is imprinted and young fish learn where to spawn from older fish (social facilitation), then if the tested spawning location is suboptimal for survival, it will represent a population trap that attracts young fish from other spawning locations. The behavioral change required to modify such suboptimal spawning decisions may require several generations of failure before it is realized.

EVIDENCE

We provide evidence from the literature of changes in spatial structure and relative population and community dynamics. Attributing each case study to a population type has been challenging, a fact that underscores the complex nature of population genetic and demographic structures. Yet, grouping populations based on their spatial, demographic and genetic structures is a common practice in ecology (e.g. Pulliam 1988, Smedbol et al. 2002) and in this review has been instrumental to describe the genesis and maintenance of spatial structure and the consequences of its erosion. However, in nature, individuals are not aware of our theoretical boundaries and behave in ways that may challenge their premises (Thomas & Kunin 1999). This does not invalidate the classification but rather underscores the need to recognize its limits when applied to wild populations. In the following case studies, the main intent of the grouping is to provide a general framework for understanding the consequences of spatial erosion across a wide range of genetically and demographically connected populations.

Sympatric populations: Alaska walleye pollock (Fig. 2)

Alaska pollock *Theragra chalcogramma* is North America's most abundant and lucrative fishery, representing ~40% of the total US fisheries landings, with a gross annual value of over US$ 1 billion (Ianelli et al. 2011). It is the world's largest human food fishery. Pollock is a gadid species, closely related to Atlantic cod, and often dominates the coastal ecosystems of the North Pacific Ocean. Pollock is usually considered a semi-demersal inhabitant of the continental shelf, but the species can occupy a wide range of habitats and environmental conditions, such as inshore seagrass beds, large estuaries, coastal embayments and offshore oceanic waters (Bailey et al. 1999). It is a subarctic species (Mueter & Litzow 2008), living in water temperatures ranging from 1° to 10°C. Pollock reach maturity at 3 to 4 yr of age, and individual females spawn millions of eggs each year (Hinckley 1987). There are several pollock spawning aggregations in the Alaska, USA, region (Fig. 2). Throughout the entire range of pollock distribution, there is good evidence of genetic separation at large scales, such as the eastern versus western Pacific or Alaska versus Puget Sound (Washington, USA) aggregations, and weaker evidence for separation at smaller scales within the Alaska region, such as between the Gulf of Alaska and the Bering Sea (Bailey et al. 1999). At even smaller scales, such as within the Gulf of Alaska or Bering Sea, the genetic structure is still unresolved, and the picture that emerges can vary with the use of different genetic markers (e.g. O'Reilly et al. 2004, Canino et al. 2005). However, it is clear that the Alaskan pollock forms a complex population structure with sympatric reproductively isolated stocks at larger scales and with several degrees of mixing at smaller scales. It is possible that this picture may be more common than assumed in many management scenarios.

Pollock populations in the Alaska region provide comparisons of situations where climate change or overfishing, as well as synergism between the 2 forces, have caused a decline in spatial structure. At the northern end of the pollock stock, one major population existed in the Aleutian Basin of the central Bering Sea, although its relationship to adjacent shelf populations is still unresolved and controversial (Bailey 2011). In the early part of the 1980s, population assessment models indicated a biomass of nearly 13 million t of pollock over age 5 yr in the US zone of the central Bering Sea alone. Americanization of the fishery occurring in the US zone in the mid-1980s forced the substantial foreign fishery into the international Donut Hole zone (Bailey 2011). The highest reported annual catch from the Aleutian basin fisheries was 1.7 million t in 1987, but it was likely higher than that

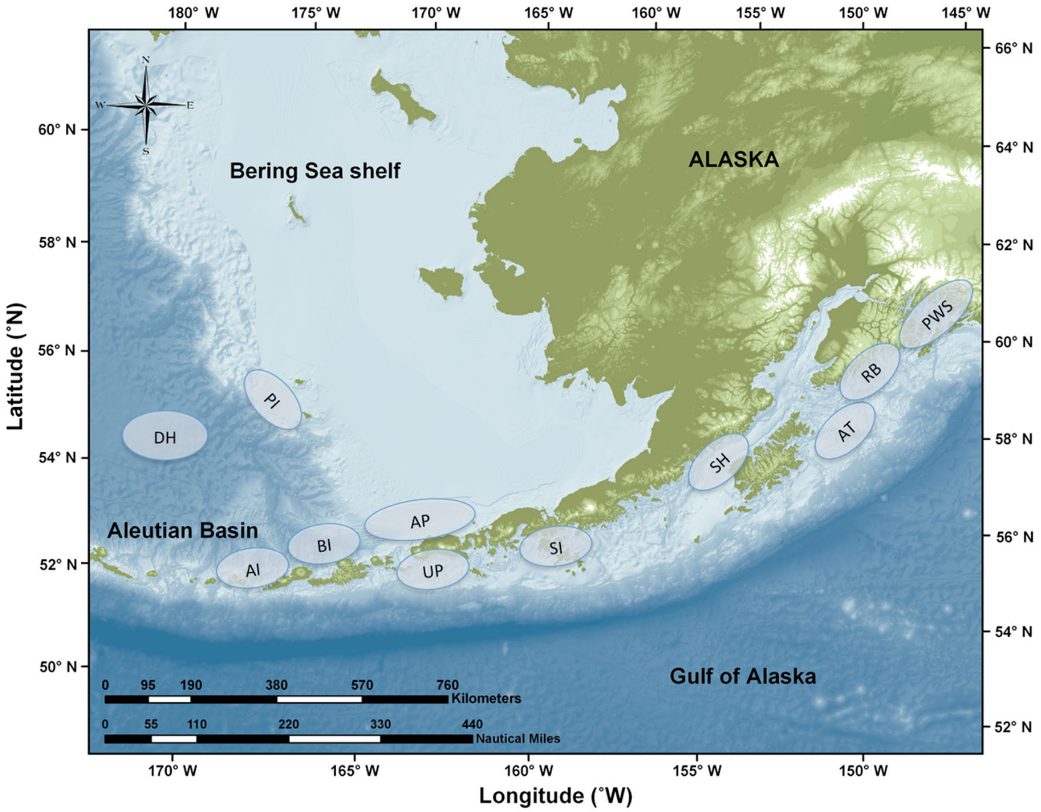

Fig. 2. Alaska, USA, region with known locations of walleye pollock *Theragra chalcogramma* spawning activity in the western Gulf of Alaska and eastern Bering Sea. The size of the location is not proportional to the spawning stock. PWS: Prince William Sound; RB: Resurrection Bay; AT: Amatuli Trough; SH: Shelikof Strait; SI: Shumagin Islands; UP: Unimak Pass; AP: Alaska Peninsula; BI: Bogoslof Island; AI: Aleutian Islands; DH: Donut Hole; PI: Pribilof Islands

(Bailey 2011). Noticeably, the peak of the landings occurred when the decline of the population biomass was already underway. In 1988, the Aleutian Basin biomass plunged to 50% of its peak value and by 1992 was only 6% of the maximum. In 2007, the population was estimated at 309 000 t, a drop of 98% from its peak. The Aleutian Basin population of pollock is currently commercially extinct. It has remained at this depleted level for 20 yr. This represents a depopulation covering ~1 million square miles. Because the fishery was so remote, the consequences to the ecosystem are unknown but could be substantial. There was no recognized trend in temperature or zooplankton abundance during the period of steep decline, so the major factor appears to be overfishing and poor recruitment (Bailey 2011). In recent years, the Pacific fur seal *Callorhinus ursinus* population of Bogoslof Island in the southeastern corner of the Aleutian Basin has been increasing at a dramatic pace. Pollock is usually an important component of the fur seal diet, but in this case they are eating mainly squid and deep-sea smelts. It is unknown whether these species have increased in abundance since the demise of pollock.

Still in the Bering Sea, but in the slope and shelf areas, there are several known pollock spawning aggregations (Bacheler et al. 2010) (Fig. 2). Collectively, the Bering Sea shelf and slope pollock have waxed and waned but remain reasonably abundant, and in fact, the commercial stock exhibited signs of a modest recovery in 2011 from a low point in 2008 to 2010. Changes in the spatial distribution of these populations have been linked to both abundance and climate (Bacheler et al. 2010). While the recruitment dynamics and stock size of pollock in the eastern Bering Sea remain fairly constant, this population has lost much of its spatial structure, especially during the larval and juvenile phase. For example, the once abundant larval aggregation around Bogoslof Island is much reduced in more recent years (Bacheler et al. 2010). Also, while juveniles (age ≥1 yr) were mostly distributed throughout the shelf, they are mostly localized in the northwest portion of the shelf in more recent years. These facts provide some evidence of reduced spatial structure over different life history stages and should be taken as early warning for potential additional negative effects at the population level. Causes of concern for the pollock stocks in the region also arise from the continuous increase in abundance of arrowtooth flounder *Atherestes stomias* (a piscivorous flatfish), which has caused an expansion of its habitat (Ciannelli et al. 2012) and a greater overlap (Hunsicker et al. 2010) and predatory impact (Zador et al. 2011) on its prey, the juvenile stage of walleye pollock, particularly in the northwest shelf region.

In the western Gulf of Alaska, potential overfishing and ecosystem reorganizations have caused changes in the spatial distribution of pollock. As in the Bering Sea, there are several recognized spawning populations of pollock in the Gulf of Alaska (Ciannelli et al. 2007b) (Fig. 2), mostly associated with deepwater bays or deep canyons and sea valleys intruding into the continental shelf. The largest population has historically been in the Shelikof Strait. This population was at a peak of 2.8 million t in 1981 from acoustic estimates of biomass during the prespawning period. Catch rates peaked in 1984 at 307 000 t as the population was already in decline. In 2007, the biomass was reduced to 180 000 t, and catches were ~50 000 t. Ciannelli et al. (2007b), analyzing egg distribution, showed that the spatial structure of the population had considerably decreased after the 1990s. The once conspicuous Shelikof Strait spawning aggregation is no longer dominant. Biomass levels of the population are now ~10% of the maximum observed. Bacheler et al. (2009) showed that with a decreased spawning biomass, spawning areas (as detected by egg density) were also reduced. As a result of the declines in this local concentration and other factors, such as management strategies to spread fishing effort and thus protect local Steller sea lions *Eumetopias jubatus*, the commercial fishery has shifted to the harvest of other smaller local populations, including those off Sanak and the Shumagin Islands. There has been considerable controversy about the effects of the pollock depletion on marine mammal and seabird populations, with the greatest concern for its effect on the endangered Steller sea lion. This issue remains unresolved.

Metapopulation: eastern Scotian Shelf cod (Figs. 3 & 4)

Cod resident on the eastern Scotian Shelf supported an important commercial fishery with average landings close to 50 000 t during the 1970s and 1980s (Fig. 3). Mobile gear fisheries, specifically otter trawling, typically accounted for 70% of the catch. Landings peaked in the mid 1980s, when the biomass had already started its decline. Annual instantaneous fishing mortality increased monotonically from ~0.2 in the late 1970s to 1.6 in 1992, the year before the population collapsed (Frank et al. 1994). Distribution patterns of adult cod prior to collapse were wide-

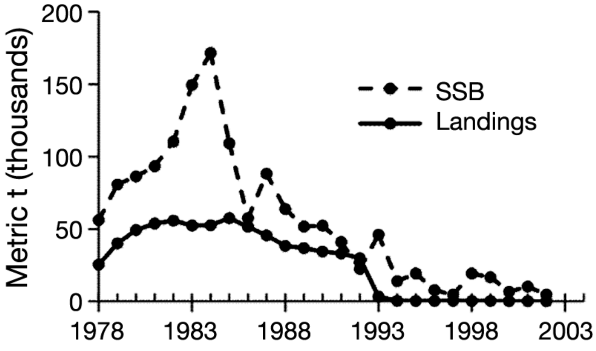

Fig. 3. *Gadus morhua*. Spawning stock biomass (SSB) and landings of the eastern Scotian Shelf cod (DFO 2011)

spread with major concentrations on most of the offshore banks along the shelf edge and Laurentian channel (Fig. 4A). After the collapse (Fig. 4B), nearly all of the banks were devoid of cod, and the few remaining concentrations were being protected by a moratorium on directed fishing for cod that was established in September of 1993. The moratorium remains in effect at present, and recovery has been very slow.

In addition to the spatial constriction, there has been a reduction in the temporal structure of spawning. Historically, the offshore banks were areas where spawning occurred during both spring and fall.

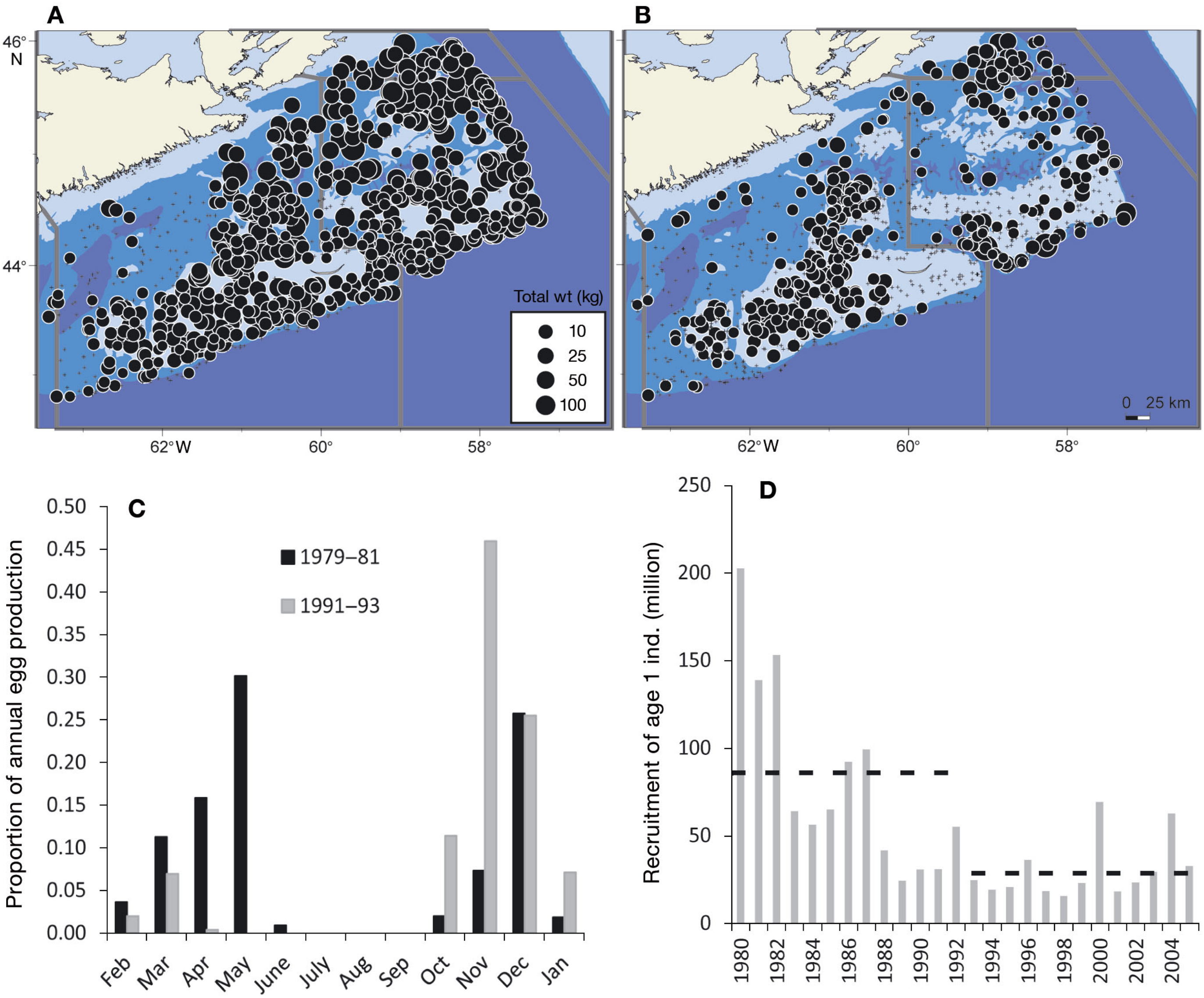

Fig. 4. Eastern Scotian Shelf cod *Gadus morhua*. Spatial distribution patterns of adult cod (A) before and (B) after the collapse in 1993. Proportion of cod eggs by month on the eastern Scotian Shelf from (C) 1979 to 1981 and 1991 to 1993 and (D) cod recruitment at age 1 yr. Grey lines in (A) and (B) show the boundaries of the Northwest Atlantic Fishery Organization. Horizontal dashed lines in (D) show the average recruitment during the pre- and post-collapse periods

Fig. 4C shows the proportion of cod eggs by month on the eastern Scotian Shelf from 1979 to 1981 and from 1991 to 1993. Distinct bi-modality was evident in the earlier period, while the spring (May to June) production was virtually absent in the latter period (Miller et al. 1995). This was one of the earliest indications of the erosion of population structure. The loss of the spring component was considered to have had a major impact on population renewal, given the capacity of the spring bloom and following events to generate new recruits in this and virtually all other temperate marine ecosystems. The loss of the spring spawning component as well as the overall reduction in spawning stock biomass were associated with a dramatic decline in annual recruitment (Fig. 4D).

Historically, and on a larger scale, cod recruitment in the Northwest Atlantic was synchronous at scales in excess of 500 km due, in part, to dispersal among adjacent stocks. Coincident with the cod collapse was a halving of the spatial scale of recruitment synchrony, suggesting an erosion of inter-stock connectivity and a further limitation to local recovery by reducing the probability of immigration from neighboring stocks (Kelly et al. 2009), i.e. the rescue effect. The collapse of cod on the eastern Scotian Shelf resulted in substantial changes in the composition of the fishery as several fisheries were newly created and some existing fisheries became extremely profitable. For example, as the percentage contribution of groundfish to the total landed value steadily declined from >70 to <10% from the 1980s to the early 2000s, invertebrate fisheries (mainly snow crab and shrimp) rose from 12 to 85% (DFO 2003). Ironically, the cod collapse produced a new fishery regime in which the inflation-adjusted monetary value of the combined shrimp and crab landing alone far exceeded that of the groundfish fishery it replaced. From an economic perspective, this may be a more attractive situation, but one cannot ignore the ecological risks of fishing down the food chain and the possibility that a focused fishery on the prey of the former groundfish could further impede recovery.

Panmictic population: Norwegian spring spawning herring (Figs. 5 & 6)

The Norwegian spring spawning (NSS) herring is a long-lived, pelagic fish with historic maximum stock levels at 15 to 20 million t and has in periods been the most important fish resource in the Northeast Atlantic (Hamre 1990). Unlike other case studies that we review in the present article, the NSS is a success story due to the spectacular recovery of both demographic and spatial structures following a collapse. The NSS is also a fascinating case study because it elucidates how human harvest and environmental variability interact with internal behavioral mechanisms to affect migratory pathways and the overall spatial structure and occupancy of a panmictic population.

Between 1 and 2 million t were landed annually in the 1950s and 1960s (Nakken 2008). The peak of the catch occurred in the late 1960s, when the biomass decline was already underway (Fig. 5). NSS herring have a complex spatial ecology, including distribution shifts with ontogenetic shifts and extensive and variable seasonal migrations as adults. The NSS herring spawn in spring along the Norwegian coast. The larvae drift with currents into nursery areas along the coast and into the Barents Sea, where they remain until ~4 yr of age. Thereafter, young herring migrate to the Norwegian Sea and take part in summer foraging, winter and spring spawning migrations. However, the areas used for spawning, foraging and wintering have varied considerably over the last decades (Dragesund et al. 2008) (Fig. 6). Due to the spatial complexity of herring stocks, the proposed population structures have ranged from discrete populations associated with the different spawning areas to a spatially complex panmictic population for which the structure, persistence and dynamics are best explained by behavioral rather than genetic mechanisms (Slotte & Fiksen 2000 and references therein). More recent studies support the latter stock structure and the hypothesis that behavioral and density-dependent mechanisms play a dominant role in de-

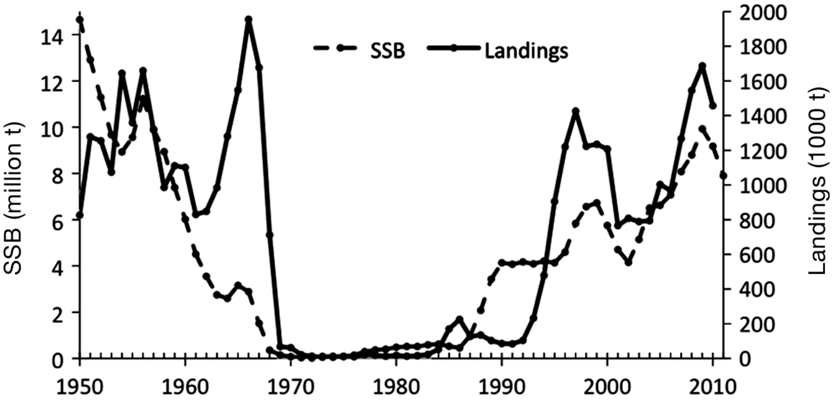

Fig. 5. *Clupea harengus*. Spawning stock biomass (SSB) and landings of Norwegian spring spawning herring (ICES 2011)

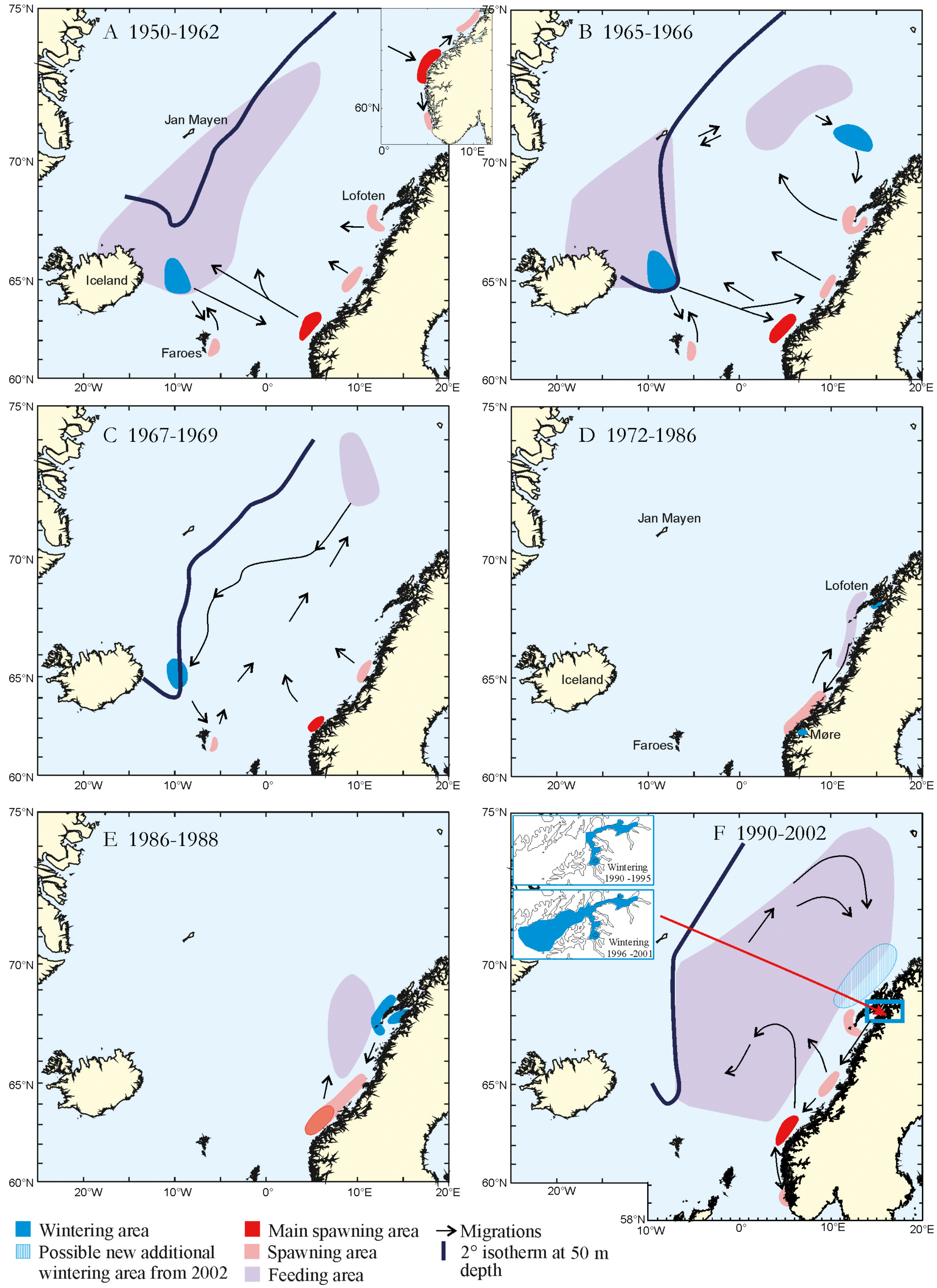

Fig. 6. *Clupea harengus*. Main migration patterns of the Norwegian spring spawning herring from 1950 to 2003. From Holst et al. (2004), with permission

termining the spatial structure of the NSS herring (e.g. Slotte & Fiksen 2000, Huse et al. 2010).

After 2 decades of rapid population decline, the NSS herring collapsed around 1970 due to high fishing mortality and adverse environmental conditions negatively impacting recruitment (Toresen & Østvedt 2000, Dragesund et al. 2008) (Fig. 5). Prior to the decline, spawning occurred from northern to southwestern Norway (Fig. 6A,B). The summer feeding migrations were long and directed toward the polar front in the Iceland and Jan Mayen areas. Wintering areas were mainly east of Iceland. During the population decline, the geographic range of the spawning areas shrunk, and no spawning occurred in the northern areas (Fig. 6C). The summer feeding areas shifted north and eastward toward the Norwegian coast. By the time of the collapse, the oceanic feeding migrations had ceased, and the summer feeding occurred only along the Norwegian coast (Fig. 6C). The herring also vacated the traditional wintering areas and started wintering along the Norwegian coast. Thus, after the collapse, the herring remained in coastal waters all year (Fig. 6D).

The changes in both spawning and feeding migrations appear to have been density-dependent, although unfavorable environmental conditions may also have had some influence (Slotte & Fiksen 2000, Holst et al. 2004). At lower densities, herring are generally in better condition and perform longer spawning migrations to southern spawning habitats (Slotte & Fiksen 2000). These habitats likely have favorable physical conditions that promote growth and survival of the fry (Slotte & Fiksen 2000). In contrast, at high abundances, the feeding migrations are longer, likely propelled by prey depletion (Holst et al. 2004). Following the collapse, the few remaining herring had likely met their energetic requirements in the coastal areas. Thus, in the NSS herring, reduced migration distances and costs, improved condition and an increasing use of optimal spawning habitats are parts of spatial processes that could positively influence recruitment at low stock abundances. However, the recruitment in NSS herring is highly variable and poorly understood, and reduced population-level resilience by spatial contraction of spawning distribution has also been discussed for this species (Dragesund et al. 2008).

The changes in wintering areas, however, are likely linked to behavioral mechanisms. Herring remain in wintering areas in dense concentrations for ~5 mo without feeding. Also, the coastal wintering areas have varied considerably during the last decades. Huse et al. (2010) demonstrated that each shift in wintering areas has been associated with a new and strong year class entering the spawning stock. Huse et al. (2010) suggested that there is a cultural transfer of the use of wintering areas, which breaks down when the proportion of recruits is high relative to that of older herring, resulting in establishment of new wintering areas.

In the 1970s, the herring fisheries were strictly regulated, and <20 000 t were landed each year (Fig. 5). However, due to the spatial contraction of herring in coastal areas during spawning, feeding and wintering, the fishermen found herring on the coast all year round, occasionally at high densities. This resulted in strong disagreements between scientists and fishermen concerning the state of the herring stock and how much could be harvested (Dragesund et al. 2008). Until the late 1970s, the technical equipment and the efficiency of the herring fisheries had developed more rapidly than the stock assessment tools available for the scientists. However, in 1979, an abundance estimate for the spawning stock was produced, revealing that the stock was at a very low level, and the strict regulations continued (Dragesund et al. 2008).

The herring started recovering in the late 1980s. The stock is currently at 9 million t and is considered to be fully recovered, although a reduction in abundance has been observed in recent years (Fig. 5). Weak recruitment since 2004 and reduction of older, abundant cohorts due to fishing and natural mortality is causing the stock decline. However, the westward, oceanic feeding migrations have resumed, spawning distributions have expanded northward (Fig. 6E,F), and the wintering areas have shifted westward from the inner fjords to off the shelf. Thus, the herring appears to have been fully able to recolonize historically used areas and habitats.

CONSERVATION

Although species are adapted to the natural variability of the environment that they inhabit, the effects of fishing and climate on the erosion of population structure interact and are at times synergistic. For instance, fishing impacts the geographic extent of a population as well as the demographic structure (e.g. truncated age/size classes) and thereby weakens the remaining population's capacity to buffer the effects of unfavorable environmental conditions (Perry et al. 2010, Planque et al. 2010). Also, climate-induced spatial contractions or merging of exploited fish stocks can lead to increases in local fish densities and catchability, which in turn make stocks more vulnerable to overfishing (Atkinson et al. 1997, Rose et al. 2000). These effects are very dependent on the life history adaptations that species or stocks have evolved to deal with environmental variability, predation pressure and ontogenetic division of prey resources. The link between climate- and fishing-induced changes of population structure and the ensuing effects on species abundance calls for a more integrated approach to the study of fish spatial distributions, one that takes into account human and environmental drivers. It also calls for a more comprehensive management approach, in which the spatial structure of a population is monitored and catches are numerically and also geographically accounted for (Link et al. 2011).

It is interesting that there is the fractal view of lumpers and splitters in both species differentiation and in population structure. We realize that our own classification of the 3 case studies to a specific population type (Table 1) may draw counter-opinions. We wish there was a way to unequivocally distinguish the demographic and genetic structure of populations, but the results to date only point to the controversial nature of these classifications. However, we contend that this controversy is counterproductive and hampers the establishment of management frameworks that integrate population structures. Genetic techniques may provide blurred pictures of the degree of separation between different subgroups in a population. Similarly, non-genetic techniques, such as otolith microchemistry, may give conflicting results (Secor 2010). Does that mean that populations are not structured or that some level of structure should not be considered in management?

Our review was motivated by 2 simple questions, namely (1) Is a change of population spatial structure a mere manifestation of removing individuals from a population, or is it also a prelude to further changes in population abundance? and (2) Is the spatial structure of fish populations that are commercially harvested an attribute that is worth monitoring and preserving? Throughout our review, we have shown how populations can be spatially structured, regardless of their genetic and demographic connections. It is also important to note that in the 3 case studies examined here, the landings peaked several years after a declining trend of abundance commenced (Figs. 3 & 5) (Bailey 2011, DFO 2011). Of course, it is simple to unveil these temporal discrepancies between harvest and abundance trends when many years have gone by and population abundance estimates have improved with retrospection. Similar downward population trends may have not been apparent at the time the trend started. However, what we have learned from hindsight highlights the fact that biomass and recruitment estimates alone are not good predictors of future population trends and underscores the importance of supplementing management with additional spatial indices of population status. We have also reviewed cases in which the erosion of this spatial structure is a prelude to further changes of population abundance for reasons that go beyond, and are more long lasting, than the removal of individuals from a location. Therefore, the monitoring and preservation of a population's spatial structure should be an explicit management goal. The upside is that in marine populations, spatial structures are easier to monitor and characterize (e.g. Woillez et al. 2007) than demographic and genetic structures. Many commercially exploited stocks are surveyed often multiple times in a year and over different life history stages. There is already a large body of available information that can be integrated in management scenarios and that is less controversial than other metrics of population structures.

Acknowledgements. We thank the Research Council of Norway for funding the workshop Tropharct through the MICO project (number 186310, Match/Mismatch and Ecosystem). L.C. and M.H. acknowledge support from the National Science Foundation – Research Coordination Network grant number 1140207. M.S.M. acknowledges support from grant number 20049/130 of the Norwegian Research Council's 'Adaptive management of living marine resources by integrating different data sources and key ecological processes (ADMAR)' program. We are indebted to J. Hutchings and P. Spencer, who reviewed earlier versions of this article, and to 4 anonymous reviewers, who provided insightful comments. Finally, we thank C. Vestfals, who is the author of Fig. 2.

LITERATURE CITED

Atkinson DB, Rose GA, Murphy EF, Bishop CA (1997) Distribution changes and abundance of northern cod (*Gadus morhua*), 1981–1993. Can J Fish Aquat Sci 54:132–138

➤ Bacheler NM, Bailey KM, Ciannelli L, Bartolino V, Chan KS (2009) Density-dependent, landscape, and climate effects on spawning distribution of walleye pollock *Theragra chalcogramma.* Mar Ecol Prog Ser 391:1–12

➤ Bacheler NM, Ciannelli L, Bailey KM, Duffy-Anderson JT (2010) Spatial and temporal patterns of walleye pollock spawning in the eastern Bering Sea inferred from egg and larval distributions. Fish Oceanogr 19:107–120

Bailey KM (2011) An empty donut hole: the great collapse of a North American fishery. Ecol Soc 16:28

➤ Bailey KM, Quinn T, Grant WS, Bentzen P (1999) Population structure and dynamics of walleye pollock, *Theragra chalcogramma.* Adv Mar Biol 37:179–255

➤ Bailey KM, Abookire A, Duffy-Anderson JT (2008) Ocean transport paths for the early life stages of offshore-spawning flatfishes: a case study in the Gulf of Alaska. Fish Fish 9:44–66

Bartolino V, Ciannelli L, Spencer P, Wildebauer T, Chan KS (2012) Scale-dependent detection of the effects of harvesting a marine fish population. Mar Ecol Prog Ser 444: 251–272

Berryman A (2002) Populations: a central concept for ecology? Oikos 97:439–442

Betts MG, Forbes GJ, Diamond AW, Taylor PD (2006) Independent effects of fragmentation on forest songbirds: an organism-based approach. Ecol Appl 16:1076–1089

Borregaard MK, Rahbek C (2010) Causality of the relationship between geographic distribution and species abundance. Q Rev Biol 85:3–25

Brander K (2010) Impacts of climate change on fisheries. J Mar Syst 79:389–402

Brander K, Botsford L, Ciannelli L, Fogarty M and others (2010) Human impacts on marine ecosystems. In: Barange M, Field JG, Harris RP, Hofmann EE, Perry IR, Werner F (eds) Marine ecosystems and global change. Oxford University Press, New York, NY, p 41–72

Brown JH, Mehlman DW, Stevens GC (1995) Spatial variation in abundance. Ecology 76:2028–2043

Cadrin SX, Secor DH (2009) Accounting for spatial population structure in stock assessment: past, present, and future. In: Beamish RJ, Rothschild BJ (eds) The future of fisheries science in North America. Springer, Dordrecht, p 405–426

Canino MF, O'Reilly PT, Hauser L, Bentzen P (2005) Genetic differentiation in walleye pollock (*Theragra chalcogramma*) in response to selection at the pantophysin (*Pan*I) locus. Can J Fish Aquat Sci 62:2519–2529

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Zeller D, Pauly D (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. Glob Change Biol 16:24–35

Ciannelli L, Dingsør G, Bogstad B, Ottersen G and others (2007a) Spatial anatomy of species survival rates: effects of predation and climate-driven environmental variability. Ecology 88:635–646

Ciannelli L, Bailey K, Chan KS, Stenseth NC (2007b) Phenological and geographical patterns of walleye pollock spawning in the Gulf of Alaska. Can J Fish Aquat Sci 64:713–722

Ciannelli L, Fauchald P, Chan KS, Agostini VN, Dingsør GE (2008) Spatial fisheries ecology: recent progress and future prospects. J Mar Syst 71:223–236

Ciannelli L, Knutsen H, Moland E, Espeland SH and others (2010) Small-scale genetic structure in a marine population in relation to water circulation and egg characteristics. Ecology 91:2918–2930

Ciannelli L, Bartolino V, Chan KS (2012) Nonadditive and nonstationary properties in the spatial distribution of a large marine fish population. Proc R Soc Lond B 279: 3635–3642

Corten A (2001) The role of 'conservatism' in herring migrations. Rev Fish Biol Fish 11:339–361

Cury P (1994) Obstinate nature: an ecology of individuals. Thoughts on reproductive behavior and biodiversity. Can J Fish Aquat Sci 51:1664–1673

DFO (Canadian Department of Fisheries and Oceans) (2011) Recovery potential assessment for the Laurentian South designatable unit of Atlantic cod (*Gadus morhua*). DFO Can Sci Advis Sec Sci Advis Rep 2011/028, DFO, Ottawa

Dragesund O, Østvedt OJ, Toresen R (2008) Norwegian spring spawning herring: history of fisheries, biology and stock assessment. In: Nakken O (ed) Norwegian spring spawning herring and northeast arctic cod. Tapir Academic Press, Trondheim, p 41–82

Duffy-Anderson J, Blood DM, Cheng W, Ciannelli L and others (2013) Combining field observations and modeling approaches to examine Greenland halibut (*Reinhardtius hippoglossoides*) early life ecology in the southeastern Bering Sea. J Sea Res 75:96–109

Dunning JB, Danielson BJ, Pulliam RH (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169–175

Eby LA, Crowder LB, McClellan CM, Peterson CH, Powers MJ (2005) Habitat degradation from intermittent hypoxia: impacts on demersal fishes. Mar Ecol Prog Ser 291:249–262

Fabry VJ, Seibel BA, Feely RA, Orr JC (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. ICES J Mar Sci 65:414–432

Fauchald P, Erikstad KE, Skarsfjord H (2000) Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology 81: 773–783

Fauchald P, Mauritzen M, Gjosaeter H (2006) Density-dependent migratory waves in the marine pelagic ecosystem. Ecology 87:2915–2924

Fisher JAD, Frank KT (2004) Abundance-distribution relationships and conservation of exploited marine fishes. Mar Ecol Prog Ser 279:201–213

Frank KT, Drinkwater KF, Page FH (1994) Possible causes of recent trends and fluctuations in Scotian Shelf/Gulf of Maine cod stocks. ICES Mar Sci Symp 198:110–120

Frank KT, Petrie B, Shackell NL (2007) The ups and downs of trophic control in continental shelf ecosystems. Trends Ecol Evol 22:236–242

Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distributions in birds. I. Theoretical development. Acta Biotheor 19:16–36

Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH (2000) Abundance–occupancy relationships. J Appl Ecol 37(Suppl 1):39–59

Gonzalez A, Lawton JH, Gilbert FS, Blackburn TM, Evans-Freke I (1998) Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281: 2045–2047

Goodwin BJ, Fahrig L (1998) Spatial scaling and animal population dynamics. In: Peterson DL, Parker VT (eds) Ecological scale: theory and applications. Columbia University Press New York, NY, p 193–206

Hamre J (1990) Life history and exploitation of the Norwegian spring spawning herring. Section I. In: Monstad T (ed) Biology and fisheries of the Norwegian spring-spawning herring and blue whiting in the northeast Atlantic. Proc 4th Soviet-Norwegian Symp, Bergen, 12–16 June 1989. Institute of Marine Research, Bergen, p 5–39

Hauser L, Carvalho GR (2008) Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts. Fish Fish 9:333–362

Heath MR, Kunzlik PA, Gallego A, Holmes SJ, Wright PJ (2008) A model of meta-population dynamics for North Sea and West of Scotland cod—the dynamic consequences of natal fidelity. Fish Res 93:92–116

Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. Proc Natl Acad

Sci USA 100:6564–6568

Hinckley S (1987) The reproductive biology of walleye pollock, *Theragra chalcogramma*, in the Bering Sea, with reference to spawning stock structure. Fish Bull 85: 481–498

Holst JC, Røttingen I, Melle W (2004) The herring. In: Skjoldal HR (ed) The Norwegian Sea ecosystem. Tapir Academic Press, Trondheim, p 203–226

Hsieh CH, Reiss SC, Hewitt RP, Sugihara G (2008) Spatial analysis shows fishing enhances the climatic sensitivity of marine fishes. Can J Fish Aquat Sci 65:947–961

Hsieh CH, Yamauchi A, Nakazawa T, Wang WF (2010) Fishing effects on age and spatial structures undermine population stability of fishes. Aquat Sci 72:165–178

Hunsicker ME, Ciannelli L, Bailey KM, Zador S (2010) Processes driving differences in major food web linkages of the Gulf of Alaska and eastern Bering Sea ecosystems. ICES Annu Sci Conf 2010, Nantes

Huse G, Fernö A, Holst JC (2010) Establishment of new wintering areas in herring co-occurs with peaks in the 'first time/repeat spawner' ratio. Mar Ecol Prog Ser 409: 189–198

Hutchings JA (2000) Collapse and recovery of marine fishes. Nature 406:882–885

Hutchings JA, Swain DP, Rowe S, Eddinton JD, Puvanendran V, Brown JA (2007) Genetic variations in life-history reaction norms in a marine fish. Proc Biol Sci 274:1 693–1699

Ianelli JN, Barbeaux S, Honkalehto T, Kotwicki S, Aydin K, Williamson N (2011) Assessment of the walleye pollock stock in the eastern Bering Sea. Alaska Fisheries Science Center, National Marine Fisheries Services Seattle, WA

ICES (2011) Report of the Working Group on Widely Distributed Stocks (WGWIDE). ICES CM 2011/ACOM:15. ICES, Copenhagen

Iles TD, Sinclair M (1982) Atlantic herring: stock discreteness and abundance. Science 215:627–633

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. Nature 402: 802–804

Kelly JE, Frank KT, Leggett WC (2009) Degraded recruitment synchrony in Northwest Atlantic cod stocks. Mar Ecol Prog Ser 393:131–146

Kempf A, Floeter J, Temming A (2008) Predator–prey overlap induced Holling type III functional response in the North Sea fish assemblage. Mar Ecol Prog Ser 367: 295–308

Knutsen H, Olse EM, Jorde PE, Espeland SH, Andre C, Stenseth NC (2011) Are low but statistically significant levels of genetic differentiation in marine fishes 'biologically meaningful'? A case study of coastal Atlantic cod. Mol Ecol 20:768–783

Kokko H, Lopez-Sepulcre A (2006) From individual dispersal to species ranges: perspectives for a changing world. Science 313:789–791

Köster FW, Möllmann C, Hinrichsen HH, Tomkiewicz J and others (2005) Baltic cod recruitment—the impact of climate and species interaction. ICES J Mar Sci 62: 1408–1425

Lawton JH (1993) Range, population abundance and conservation. Trends Ecol Evol 8:409–413

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Link JS, Nye JA, Hare JA (2011) Guidelines for incorporating fish distribution shifts into a fisheries management context. Fish Fish 12:461–469

Litzow MA, Ciannelli L (2007) Oscillating trophic control induces community reorganization in a marine ecosystem. Ecol Lett 10:1124–1134

MacCall AD (1990) Dynamic geography of marine fish populations. University of Washington Press, Seattle, WA

McFarlane GA, Smith PE, Baumgartner TR, Hunter JR (2002) Climate variability and Pacific sardine populations and fisheries. Am Fish Soc Symp 32:195–214

McQuinn IH (1997) Metapopulations and the Atlantic herring. Rev Fish Biol Fish 7:297–329

Miller TJ, Herra T, Leggett WC (1995) An individual-based analysis of the variability of eggs and their newly hatched larvae of Atlantic cod (*Gadus morhua*) on the Scotian Shelf. Can J Fish Aquat Sci 52:1083–1093

Mueter FJ, Litzow MA (2008) Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecol Appl 18:309–320

Murawski SA (2010) Rebuilding depleted fish stocks: the good, the bad, and, mostly, the ugly. ICES J Mar Sci 67: 1830–1840

Nakken O (2008) Introduction. In: Nakken O (ed) Norwegian spring spawning herring and northeast arctic cod. Tapir Academic Press, Trondheim, p 9–16

Nøttestad L, Giske J, Holst JC, Huse G (1999) A length-based hypothesis for feeding migrations in pelagic fish. Can J Fish Aquat Sci 56:26–34

Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Mar Ecol Prog Ser 393:111–129

O'Reilly PT, Canino MF, Bailey KM, Bentzen P (2004) Inverse relationship between F_{ST} and microsatellite polymorphism in the marine fish, walleye pollock (*Theragra chalcogramma*): implications for resolving weak population structure. Mol Ecol 13:1799–1814

Olsen EM, Knutsen H, Gjøsæter J, Jorde PE, Knutsen JA, Stenseth NC (2008) Small-scale biocomplexity in coastal Atlantic cod supporting a Darwinian perspective on fisheries management. Evol Appl 1:524–533

Palumbi S (2003) Population genetics, demographic connectivity, and the design of marine reserves. Ecol Appl 13: 146–158

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915

Perry RI, Cury P, Brander K, Jennings S, Mollmann C, Planque B (2010) Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. J Mar Syst 79:427–435

Planque B, Fromentin JM, Cury P, Drinkwater KF, Jennings S, Perry RI, Kifani S (2010) How does fishing alter marine populations and ecosystems sensitivity to climate? J Mar Syst 79:403–417

Planque B, Loots C, Petitgas P, Lindstrom U, Vaz S (2011) Understanding what controls the spatial distribution of fish populations using a multi-model approach. Fish Oceanogr 20:1–17

Pulliam HR (1988) Sources, sinks, and population regulation. Am Nat 132:652–661

Reiss H, Hoarau G, Dickey-Collas M, Wolff WJ (2009) Genetic population structure of marine fish: mismatch between biological and fisheries management units. Fish Fish 10:361–395

Rose GA, deYoung B, Kulka DW, Goddard SV, Fletcher GL

(2000) Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Can J Fish Aquat Sci 57:644–663

Rowe S, Hutchings JA (2003) Mating systems and the conservation of commercially exploited marine fish. Trends Ecol Evol 18:567–572

Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS (2010) Population diversity and the portfolio effect in an exploited species. Nature 465: 609–612

Secor DH (2010) Is otolith science transformative? New views on fish migration. Environ Biol Fishes 89:209–220

Shackell NL, Frank KT, Brickman DW (2005) Range contraction may not always predict core areas: an example from marine fish. Ecol Appl 15:1440–1449

Shepherd TD, Litvak MK (2004) Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: considerations and cautions. Fish Fish 5:141–152

Slotte A, Fiksen Ø (2000) State-dependent spawning migration in Norwegian spring-spawning herring. J Fish Biol 56:138–162

Smedbol RK, McPherson A, Hansen MM, Kenchington E (2002) Myths and moderation in marine 'metapopulations'. Fish Fish 3:20–35

Swain DP (1999) Changes in the distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence—effects of environmental change or change in environmental preferences? Fish Oceanogr 8:1–17

Thomas CD, Kunin WE (1999) The spatial structure of populations. J Anim Ecol 68:647–657

Toresen R, Østvedt J (2000) Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus, Clupeidae*) throughout the 20th century and the influence of climatic fluctuations. Fish Fish 1:231–256

Voss R, Hinrichsen HH, Stepputtis D, Bernreuther M, Huwer B, Neumann V, Schmidt JO (2011) Egg mortality: predation and hydrography in the central Baltic. ICES J Mar Sci 68:1379–1390

Walters CJ, Martell SJD (2004) Fisheries ecology and management. Princeton University Press, Princeton, NJ

Watanabe Y, Zenitani H, Kimura R (1997) Variations in spawning ground area and egg density of the Japanese sardine in Pacific coastal and oceanic waters. Fish Oceanogr 6:35–40

Woillez M, Poulard JC, Rivoirad J, Petitgas P, Bez N (2007) Indices for capturing spatial patterns and their evolution in time, with application to the European hake (*Merluccius productus*) in the Bay of Biscay. ICES J Mar Sci 64:537–550

Zador S, Aydin K, Cope J (2011) Fine-scale analysis of arrowtooth flounder *Atherestes stomias* catch rates reveals spatial trends in abundance. Mar Ecol Prog Ser 438:229–239

Submitted: April 27, 2012; Accepted: September 21, 2012

Proofs received from author(s): January 21, 2013

Vol. 480: 245–261, 2013
doi: 10.3354/meps10246

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 22

Contribution to the Theme Section 'Harvested fish stocks in a changing environment'

Predicting fish recruitment from juvenile abundance and environmental indices

Leif Christian Stige[1,*], Mary E. Hunsicker[2], Kevin M. Bailey[3], Natalia A. Yaragina[4], George L. Hunt Jr[5]

[1]Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, Oslo 0316, Norway
[2]College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, Oregon 97331, USA
[3]Alaska Fisheries Science Center, Seattle, Washington 98115, USA
[4]Polar Research Institute of Marine Fisheries and Oceanography, Murmansk 183038, Russia
[5]School of Aquatic and Fishery Science, University of Washington, Seattle, Washington 98195, USA

ABSTRACT: Prediction of year-class strength is a critical challenge for fisheries managers. Theoretically, predictions of recruitment should be better when they are based on estimates of cohort size taken close to the age of recruitment and may improve if the effects of environmental factors that influence pre-recruit mortality are accounted for. In practice, measurement error and difficulties in establishing robust recruitment–environment relationships complicate the picture. For 5 fish stocks of 4 species in 3 ecosystems, we examined the usefulness of indices of juvenile abundance relative to larval abundance for predicting recruitment. Further, we examined whether the use of environmental covariates improved predictions. For 2 of 4 stocks with sufficient data (1 stock did not have larval data), juvenile abundance was a better predictor of recruitment compared to larval indices. For the 2 other stocks, we found that juvenile indices were not superior to larval indices, possibly because of error in the measurement of juvenile abundance. In all 5 of these stocks, regression analysis showed that inclusion of environmental correlates contributed significantly to explaining recruitment variation compared to models based on juvenile indices alone. Further, cross validation showed that forecasts of future recruitment were either improved or qualitatively unchanged by including environmental correlates. This was despite apparent nonstationarity in the recruitment–environment relationships; most of the environmental variables and pre-recruit abundance indices were significantly correlated with recruitment for only parts of the studied period. Such complex responses to environmental changes are difficult to anticipate, yet the environmental information should not be ignored altogether.

KEY WORDS: Fish recruitment · Environmental covariates · Predicting recruitment · Gulf of Alaska walleye pollock · Bering Sea walleye pollock · Barents Sea capelin · Northeast Arctic cod · Northeast Arctic haddock

INTRODUCTION

The recruitment to many fish stocks is highly variable because of large interannual fluctuations in survival during early life stages (Hjort 1914, Cushing 1995, Chambers & Trippel 1997). To understand the causes of and, if possible, predict these fluctuations, the abundances of spawners, eggs, larvae, and juveniles of many stocks are monitored regularly, along with various biotic and abiotic environmental factors potentially linked to survival. If the recruitment strength, that is, the abundance of a cohort as it enters into the fishery, can be accurately predicted ≥1 yr in advance, the managers of the stocks can better evaluate the consequences of alternative management actions (e.g. Logerwell et al. 2003, Bailey et al. 2005, MacKenzie et al. 2008).

---

*Email: l.c.stige@bio.uio.no

Assuming that all measures of year-class strength are equally accurate, the closer the measurement is taken to the time of recruitment, the more likely it will provide an accurate index of recruitment (Bradford 1992). The vulnerability of egg and larval stages to environmental perturbations may further diminish their value as indices for predicting recruitment (Bailey et al. 2005, Houde 2008). For example, these stages may be particularly vulnerable to adverse temperatures, predation, and mismatch with prey because they lack sufficient behavioral mechanisms to respond to poor environmental conditions (e.g. Sinclair & Tremblay 1984, Houde 1994, Blood 2002, Beaugrand et al. 2003, Fiksen et al. 2007). Juvenile fish may be more resilient to environmental perturbation. They are larger and have more energy reserves than eggs or larvae, and they can search effectively for more favorable conditions (Sogard 1997). One may therefore expect that indices of juvenile abundance provide considerably better predictions of the eventual recruitment to a fishery than indices of eggs or larvae, unless egg or larval abundances are measured with much higher accuracy. It should be noted that large differences in measurement error are indeed possible, as very different survey types and gears are needed to survey different life-history stages, and each of these methods have different shortcomings, types of error, and other problems (Heath 1992, Godø 1998).

For any given pre-recruit life stage, it would also seem reasonable that the inclusion of environmental variables, such as water temperature and indices of predator or competitor abundance, should increase the ability to predict the survival of that life stage to recruitment. Understanding the effects of climate on fisheries has been a central research topic since the foundation of the International Council for the Exploration of the Sea (ICES) in 1902 (e.g. Cushing 1982, Beamish 1993, Alheit & Hagen 1997, Borja et al. 1998, Rothschild 2000, Drinkwater et al. 2005, Hollowed et al. 2011). In recent years, there has been an effort to develop models incorporating climate and other environmental indices for the prediction of recruitment (e.g. Chen & Ware 1999, Borja et al. 2008, MacKenzie et al. 2008, Andonegi et al. 2011, Mueter et al. 2011). For example, Zabel et al. (2011), working with bocaccio *Sebastes paucispinis* in the California Current system, found that a recruitment model, which included juvenile abundance and climate and the interaction of these factors, explained 68% of the recruitment variation, whereas a model with population density alone explained only 1.4% of the recruitment variance. Using cross validation (i.e. separating the data set into 'training' and 'testing' data sets and using the training data set to predict the response in the testing data set), Zabel et al. (2011) found that the interaction model was also better at predicting 'new' observations not used when estimating the parameters in the model. In the Barents Sea, a number of recruitment models have been developed for cod *Gadus morhua* that have included environmental variables, such as the yearly average temperature along the Kola line (0 to 200 m) and predator and prey biomasses (e.g. Hjermann et al. 2007, Dingsør et al. 2010). To assess accurately the stock size and advise corresponding catch limits for the management of this stock, analogous recruitment models are used to predict the recruitment of 3 yr olds to the fishery in the coming 3 yr (ICES 2010). In the management of most other stocks, environmental information is not routinely used (De Oliveira & Butterworth 2005), which can be partly explained by the difficulty in identifying recruitment–environment correlations that remain robust over time (Myers 1998).

For the present paper, we tested the hypothesis that indices of juvenile abundance are better predictors of recruitment than indices of earlier life stages for 3 fish species in the Barents Sea, 1 in the Gulf of Alaska, and 1 in the eastern Bering Sea. We also examined whether inclusion of environmental covariates of juvenile survival (e.g. predator and competitor abundance, prey availability, water temperature, and climate patterns) in the models of juvenile survival significantly improved both hindcasts and predictions of recruitment. We expected that predictions for 'new' observations are not necessarily better if the recruitment–environment correlations are spurious or nonstationary. To detect nonstationarity, we investigated whether the correlations between recruitment on the one hand and the environmental indices and the early life stage abundance indices on the other were stable over time. To assess the predictive value of the environmental information, predictive models with and without environmental variables were developed for each year based only on data collected prior to the year predicted. We then examined how closely these 1 yr prior predictions matched the observations. By testing the same hypotheses for 5 different stocks, we aimed to disclose general patterns relating to the predictability of fish recruitment from pre-recruit abundance and environmental indices—under the influence of measurement errors and uncertain or changing relationships between these indices and recruitment.

MATERIALS AND METHODS

Data on fish abundance

Barents Sea cod, haddock, and capelin

To examine the relationships between indices at different life stages and recruitment of 3 fish stocks in the Barents Sea, we obtained data from several sources (Table 1). For northeast Arctic (NEA) cod *Gadus morhua* and NEA haddock *Melanogrammus aeglefinus*, we considered the following indices: spawning stock biomass (SSB$_t$), egg abundance in April to May (E_t), larval abundance in April to July (L_t), Age 0 abundance in August to September ($N0_t$), Age 1 and Age 2 abundances in January to March ($N1_t$ and $N2_t$), and recruitment at Age 3 year (R_t). For the Barents Sea (BS) capelin *Mallotus villosus*, we considered spawning stock biomass (SSB$_t$), larval abundance in April to July (L_t), Age 0 abundance in August and September ($N0_t$), and recruitment in September to October at Age 1 year (R_t). Sources and manipulation of abundance data for the Barents Sea stocks are described in Appendix 1.

Table 1. Description and sources of data used to examine the relationship between indices at different life stages and recruitment of 5 fish stocks in the Barents Sea (BS), the Gulf of Alaska (GOA), and the eastern Bering Sea (EBS). ATF: arrowtooth flounder; NEA: northeast Arctic; SST: sea surface temperature; SSB: spawning stock biomass

Data type	Years	Source	Reference
BS NEA cod and haddock			
Egg	1959–1990	Russian (PINRO) ichthyoplankton surveys	Mukhina (1992), Mukhina et al. (2003)
Larvae	1959–1990	Russian (PINRO) ichthyoplankton surveys	Mukhina (1992), Mukhina et al. (2003)
Age 0	1966–2009	International 0-group surveys	ICES (2007), (2010), their Table 1.2
Age 1 and Age 2	1981–2008	Norwegian acoustic surveys	ICES (2010), their Tables A2 & B3
Recruitment (Age 3)	1962–2009	VPA stock assessment	ICES (2010), their Tables 3.25 & 4.18
SSB	1959–2008	VPA stock assessment	ICES (2010), their Tables 3.25 & 4.18
Predator (Age 3–6 NEA cod)	1946–2010	VPA stock assessment	ICES (2010), their Table 3.22
BS capelin			
Larvae	1959–2009; except 2007, 2008	Combined from Russian (PINRO) ichthyoplankton surveys and Norwegian surveys	Mukhina (1992), Mukhina et al. (2003), ICES (2010), their Table 9.4
Age 0	1965–2009	International 0-group surveys	ICES (2007), (2010), their Table 1.2
Recruitment (Age 1)	1973–2010	September–October acoustic surveys	ICES (2010), their Table 9.6
SSB	1959–2009	September–October acoustic surveys	ICES (2010), their Table 9.6
Predator (Age 1–2 herring)	1973–2009	VPA stock assessment	ICES (2010), their Table 9.6
Mean December to March temperature; 0–200 m at Kola	1921–2009	PINRO	Tereshchenko (1996), www.pinro.ru
GOA pollock			
Larvae	1979–2008; except 1980, 1984	NOAA Fisheries Echo Integration trawl survey	Bailey (2000), Zhang et al. (2010)
Age 1 and Age 2	1981–2008; except 1982, 1987, 1999	NOAA Fisheries acoustic survey	Dorn et al. (2010), their Table 1.10
Recruitment (Age 4)	1977–2009	NOAA Fisheries stock assessment	Dorn et al. (2010), their Table 1.17
SSB	1977–2009	NOAA Fisheries stock assessment	Dorn et al. (2010), their Table 1.18
Predator (Age 3+ ATF)	1977–2009	NOAA Fisheries stock assessment	Turnock & Wilderbuer (2009), their Table 7.9
Mean April to June SST	1977–2009	NOAA Climate Diagnostics Center	www.cdc.noaa.gov/cdc/reanalysis/
EBS pollock			
Age 1 and Age 2	1982–2010	NOAA Fisheries groundfish trawl survey	Ianelli et al. (2010), their Table 1.12
Recruitment (Age 4)	1976–2009	NOAA Fisheries stock assessment	Ianelli et al. (2010), their Table 1.21
SSB	1976–2010	NOAA Fisheries stock assessment	Ianelli et al. (2010), their Table 1.23
Predator (Age 1+ ATF)	1977–2010	NOAA Fisheries stock assessment	Wilderbuer et al. (2010), their Table 6.10
Predator (Age 3+ pollock)	1977–2010	NOAA Fisheries stock assessment	Ianelli et al. (2010), their Table 1.23
Predator (Age 0+ Pacific cod)	1977–2010	NOAA Fisheries stock assessment	Thompson et al. (2010), their Table 2.25a
Predator (Age 3+ flathead sole)	1977–2010	NOAA Fisheries stock assessment	Stockhausen et al. (2010), their Table 8.15
Mean May SST	1948–2010	NOAA Bering Climate	www.beringclimate.noaa.gov
Ice cover index	1979–2008	NOAA Bering Climate	www.beringclimate.noaa.gov

Gulf of Alaska and eastern Bering Sea walleye pollock

We examined the relationship between indices at different life stages and recruitment of walleye pollock *Theragra chalcogramma* in the Gulf of Alaska (GOA) and Eastern Bering Sea (EBS). We defined recruits (R_t) as Age 4 pollock because that is the age at which pollock start to recruit to the fishery in most years. For the GOA, we used abundance estimates available for pollock larvae (L_t), juveniles ($N1_t$: Age 1 and $N2_t$: Age 2), spawning stock biomass (SSB_t), and recruits (Table 1). Sources, manipulation, and assumptions concerning pollock larvae data are described by Bailey (2000) and Zhang et al. (2010). For the EBS, we used indices of $N1_t$, $N2_t$, SSB_t, and R_t (Table 1). Pollock L_t indices are not available for the EBS.

Environmental correlates

We focused on temperature and predator abundance as the main environmental correlates (Table 1). Water temperatures (integrated water column or sea surface temperature [SST]) were used as the main oceanographic correlates because fish are ectothermic organisms, with temperature strongly influencing all life stages. Moreover, temperatures are the most frequently recorded environmental parameters with available long-term time series. Temperatures during the spawning season were used in the analyses, except for the Barents Sea stocks, where temperature for the winter following spawning correlated more strongly with recruitment. The environmental covariates considered for the different stocks are listed below (see Table 1 for data sources).

Barents Sea cod, haddock, and capelin

(1) $\mathrm{COD}_{3-6,t}$: ln(abundance) of cod aged 3 to 6 yr was used as an index of a key predator on juvenile cod and haddock (following e.g. Stige et al. 2010).

(2) $\mathrm{HER}_{1-2,t}$: ln(biomass) of Age 1 and 2 herring *Clupea harengus* was used as an index of a key predator/competitor of juvenile capelin (e.g. Stige et al. 2010).

(3) TEMP_t: For a climate index for all 3 stocks, we used the integrated water column temperature at 0 to 200 m depth at the Kola section (70.5 to 72.5° N, 33.5° E) in the south-central Barents Sea. Annual mean winter temperatures for 1921 to 2006 were computed from monthly averages of December (year t) through March (year $t+1$) temperatures. Kola temperature correlates positively to recruitment of all 3 species (e.g. Stige et al. 2010).

Gulf of Alaska walleye pollock

(1) ATF_t: ln(abundance) of arrowtooth flounder *Atheresthes stomias*, an index of potential predation. Arrowtooth flounder is the dominant groundfish species in the GOA, and it exerts a significant predation pressure on juvenile walleye pollock (Bailey 2000, Dorn et al. 2010). Only arrowtooth flounder was used as predation index in the GOA because of its overwhelming abundance there.

(2) SST_t: mean April to June SST, derived from average monthly temperatures interpolated across a longitude band in the GOA from 155.6° W to 157.5° W centered at latitude 56.2° N (data source: A. Macklin, Pacific Marine Environmental Laboratory, Seattle, WA, pers. comm., www.cdc.noaa.gov/cdc/reanalysis).

Eastern Bering Sea walleye pollock

(1) PRED_t: ln(total abundance) of adult walleye pollock (Age 3+), arrowtooth flounder (Age 1+), Pacific cod *Gadus macrocephalus* (Age 0+), and flathead sole *Hippoglossoides elassodon* (Age 3+) (an index of an aggregate of potential predators; Aydin et al. 2007).

(2) SST_t: mean May SST. A relationship between EBS pollock recruitment and SST was reported by Quinn & Niebauer (1995).

(3) ICE_t: sea ice cover index.

Modeling and statistical analyses

Correlation analysis

To determine the predictive value of abundance indices representative of different early life stages, we computed the correlations between the recruitment ($\ln(R_t)$) and each of the alternative indices ($\ln(\mathrm{SSB}_{t-a})$, $\ln(E_{t-a})$, $\ln(L_{t-a})$, $\ln(N0_{t-a})$, $\ln(N1_{t-a+1})$, $\ln(N2_{t-a+2})$, where a is the recruitment age).

To explore if and how the correlation between recruitment and early life-stage abundance or environmental indices varied over time, we computed correlations between interannual variability in recruitment and the different indices in 15 yr moving windows and displayed the results graphically. That is, we sliced the time-range into overlapping time-slots of 15 yr (years 1,…,15; years 2,…,16; … ; years (n − 14),…, n), computed the correlation for each time-slot, and plotted the resulting series of correlation coefficients against the mid-year of the time-slots.

Baseline and environmental recruitment models

To quantify the extent to which the incorporation of environmental indices improved recruitment prediction models, we focused on the survival from the juvenile stage to recruitment. For results to be comparable across stocks, we selected the earliest available post-larval index for each stock, that is, $N0_t$ for BS capelin, NEA cod, and NEA haddock and $N1_t$ for GOA and EBS walleye pollock. We considered ordinary least-squares linear regression models of the general form (here exemplified with the $N0_t$ juvenile index and a recruitment age of 3 yr, as for NEA cod):

$$\ln(R_t) = \alpha_0 + \alpha_1 \ln(N0_{t-3}) + \beta_1 \text{ENV1}_{t-3} + \beta_2 \text{ENV2}_{t-3} + \ldots + \varepsilon_t \qquad (1)$$

Here, $N0_t$ and R_t are abundance indices as defined earlier, ENV1_t, ENV2_t, … are environmental indices that might potentially influence recruitment (i.e. TEMP_{t-3} and $\text{COD}_{3-6,t-3}$ for NEA cod and NEA haddock; TEMP_{t-1} and $\text{HER}_{1-2,t-1}$ for BS capelin; SST_{t-4} and ATF_{t-4} for GOA walleye pollock; SST_{t-4}, ICE_{t-4}, and PRED_{t-4} for EBS walleye pollock), α_0, α_1, β_1, β_2,… are coefficients estimated from the data, and ε_t is an independent and normally-distributed error term with a mean of zero and a standard deviation of σ. The parameter α_0 is the intercept, $1 - \alpha_1$ quantifies the strength of density dependence, and β_1, β_2,… quantify the environmental effects (e.g. Stige et al. 2010). Note that for simplicity, we assumed a log-linear relationship between past and present cohort size (a 'Gompertz' model). To check for strong departures from this assumption (e.g. reduced R_t at high $N0_{t-3}$ because of overcompensatory density dependence), we inspected plots of model residuals vs. $\ln(N0_{t-3})$. As these residual diagnostics (not shown) failed to reveal any systematic departures, we deemed the model formulation sufficient for our purposes.

We compared 2 alternative formulations of the model above. In the 'baseline' model, no environmental covariates were included, so that the model simplified to the following relation:

$$\ln(R_t) = \alpha_0 + \alpha_1 \ln(N0_{t-3}) + \varepsilon_t \qquad (2)$$

In the 'environmental' model, the covariates were selected using an information theoretic approach: we started with a model with all terms included (Eq. 1), then removed (or added back) terms one by one until we found the model formulation that provided the lowest value of Akaike's information criterion corrected for small sample size (AIC_C; Hurvich & Tsai 1989).

Measuring hindcast strength

To measure the performance of the 2 alternative model formulations, the baseline and the environmental, we considered both hindcast and forecast strengths. The hindcast strength of a model refers to the degree to which the model can reproduce the observed pattern in the response retrospectively, whereas the forecast strength refers to its ability to make accurate predictions for observations not used when fitting the model. The contribution of the environmental information to the hindcast strength was measured by the difference in explained variance (R^2) between the baseline and the environmental models, fitted to the maximum year range for which both environmental and abundance information was available for each stock (from 23 to 41 yr; see Table 3). An F-test was used to test whether this difference in R^2 was statistically significant (as this test required nested models, the juvenile index was added back to the environmental models prior to testing if this variable had been removed during AIC_C selection). Further, the difference in AIC_C was used to indicate which model provided the best compromise between explanatory power and model parsimony. In principle, the difference in AIC_C should also indicate which model would make the best predictions for new observations (Burnham & Anderson 2002), but that is not necessarily correct if the model assumptions are not met, for example, if the relationship between the response and the predictors change over time (i.e. in the presence of nonstationarity).

Measuring forecast strength

To assess the forecast strengths of the baseline and environmental models, we computed 1 yr prior predictions using a sequential approach. We compared 2 approaches to forecast recruitment, one based on juvenile indices ($N0_t$ or $N1_t$) alone and one that considers environmental information. For each year from the 11th year onward for each stock, 2 regression models were constructed based on the data from the years collected up until that point. The first was the 'baseline' model (Eq. 2). The second was the 'environmental' model, with the terms selected based on AIC_C. From each model, the next year's recruitment was forecast, i.e. the 11th observation was predicted based on the first 10 yr with observations, the 12th observation based on first 11 yr, etc. The selection of terms to be included in the environmental model was repeated for each year. To reduce identifiability problems, the model selection was modified slightly from that described above (see 'Baseline and environmental recruitment models'), in that model selection started with a model with no predictors instead of one with all terms. This way, we obtained 2 time series of predictions, one from the baseline model and one from the environmental model, which were compared to the observations by calculating R^2 (calculated as the correlation coefficient squared), root-mean-square error (RMSE) and mean absolute prediction error (MAPE). Both RMSE and MAPE measure the 'typical' differences between predicted and observed recruitment, with RMSE being more influenced by the extreme values. As the RMSE values were not normally distributed, a bootstrap test was used to assess whether the difference in RMSE between the 2 modeling approaches was statistically significant from zero. We generated a bootstrap distribution of the test statistic by sampling with replacement the time series of predictions and observations 10 000 times, each sample being of the same size as the original series.

Only linear and additive effects of the environmental variables were considered in the statistical models used to forecast or hindcast recruitment. Quantification of nonlinear and nonadditive effects demands long time series and was not feasible with the forecasting approach used here, starting with only 10 yr of data on which to base the first prediction (see above). Moreover, we wanted to assess to what degree simple, linear approaches might still be helpful, even if the true effects of the environmental factors are likely to be considerably more complex than modeled. The programming environment R was used for all statistical analyses (R Development Core Team 2010). The R code and data used for the analyses are available in an electronic supplement that accompanies the online version of the paper (see Supplement at www.int-res.com/articles/suppl/m480p245_supp/).

RESULTS

Use of egg and larvae surveys vs. juvenile surveys

Our examination of the hypothesis that measurement at a late life stage should provide an equally good or better prediction of recruitment than measurements at earlier life stages revealed mixed results. Estimates of recruitment for some stocks showed an improved prediction when older ages of pre-recruits were used, while for some other stocks, indices of larval abundance were better predictors of recruitment than later life stages (Table 2, Figs. 1 & 2). Among the Barents Sea stocks, capelin supported our hypothesis: the Age 0 index was more strongly correlated with recruitment than was the larval index and spawning stock biomass (Table 2, Fig. 1). However, for NEA cod and NEA haddock, the larval index, counterintuitively, was more strongly correlated with recruitment than was the Age 0 index (Table 2, Fig. 1). When looking at the whole series of indices for NEA

Table 2. Correlations between recruitment and early life-stage abundance indices for 5 fish stocks (see Table 1 for abbreviations). Spawning stock biomass (SSB) quantifies egg production potential. The values are product–moment correlation coefficients, calculated for the same years for each row in the table (except the first row for GOA walleye pollock). Correlations for different year ranges are shown for some stocks because of limited overlap among time series (Table 1). $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

Stock	Correlation coefficient						n (years)	Year range
	SSB	Eggs	Larvae	Age 0	Age 1	Age 2		
NEA cod	0.42^{*}	0.61^{**}	0.61^{**}	0.47^{*}			25	1966–1990
	0.67^{***}			0.50^{**}	0.68^{***}	0.70^{***}	27	1980–2006
NEA haddock	0.33	0.17	0.63^{***}	0.46^{*}			25	1966–1990
	0.46^{*}			0.78^{***}	0.56^{**}	0.94^{***}	27	1980–2006
BS capelin	0.00		0.32	0.71^{***}			35	1973–2009
GOA walleye pollock	0.49^{**}		0.19		0.49^{*}	0.64^{***}	23–25	1979–2005[a]
	0.41		0.07		0.45	0.54^{*}	19	1982–2005[a]
EBS walleye pollock	–0.31				0.72^{***}	0.48^{*}	25	1981–2005

[a] Missing larval data for years 1980 and 1984 and missing Age 1 and Age 2 data for years 1982, 1987, and 1999. Only the correlations in the second row for GOA walleye pollock are calculated for exactly the same years

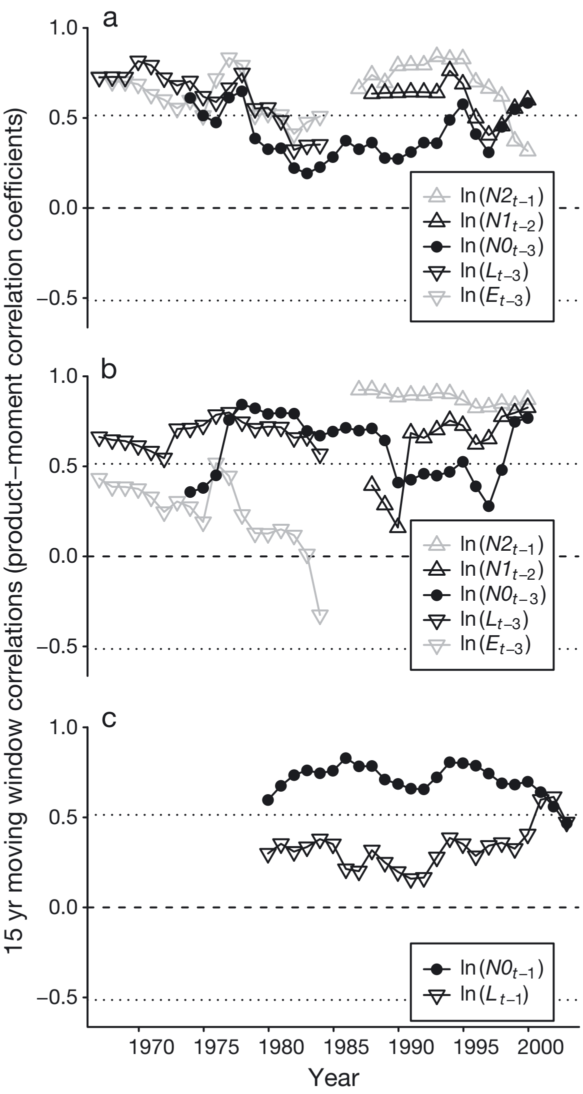

Fig. 1. Temporal change in the correlations between recruitment and early life-stage abundance indices for (a) NEA cod, (b) NEA haddock, and (c) BS capelin. Correlation coefficients (r) were calculated for 15 yr moving windows centered at the *x*-axis values. The symbols indicate with which early life-stage abundance index recruitment ($\ln(R_t)$) was correlated (*E*: eggs, *L*: larvae, *N0*: Age 0, *N1*: Age 1, *N2*: Age 2; see 'Materials and methods' for details). Broken lines: r = 0. Stippled lines: r = ±0.51. The 15 yr correlations larger than ±0.51 are statistically significant ($p < 0.05$, ignoring autocorrelation)

cod and haddock, from spawning stock biomass, to the egg, larval, and Age 0, 1, and 2 indices, there seems to be a tendency toward stronger correlations with recruitment for the later life stages, but with the correlations for the Age 0 (and for haddock, Age 1) indices being somewhat weaker than expected from such a pattern (Table 2) and with the ranking of the indices, in terms of their correlation with recruitment, varying with time (Fig. 1).

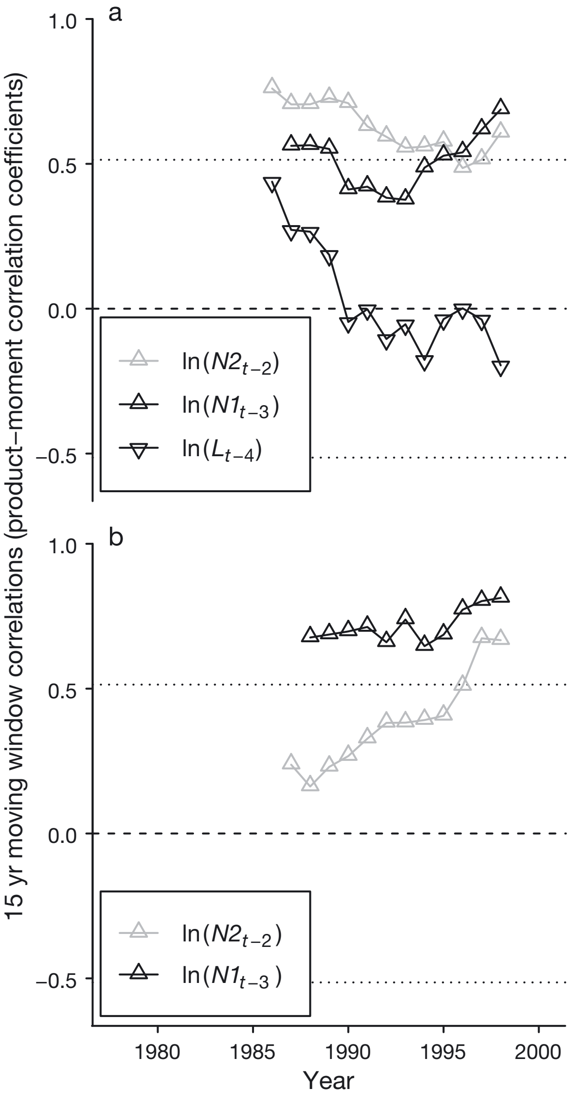

Fig. 2. Temporal change in correlations between walleye pollock recruitment and early life-stage abundance indices in the (a) Gulf of Alaska and (b) eastern Bering Sea. Correlation details as in Fig. 1

In the GOA, walleye pollock recruitment was most strongly correlated with the Age 2 index, followed by the Age 1 index, spawning stock biomass, and the larval index (Table 2). Fig. 2 supports this finding and also shows that there is some variation in the correlation of pollock life stage abundances and recruitment over time. Our GOA pollock results thus mostly agree with those of the BS capelin in that measurements of later life stages provided better predictions of recruitment (the exception being the lower correlation when going from spawning stock biomass to the larval index). In the EBS, we do not have larval pollock data. However, we found that the Age 1 index was strongly correlated with recruitment and, counter to that expected, more strongly correlated with recruitment than the Age 2 index (Table 2, Fig. 2).

Temporal stability of correlations between pre-recruit indices and recruitment

In all stocks examined, the correlations between indices of pre-recruit abundances and recruitment strength varied over time, with the relationship in some stocks reversing sign (Figs. 1 & 2). For example, for NEA cod in the Barents Sea, the Age 0 recruitment correlation was stronger toward the start and end of the period studied and non-significant in the intervening period (Fig. 1a). In comparison, the corresponding correlation for NEA haddock (Fig. 1b) showed 2 periods with non-significant correlations (around the early 1970s and 1990s), while that for BS capelin was statistically significant throughout the period studied (Fig. 1c).

For walleye pollock in the GOA and EBS, most correlations between pollock early life stages and recruitment varied considerably over time (Fig. 2). The one exception was the correlation between Age 1 pollock and pollock recruitment in the EBS (Fig. 2b). That relationship was strong (correlation coefficient > 0.5) for the duration of the time series. In the GOA, walleye pollock showed a positive correlation between larvae and recruitment in the 1980s, but the correlation weakened and became negative in the 1990s (Fig. 2a), a pattern similar to that found by Bailey (2000).

Inclusion of environmental correlates in hindcasts and forecasts

The results of applying linear regression models to explain recruitment variation using juvenile indices, with and without the addition of environmental correlates, are presented in Table 3. In all cases, both the R^2 and the AIC_C of the model were substantially improved with the addition of the environmental correlates. With these encouraging results, we then examined forecasts using a sequential approach to compute predictions for 'new' observations not used when fitting the model.

Barents Sea cod, haddock, and capelin

Environmental variables (TEMP for cod and haddock, HER_{1-2} for capelin) significantly improved hindcasts for all 3 Barents Sea stocks tested (Table 3). This was also true when the analysis was restricted to the range of years for which forecast strength was assessed (left-side columns in Table 4; here also COD_{3-6}, representing cannibalism, was selected for cod). The strength of the correlations between the environmental variables and recruitment varied with time, however (Fig. 3), potentially reducing the value of the environmental indices as predictors of recruitment.

In the Barents Sea, forecasts of 'new' observations from the 11th sampling year onward showed that forecasts were significantly improved by utilizing environmental information for the NEA haddock (right-side columns in Table 4, Fig. 4). For this stock, the inclusion of the environmental correlates resulted in higher correlations between predictions and observations (R^2 increasing from 0.44 to 0.64), 23% lower RMSE, and 20% lower MAPE (Table 4). For the NEA cod and the BS capelin, the inclusion of environmental correlates resulted in no practical difference in forecast strength (<4% change in RMSE and MAPE; Table 4, Fig. 4).

Table 3. Contribution of environmental variables to the hindcast strength of statistical models describing the interannual fluctuations in the recruitment to 5 fish stocks (see Table 1 for abbreviations). Baseline model: linear regression model with juvenile abundance index ($N0_t$ or $N1_t$) the only predictor. Environmental model: covariates (juvenile abundance and environmental indices) were selected using an information theoretic approach. Akaike's information criterion corrected for small sample size (AIC_C). ΔAIC_C: difference in AIC_C between the baseline and the environmental model; negative values mean stronger statistical support of the environmental model. By considering environmental information, from 12.6% (for BS Capelin) to 24.0% (for GOA walleye pollock), more of the variance in recruitment (R^2) could be explained. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$; for improvement in model fit by inclusion of environmental variables

Stock	n (years)	Baseline model	R^2	Environmental model	R^2	ΔAIC_c
NEA cod	41	$\ln(R_{t+3}) \sim \ln(N0_t)$	0.338	$\ln(R_{t+3}) \sim \ln(N0_t) + TEMP_t$	0.509	-9.9^{***}
NEA haddock	41	$\ln(R_{t+3}) \sim \ln(N0_t)$	0.395	$\ln(R_{t+3}) \sim TEMP_t$	0.620	-19.0^{***}
BS capelin	37	$\ln(R_{t+1}) \sim \ln(N0_t)$	0.494	$\ln(R_{t+1}) \sim \ln(N0_t) + HER_{1-2,t}$	0.616	-7.8^{**}
GOA walleye pollock	23	$\ln(R_{t+4}) \sim \ln(N1_t)$	0.235	$\ln(R_{t+4}) \sim \ln(N1_t) + ATF_t$	0.475	-6.0^{**}
EBS walleye pollock	25	$\ln(R_{t+4}) \sim \ln(N1_t)$	0.524	$\ln(R_{t+4}) \sim \ln(N1_t) + PRED_t + ICE_t$	0.671	-3.8^{*}

Table 4. The contribution of environmental variables to both hindcast and forecast strengths of recruitment models for 5 fish stocks (see Table 1 for abbreviations). Hindcast strength: results of linear regression models as in Table 3, but excluding the first 10 yr (note resulting smaller sample size compared to Table 3). The predictor variables selected in the environmental models differed from Table 3 in that $COD_{3-6,t}$ and $\ln(N_t)$ were selected as additional variables for NEA cod and haddock, respectively, while ATF_t and $PRED_t$ were not selected for GOA and EBS walleye pollock, respectively. Forecast strength: results of linear regression models as in Table 3, used to make 1 yr prior predictions from Year 11 onwards. Figs. 4 & 6 show which variables were selected for the environmental model for each year and stock. R^2: explained proportion of variance. RMSE: root-mean-square prediction error. MAPE: mean absolute prediction error. Lower RMSE and MAPE values are better. (*)$p < 0.10$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$; for improvement in model fit or predictions by inclusion of environmental variables (hindcast: *F*-test, forecast: bootstrap test)

Stock		Hindcast strength		Forecast strength		n (years)
		Baseline model	Environ. model	Baseline model	Environ. model	
NEA cod	R^2	0.33	0.63	0.17	0.35	31
	RMSE	0.50	0.37***	0.57	0.55	
	MAPE	0.41	0.27	0.45	0.44	
NEA haddock	R^2	0.60	0.73	0.44	0.64	31
	RMSE	0.81	0.67**	1.01	0.78*	
	MAPE	0.64	0.53	0.81	0.65	
BS capelin	R^2	0.46	0.52	0.39	0.38	27
	RMSE	1.02	0.96(*)	1.17	1.19	
	MAPE	0.81	0.79	0.92	0.97	
GOA walleye pollock	R^2	0.47	0.47	0.40	0.34	13
	RMSE	0.62	0.62	0.97	0.85	
	MAPE	0.51	0.51	0.84	0.75	
EBS walleye pollock	R^2	0.66	0.75	0.65	0.63	15
	RMSE	0.39	0.33(*)	0.45	0.44	
	MAPE	0.33	0.24	0.39	0.38	

Gulf of Alaska and eastern Bering Sea walleye pollock

In developing the best model for hindcasting and forecasting walleye pollock recruitment in the GOA, we examined the value of 2 environmental indices, a predation index that was Age 3+ arrowtooth flounder abundance, and an index of SST. The correlation between recruitment and the predation index varied considerably over time, while the correlation between recruitment and temperature started with a positive relationship that gradually weakened and became negative (Fig. 5a). The correlation between EBS pollock recruitment and all initial environmental indices also varied considerably over time (Fig. 5b). The sea ice cover index was positively correlated with recruitment, whereas the correlation between temperature and recruitment was at first positive and then became negative. The correlation between predation and recruitment was relatively strong and stable until the early 1990s and subsequently decreased (Fig. 5b).

In the GOA, the addition of environmental variables (specifically, ATF) improved the hindcasts of walleye pollock recruitment (Table 3), although not when tested on the more restricted year range, when no environmental variables were selected (Table 4). Forecasts of GOA walleye pollock recruitment with and without the inclusion of environmental correlates show that, by accounting for environmental information, our predictions of pollock recruitment were generally closer to the observed values for the last years of the present study. For the earlier years, the forecasts were identical because no environmental covariates were selected in the 'environmental' model (Fig. 6). This finding is supported by the (non-significantly) 12% lower RMSE and the 11% lower MAPE in the model with environmental predictors (Table 4).

Similar to that observed for species in the other ecosystems, environmental indices (specifically, PRED and ICE) improved the hindcasts of walleye pollock recruitment in the EBS (Table 3). This was also the case when tested on the more restricted year range (but here, only SST was selected among the environmental variables; Table 4). Forecasts of EBS walleye pollock recruitment using indices of Age 1 abundance, with or without environmental correlates, showed a strong match in both the pattern and the magnitude with observed recruitment values (Fig. 6, Table 4). As for the NEA cod and the BS capelin, the inclusion of environmental correlates resulted in no practical difference in forecast strength, neither to the better nor the worse (<4% change in RMSE and MAPE).

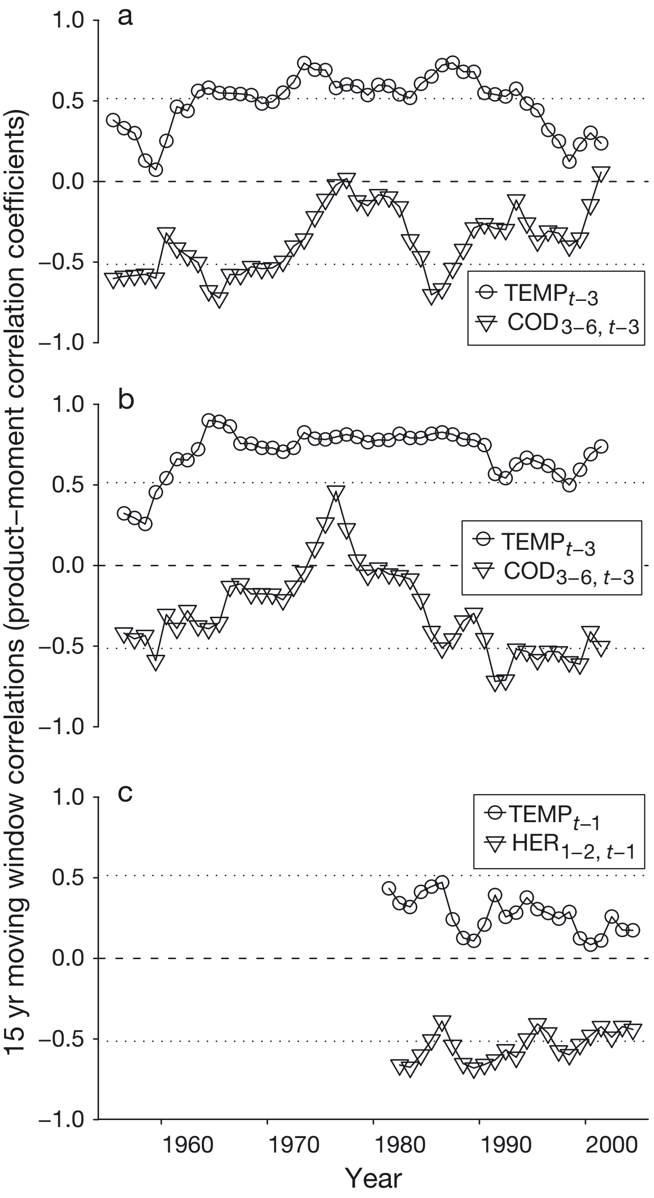

Fig. 3. Temporal change in correlations between recruitment and environmental indices for (a) NEA cod, (b) NEA haddock, and (c) BS capelin. Correlation details as in Fig. 1. TEMP: integrated water column temperature, COD$_{3-6}$: Age 3 to 6 cod abundance

DISCUSSION

Our results suggest that large and variable measurement errors and nonstationary dynamics are the rule rather than the exception in investigations of fish recruitment. Determining the predictive value of alternative pre-recruit abundance and environmental indices then remains an empirical question, which we have assessed using a comparative approach for 5 fish stocks.

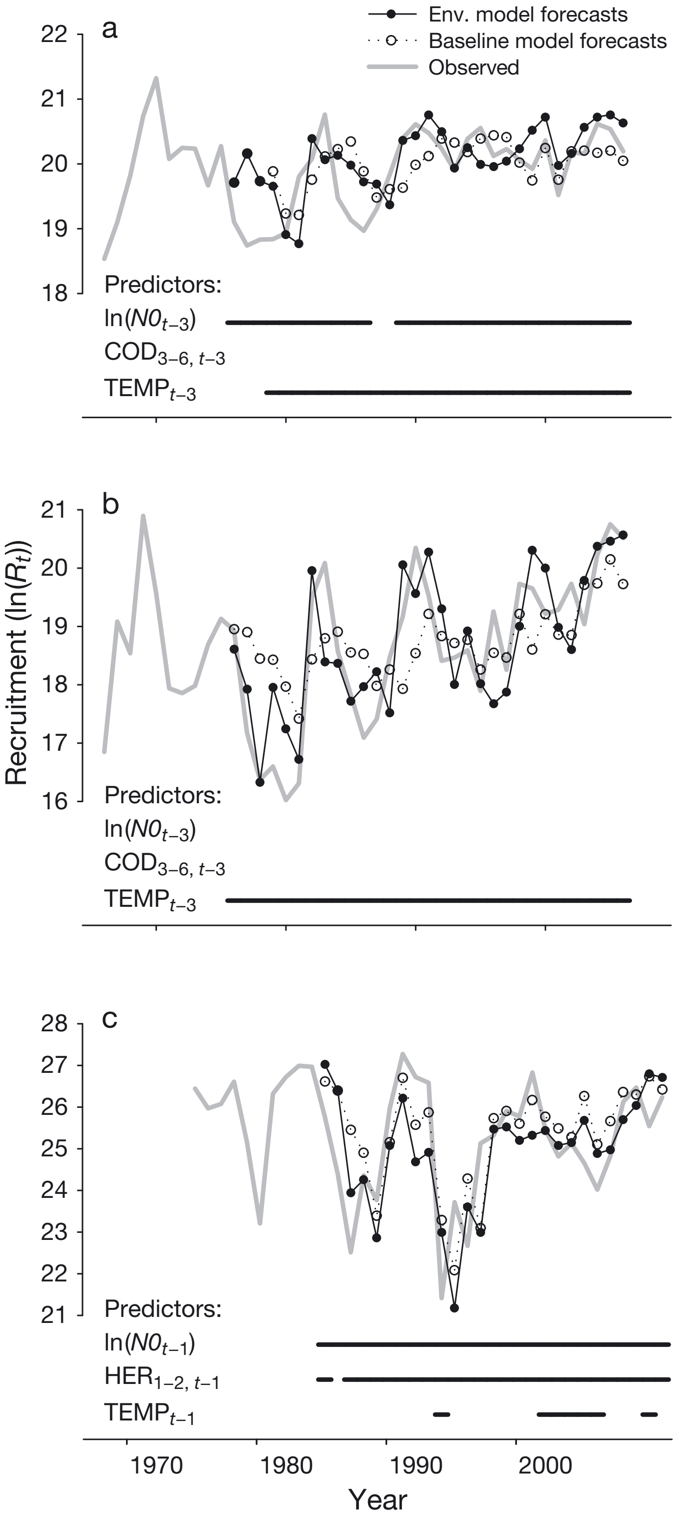

Fig. 4. Observed recruitment time series and recruitment forecast from early life-stage abundance and environmental indices for (a) NEA cod, (b) NEA haddock, and (c) BS capelin. Models and variables as detailed in Tables 3 & 4. The horizontal lines near the lower end of each panel indicate when each variable (Age 0 and environmental) entered the environmental models

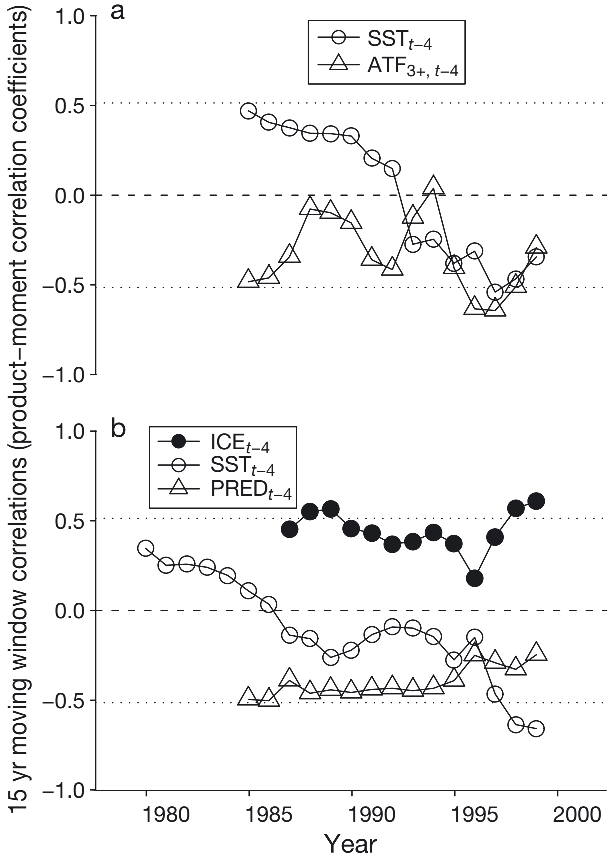

Fig. 5. Temporal change in correlations between walleye pollock recruitment and environmental indices in the (a) Gulf of Alaska and (b) eastern Bering Sea. SST: sea surface temperature, ICE: ice cover index, ATF: Age 3+ arrowtooth flounder abundance, PRED: aggregated predator index. Further details as in Fig. 1

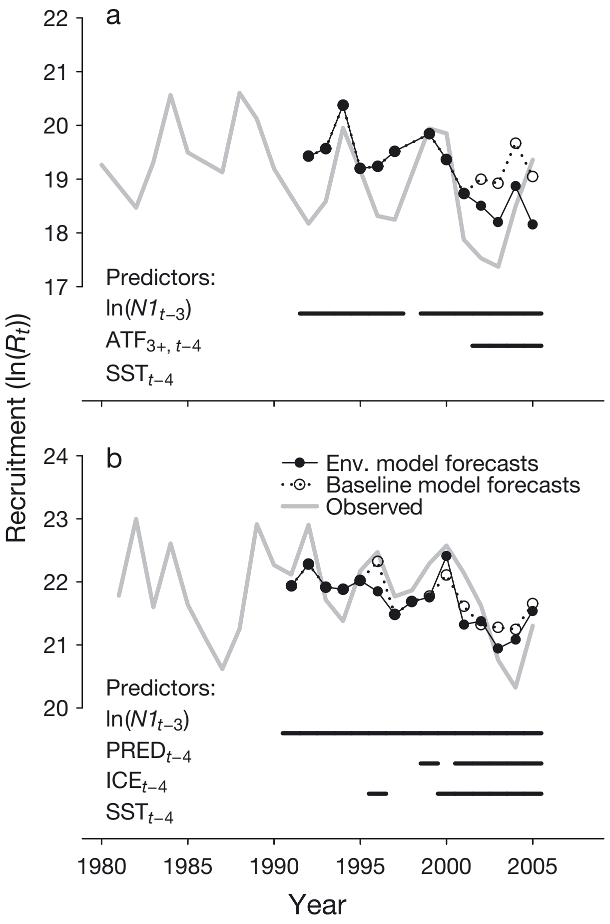

Fig. 6. Observed recruitment time series and recruitment forecast from pollock early life-stage abundance (Age 1) and environmental indices in the (a) Gulf of Alaska and (b) eastern Bering Sea. Models and variables as detailed in Tables 3 & 4. The horizontal lines near the lower end of each panel indicate when each variable (Age 1 and environmental) entered the environmental models

Predictive value of larval compared to juvenile abundance indices

Our findings show that different life-history stages predict recruitment better in different populations. Indices of the abundance of older life-history stages in some cases (BS capelin, GOA walleye pollock), but not all (NEA cod, NEA haddock, and EBS walleye pollock), provided better bases for predicting recruitment than earlier life-history stages such as indices of egg or larval abundance. Low correlation between the recruitment and the larval index for the BS capelin is consistent in particular with variable predation by immature herring on capelin larvae (e.g. Hjermann et al. 2004). This low correlation is probably not only due to noise. In a regression analysis using the same larval index, it was found that 64 % of its variability could be explained by capelin stock size and indices of prey (zooplankton) and predators (cod, feeding on the spawners, and herring, feeding on the larvae) (Stige et al. 2010), suggesting that the index indeed contains a biological signal. Likewise, low correlation between the recruitment and the larval index for the GOA walleye pollock is consistent with high and variable juvenile mortality in this system (Bailey 2000). This finding is in agreement with the results of Bailey et al. (2005), who showed that, over the range of population abundances available at the time, there was no correlation between estimated natality (egg abundance) and recruitment and that the relationship between recruitment and estimates of stage-specific abundances from life tables (some values were interpolated) became stronger for the older predictor variables. The authors found a weakly positive correlation of recruitment with estimated late-stage larval abundance, and the strength of the relationship increased for Age 0 abundance and Age 1 abundance. These results matched our *a priori* expectations, as the forecast should improve with both more accuracy and precision as the forecast target gets closer in time to the predictor variable (Bradford 1992).

For 3 of the 5 stocks examined in our study, NEA cod, NEA haddock, and EBS walleye pollock, the abundances of earlier life stages were better predictors of recruitment strength than were the abundances of later life-history stages. Analyzing the same data for NEA cod to determine when the signal in year-class strength could first be detected, Mukhina et al. (2003) reported that the largest improvement in explanatory power came when going from the spawning stock biomass to the egg stage and suggested that the lower predictive power of later life stages was caused by higher measurement error after the larval stage. According to Mukhina et al. (2003), the signal in year-class strength of NEA cod was thus often determined during the earliest life-history stages (i.e. as eggs), enabling early forecasts of recruitment. Also, Helle et al. (2000) found that an index of 'early juveniles' (~3 mo olds) was more strongly correlated with NEA cod recruitment than was an Age 0 index (~5 mo olds). The Age 0 cod may have begun to settle to the bottom at the time of the pelagic 0-group survey in August and September in the Barents Sea and may thus not have been fully available to the sampling gear (Mukhina et al. 2003). In fact, an Age 0 index calculated from demersal trawls in October to December provided better recruitment predictions than the pelagic Age 0 index (Mukhina et al. 2003), as did the acoustic Age 1 index for January to March (Table 2). Other possible causes of high measurement error for Age 0 cod include incomplete spatial coverage of the survey and schooling behavior (Helle et al. 2000). Likewise, the lower predictive power of Age 2 EBS walleye pollock may have been caused by higher measurement error of this life stage than for Age 1 fish. Age 2 pollock are thought to school higher in the water column, while Age 1 fish are primarily located on the bottom and available to the bottom trawl survey (Duffy-Anderson et al. 2003). Our findings suggest a need for caution when assuming that abundance indices of later life stages always provide better predictions of recruitment than earlier life stages. Our work shows that the opposite is frequently the case, most likely because older life stages may be more difficult to measure due to, for example, wider geographical and vertical distributions, aggregative behavior, and net-escapement behavior.

Consistency of correlations between juvenile indices and recruitment

In all but 2 stocks investigated (EBS walleye pollock and BS capelin), the relationship between the best index of pre-recruit abundance and the abundance of recruits varied strikingly over time. In other words, we found that the best life stage to use as a predictive indicator of eventual recruitment may change over time. One reason for such a change is that the predictive value of a given pre-recruit index can be modified by changes in the mortality during the subsequent life stages.

In the GOA, we found a positive correlation between pollock larvae and recruitment in the 1980s, but the correlation weakened and became negative in the 1990s. Bailey (2000) also investigated the relationship between different pre-recruit life-history stages and recruitment in GOA walleye pollock. He showed that, prior to 1989, larval mortality was inversely related to recruitment at Age 2 for the 1981 to 1988 year classes, but after 1988, larval mortality and recruitment became decoupled. He attributed this shift to a gradual trend of increasing juvenile mortality, which eventually surpassed the larval mortality. The increasing mortality of juveniles was presumed to be linked to a trend of increasing predation potential in the ecosystem, most closely associated with a dramatic increase in arrowtooth flounder *Atheresthes stomias*.

For the NEA cod in the Barents Sea, the Age 0 recruitment correlation appeared to break down for a period around the 1980s. One possible reason for this breakdown is the effect of cannibalism. Consistent with this hypothesis is the finding that NEA cod spawning stock biomass was correlated with calculated Age 1 but not Age 3 abundance in a virtual population analysis with cannibalism included (Yaragina et al. 2009). This result indicated that cannibalism, particularly on 1 to 2 yr olds, affected the year-class strength. However, counter to this hypothesis, analyses of stomach contents suggested that the levels of cannibalism on Age 1 to Age 3 cod were not particularly high in the 1980s (compared to high levels from 1947 to 1965 and then again in the 1990s; Yaragina et al. 2009).

The changing correlations should be interpreted with considerable caution because they are likely to reflect both biological and sampling issues, as catchability is likely to have varied over time. For example, the increasing correlation between the recruitment and the Age 2 index for the EBS walleye pollock seems unlikely to have a demographic basis, as the correlation between the recruitment and the Age 1 index was consistently strong in the same period. For the NEA cod and haddock, the correlations with egg and larval indices showed similar trends as the correlations with the Age 0 indices, supporting the hypothesis of a biological basis — a basis that should be considered for further research.

The value of using environmental correlates to predict recruitment

A fisheries management perspective

Although few stock-assessment working groups have developed predictions of recruitment based on a combination of stock and environmental variables, there appears to be a growing trend in the number of such models (ICES 2011). Our results support the findings of several previous studies that environmental variables contribute significantly to explaining recruitment variation retrospectively, both in the BS (e.g. Ottersen & Sundby 1995, Mukhina et al. 2003, Dingsør et al. 2007, Stige et al. 2010), the GOA (Duffy-Anderson et al. 2002, Ciannelli et al. 2004, Bailey et al. 2005), and the EBS (Mueter et al. 2006, 2011). Fewer studies have assessed if environmental variables improve predictions of future recruitment (but see e.g. MacKenzie et al. 2008, Zabel et al. 2011). We found that inclusion of environmental variables in some of our study cases improved recruitment forecasts considerably and in the remaining cases had only minor influence on the accuracy of the forecasts. The incorporation of environmental variables into models for predicting recruitment 1 yr ahead improved forecasts of recruitment for NEA haddock and GOA walleye pollock, although the improvement was only statistically significant for NEA haddock.

Fisheries managers may use forecasts of recruitment a few years ahead to set catch limits that buffer some of the effects of the interannual variability in productivity. For fishermen, abrupt changes in catches are clearly undesirable. In the harvest control rule for the NEA cod, for example, the total allowable catch (TAC) is set based on the stock forecasts, taking into account the predicted recruitment of 3 yr olds 3 yr ahead, with the constraint that the TAC should change by no more than 10% from the previous year (ICES 2010). The NEA haddock is managed using a 1 yr forecast with the constraint that the TAC should change by no more than 25% from the previous year (ICES 2010). Under such a scheme, improvements in forecast strength by use of environmental information, as shown here for the NEA haddock, can potentially improve the quality of the advice and reduce the uncertainty in setting the TAC. Note that such short-term predictions do not necessarily require predictions of environmental conditions, as the predictions can be based on current environmental conditions within the 3 yr forecast window.

Use of environmental information in recruitment forecasts can also potentially increase the average catches in the fisheries and reduce the risk of over-exploitation, especially for short-lived species with strong links between environmental conditions and recruitment (De Oliveira & Butterworth 2005). However, if recruitment-environment correlations are weak, accounting for environmental information may lead to more uncertain and variable recruitment predictions and to lower average catches (De Oliveira & Butterworth 2005). While our modeling accounted for some of the uncertainties arising from using environmental information to predict recruitment, the full implications of using such predictions in a management context remains to be assessed. In particular, there is a need for studies that simulate alternative management actions to evaluate both the potential gains and risks of different approaches (e.g. Roel et al. 2004, De Oliveira & Butterworth 2005).

Unstable recruitment–environment correlations

Despite the moderately positive results that we found, there are also disadvantages in the use of environmental information to predict recruitment. Reviewing published recruitment–environmental correlations that were retested when more data had become available, Myers (1998) found that few of the established correlations remained significant. There were a few exceptions, such as temperature–recruitment correlations toward the edges of the distribution ranges of species, which generally were robust.

Inconsistent correlations between the environmental indices and recruitment may have contributed to reduce the predictive value of the environmental variables in the present study. The recruitment–environment correlations for nearly all of the frequently selected environmental variables in the forecast models were found to cycle in and out of statistical significance: HER_{1-2} for BS capelin, TEMP for NEA cod and haddock, PRED and ICE for EBS walleye pollock, and ATF_{3+} for GOA walleye pollock.

It may be noted that the recruitment–temperature correlation for NEA haddock was among the more stable ones, being significant except from the very beginning of the period studied. Also, this was the only stock for which the environmental indices significantly improved the forecast for the time series as a whole. Our results regarding the changing relevance of temperature for the recruitment of the NEA cod in the Barents Sea are consistent with results of Ottersen et al. (2006), who proposed the finding to be caused by increased sensitivity of age-truncated stocks to climate fluctuations. In a recent meta-analysis of 42 North Atlantic fish stocks, Ottersen et al. 2013, this Theme Section) found that non-stationarity in the relationship between spawning stock biomass, temperature, and recruitment is the rule rather than the exception, but that age-truncation in general is not linked to changes in recruitment dynamics.

Nonlinear and nonadditive environmental effects

Nonlinear and nonadditive effects of environmental factors on juvenile survival are likely to have reduced the forecast value of the environmental indices when using the simplistic approach chosen in the present study. This can be exemplified by the GOA walleye pollock. Zhang et al. (2010) made Age 4 GOA pollock recruitment forecasts that accounted for the effects of Age 1 abundance, threshold effects of arrowtooth flounder biomass that became important when arrowtooth flounder became the dominant biomass species in the groundfish community, and autocorrelation terms that may be related to inter year-class effects. These authors found that strong, nonlinear threshold effects of environmental variables on pollock recruitment improved the amount of variability accounted for to 81%, more than accounted for by the Age 1 abundance alone (31%). Our results did not show the same improvement in explaining GOA pollock recruitment when environmental correlates were added. We suspect that our modeling framework contributes to the discrepancy in our results. Our environmental model did not account for nonlinear or threshold effects. The importance of nonlinear and nonstationary interactions will challenge those wanting to use environmental correlates in assessment models. However, their incorporation will be necessary if we are to improve our ability to account for the effects of demographic and environmental variables on the dynamics of fish populations (Rothschild 2000, Duffy-Anderson et al. 2005, Litzow & Ciannelli 2007).

Simple models of complex dynamics

Our study exemplifies that correlations between recruitment and both environmental and early life-stage abundance indices may cycle in and out of significance. For example, temperature may be an important factor for explaining recruitment variations for a while, and then this effect becomes overwhelmed by effects of an increase in the abundance of predators. Similarly, an increase in predation on juveniles can lead to a weaker link between larval abundance and recruitment (Bailey 2000). Thus, there are periods when the population seems responsive to some variables, but then the dominance seems to shift to other variables. The shifting importance of environmental factors may be due to shifting importance of the life stage they are influencing (as exemplified by the changing correlations between the various pre-recruit indices and recruitment in the present study), changes in the magnitude of the environmental factor (here exemplified by the increasing dominance of arrowtooth flounder in the GOA), and indirect or interacting effects (here exemplified by the arrowtooth flounder effect in the GOA likely being threshold-like rather than linear). The results thus reflect the complexity in specific responses to ecosystem changes. For most marine species, the available time series are too short to understand the full complexity of the many interacting factors that influence recruitment. Long time series are also needed to detect the effects of slowly changing environmental variables. Recent studies have demonstrated nonlinear changes in the Bering Sea ecosystem dynamics (Hunt et al. 2011) and a combination of a gradual increase in predator abundance and nonlinear interaction effects of predators and temperature on pollock recruitment in the Gulf of Alaska (Zhang et al. 2010). Given the simplistic approach taken in the present study, predicting recruitment from linear regression models fitted to short time series, the moderately positive results regarding the value of using environmental information is encouraging. In short, our results show that even if marine systems are complex, even simple attempts at using environmental information to predict fish recruitment may be better than ignoring such information.

Acknowledgements. We thank The Research Council of Norway (RCN) for funding the workshop Tropharct through the MICO project (Match/Mismatch and Ecosystem). We are greatly in debt to all of the people who made available the data used in the study. We are thankful for an RCN grant to L.C.S. through the ADMAR project, an NSF grant to G.L.H., and a CAMEO grant to M.E.H. This work is a product of the

IMBER regional program, Ecosystem Studies of Sub-Arctic Seas (ESSAS). The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. We thank T. J. Quinn II, J. Napp, M. Mauritzen, and 3 anonymous reviewers for helpful comments on earlier versions of the manuscript.

LITERATURE CITED

- Alheit J, Hagen E (1997) Long-term climate forcing of European sardine and herring populations. Fish Oceanogr 6: 130–139
- Andonegi E, Fernandes JA, Quincoces I, Irigoien X and others (2011) The potential use of a Gadget model to predict stock responses to climate change in combination with Bayesian networks: the case of the Bay of Biscay anchovy. ICES J Mar Sci 68:1257–1269
- Aydin K, Gaichas S, Ortiz I, Kinzey D, Friday N (2007) A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands Large Marine Ecosystems through food web modeling. NOAA Tech Memo NMFS-AFSC-178
- Bailey KM (2000) Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climate and ecosystem change. Mar Ecol Prog Ser 198:215–224
- Bailey KM, Ciannelli L, Bond NA, Belgrano A, Stenseth NC (2005) Recruitment of walleye pollock in a physically and biologically complex ecosystem. Prog Oceanogr 67: 24–42
- Beamish RJ (1993) Climate and exceptional fish production off the west coast of North America. Can J Fish Aquat Sci 50:2270–2291
- Beaugrand G, Brander KM, Alistair Lindley J, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–664
- Blood DM (2002) Low-temperature incubation of walleye pollock (*Theragra chalcogramma*) eggs from the southeast Bering Sea shelf and Shelikof Strait, Gulf of Alaska. Deep-Sea Res II 49:6095–6108
- Borja A, Uriarte A, Egaña J, Motos L, Valencia V (1998) Relationships between anchovy (*Engraulis encrasicolus*) recruitment and environment in the Bay of Biscay (1967–1996). Fish Oceanogr 7:375–380
- Borja A, Fontán A, Sáenz J, Valencia V (2008) Climate, oceanography and recruitment: the case of the Bay of Biscay anchovy (*Engraulis encrasicolus*). Fish Oceanogr 17:477–493
- Bradford MJ (1992) Precision of recruitment predictions from early life stages of marine fishes. Fish Bull 90:439–453
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY
- Chambers RC, Trippel EA (eds) (1997). Early life history and recruitment in fish populations. Chapman & Hall, London
- Chen DG, Ware DM (1999) A neural network model for forecasting fish stock recruitment. Can J Fish Aquat Sci 56: 2385–2396
- Ciannelli L, Chan KS, Bailey KM, Stenseth NC (2004) Nonadditive effects of the environment on the survival of a large marine fish population. Ecology 85:3418–3427
- Cushing DH (1995) Population production and regulation in the sea. A fisheries perspective. Cambridge University Press, Cambridge
- Cushing (1982) Climate and fisheries. Academic Press, London
- De Oliveira JAA, Butterworth DS (2005) Limits to the use of environmental indices to reduce risk and/or increase yield in the South African anchovy fishery. Afr J Mar Sci 27:191–203
- Dingsør GE, Ciannelli L, Chan KS, Ottersen G, Stenseth NC (2007) Density dependence and density independence during the early life stages of four marine fish stocks. Ecology 88:625–634
- Dingsør GE, Bogstad B, Stiansen JE, Subby S (2010) How can we assess recruitment models for (age-3) NEA cod? In: Report of the Arctic Fisheries Working Group Lisbon/Bergen, 22–28 April 2010. ICES, Copenhagen CM 2010/ACOM:05, WD 19
- Dorn M, Aydin K, Barbeaux S, Guttormsen M, Spalinger K, Wilkins M (2010) Assessment of the walleye pollock stock in the Gulf of Alaska. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea and Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage, AK
- Drinkwater KF, Loeng H, Megrey BA, Bailey N, Cook RM (2005) The influence of climate change on North Atlantic fish stocks. ICES J Mar Sci 62:1203–1204
- Duffy-Anderson JT, Bailey KM, Ciannelli L (2002) Consequences of a superabundance of larval walleye pollock *Theragra chalcogramma* in the Gulf of Alaska in 1981. Mar Ecol Prog Ser 243:179–190
- Duffy-Anderson JT, Ciannelli L, Honkalehto T, Bailey KM, Sogard SM, Springer AM, Buckley T (2003) Distribution of age-1 and age-2 walleye pollock in the Gulf of Alaska and eastern Bering Sea: sources of variation and implications for higher trophic levels. In: Browman HI, Skiftesvik AB (eds) The big fish bang: Proceedings of the 26th annual larval fish conference. Institute of Marine Research, Bergen, p 381–394
- Duffy-Anderson JT, Bailey K, Ciannelli L, Cury P, Belgrano A, Stenseth NC (2005) Phase transitions in marine fish recruitment processes. Ecol Complex 2:205–218
- Fiksen Ø, Jørgensen C, Kristiansen T, Vikebø F, Huse G (2007) Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. Mar Ecol Prog Ser 347:195–205
- Godø OR (1998) What can technology offer the future fisheries scientist — possibilities for obtaining better estimates of stock abundance by direct observations. J Northwest Atl Fish Sci 23:105–131
- Heath MR (1992) Field investigations of the early life stages of marine fish. Adv Mar Biol 28:1–174
- Helle K, Bogstad B, Marshall CT, Michalsen K, Ottersen G, Pennington M (2000) An evaluation of recruitment indices for Arcto-Norwegian cod (*Gadus morhua* L.). Fish Res 48:55–67
- Hjermann DØ, Ottersen G, Stenseth NC (2004) Competition among fishermen and fish causes the collapse of Barents Sea capelin. Proc Natl Acad Sci USA 101:11679–11684
- Hjermann DØ, Bogstad B, Eikeset AM, Ottersen G, Gjøsæter H, Stenseth NC (2007) Food web dynamics affect Northeast Arctic cod recruitment. Proc R Soc Lond B Biol Sci 274:661–669
- Hjort J (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp P-V Réun Cons Int Explor Mer 20:1–228
- Hollowed A, Barange M, Ito SI, Kim S, Loeng H, Peck MA (2011) Effects of climate change on fish and fisheries:

forecasting impacts, assessing ecosystem responses, and evaluating management strategies. ICES J Mar Sci 68: 984–985

Houde ED (1994) Differences between marine and freshwater fish larvae: implications for recruitment. ICES J Mar Sci 51:91–97

Houde ED (2008) Emerging from Hjort's shadow. J Northwest Atl Fish Sci 41:53–70

Hunt GL Jr, Coyle KO, Eisner LB, Farley EV and others (2011) Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES J Mar Sci 68:1230–1243

Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. Biometrika 76:297–307

Ianelli JN, Barbeaux S, Honkalehto T, Kotwicki S, Aydin K, Williamson N (2010) Assessment of the walleye pollock stock in the Eastern Bering Sea. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea and Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage, AK, p 54–156

ICES (International Council for the Exploration of the Sea) (2007) Report of the Arctic Fisheries Working Group (AFWG), 18–27 April 2007, Vigo, Spain. ICES CM 2007/ ACFM:16, ICES, Copenhagen

ICES (2010) Report of the Arctic Fisheries Working Group (AFWG), 22–28 April 2010, Lisbon, Portugal/Bergen, Norway. ICES CM 2010/ACOM:05, ICES, Copenhagen

ICES (2011) Report of the Study Group on Recruitment Forecasting (SGRF), 17–20 October 2011, Copenhagen, Denmark. ICES CM 2011/ACOM:31, ICES, Copenhagen

Litzow MA, Ciannelli L (2007) Oscillating trophic control induces community reorganization in a marine ecosystem. Ecol Lett 10:1124–1134

Logerwell EA, Mantua N, Lawson PW, Francis RC, Agostini VN (2003) Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fish Oceanogr 12:554–568

MacKenzie BR, Horbowy J, Köster FW (2008) Incorporating environmental variability in stock assessment: predicting recruitment, spawner biomass, and landings of sprat (*Sprattus sprattus*) in the Baltic Sea. Can J Fish Aquat Sci 65:1334–1341

Mueter FJ, Ladd C, Palmer MC, Norcross BL (2006) Bottom-up and top-down controls of walleye pollock (*Theragra chalcogramma*) on the eastern Bering Sea shelf. Prog Oceanogr 68:152–183

Mueter FJ, Bond NA, Ianelli JN, Hollowed AB (2011) Expected declines in recruitment of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea under future climate change. ICES J Mar Sci 68:1284–1296

Mukhina NV (1992) Results of the ichthyoplankton investigations in the Norwegian and Barents Seas in 1959–1990. In: Belikov SV, Mukhin AI, Savvatimsky PI, Tretyak VL, Shevelev MS, Shleinik VN (eds) Ekologicheskie problemy Barentseva moria. PINRO, Murmansk (in Russian), p 62–102

Mukhina NV, Marshall CT, Yaragina NA (2003) Tracking the signal in year-class strength of Northeast Arctic cod through multiple survey estimates of egg, larval and juvenile abundance. J Sea Res 50:57–75

Myers RA (1998) When do environment–recruitment correlations work? Rev Fish Biol Fish 8:285–305

Ottersen G, Sundby S (1995) Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fish Oceanogr 4:278–292

Ottersen G, Hjermann DØ, Stenseth NC (2006) Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod stock. Fish Oceanogr 15:230–243

Ottersen G, Stige LC, Durant JM, Chan KS, Rouyer TA, Drinkwater KF, Stenseth NC (2013) Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. Mar Ecol Prog Ser 480:205–225

Quinn TJ II, Niebauer HJ (1995) Relation of eastern Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment to environmental and oceanographic variables. In: Beamish RJ (ed) Climate change and northern fish populations. Can Spec Publ Fish Aquat Sci 121:497–507

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org

Roel BA, O'Brien CM, Basson M (2004) Management options for the Blackwater herring, a local spring-spawning stock in the Thames estuary. ICES J Mar Sci 61:297–307

Rothschild BJ (2000) 'Fish stocks and recruitment': the past thirty years. ICES J Mar Sci 57:191–201

Sinclair M, Tremblay MJ (1984) Timing of spawning of Atlantic herring (*Clupea harengus harengus*) populations and the match-mismatch theory. Can J Fish Aquat Sci 41:1055–1065

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60: 1129–1157

Stige LC, Ottersen G, Dalpadado P, Chan KS and others (2010) Direct and indirect climate forcing in a multi-species marine system. Proc R Soc Lond B Biol Sci 277: 3411–3420

Stockhausen WT, Nichol D, Lauth RR, Wilkins M (2010) Assessment of the flathead sole stock in the Bering Sea and Aleutian Islands. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea and Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage, AK, p 869–968

Tereshchenko VV (1996) Seasonal and year-to-year variations of temperature and salinity along the Kola meridian transect. ICES CM 1996/C:11, ICES, Copenhagen

Thompson GG, Ianelli JN, Lauth RR (2010) Assessment of the Pacific cod stock in the Eastern Bering Sea and Aleutian Islands area. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea and Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage, AK, p 243–424

Turnock BJ, Wilderbuer TK (2009) Gulf of Alaska arrowtooth flounder stock assessment. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea and Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage, AK, p 627–680

Wilderbuer TK, Nichol DG, Aydin K (2010) Arrowtooth flounder. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea and Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage, AK, p 697–762

Yaragina NA, Bogstad B, Kovalev YA (2009) Variability in cannibalism in Northeast Arctic cod (*Gadus morhua*) during the period 1947–2006. Mar Biol Res 5:75–85

Zabel RW, Levin PS, Tolimieri N, Mantua NJ (2011) Interactions between climate and population density in the episodic recruitment of bocaccio, *Sebastes paucispinis*, a Pacific rockfish. Fish Oceanogr 20:294–304

Zhang T, Bailey KM, Chan KS (2010) Recruitment forecast models for walleye pollock *Theragra chalcogramma* fine-tuned from juvenile survey data, predator abundance and environmental phase shifts. Mar Ecol Prog Ser 417: 237–248

Appendix 1. Sources and manipulation of abundance data for the BS stocks

NEA cod and NEA haddock

SSB_t and R_t were estimated by virtual population analysis based on catch data (Table 1). The E_t and L_t indices (given by Mukhina 1992) were constructed based on egg and larval data collected by surveys by the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Murmansk, as described by Mukhina et al. (2003). $N0_t$ was calculated from Age 0 data sampled by international 0-group surveys in the Barents Sea (ICES 2007, 2010). Several alternative indices of Age 0 abundance have been computed, but none that cover the entire year range. For 1980 to 2009, we defined $N0_t$ as $N0_{t\text{-new}}$, where $N0_{t\text{-new}}$ is the most recent index (given in Table 1.2 of ICES 2010) that corrects for catching efficiency but has, to our knowledge, not been calculated for years prior to 1980. To increase the temporal overlap with the egg and larvae indices, we therefore calculated $N0_t$ for 1966 to 1979 from the so-called 'logarithmic' Age 0 index (here referred to as $N0_{t\text{-old}}$) that has been published for 1966 to 2004 (ICES 2007). The conversion equation was calculated by ordinary least-squares regression on log-transformed data for the 25 overlapping years — cod: $\ln(N0_{t\text{-new}}) = 23.9 + 1.817 \ln(N0_{t\text{-old}} + 0.01)$, haddock: $\ln(N0_{t\text{-new}}) = 23.2 + 1.445 \ln(N0_{t\text{-old}} + 0.01)$; $R^2 = 0.83$ and 0.81, respectively; log-transformation of predictors improved fit and removed curvature in residuals-fitted plots. Finally, $N1_t$ and $N2_t$ were calculated from Norwegian acoustic surveys in the Barents Sea (ICES 2010).

BS capelin

SSB_t and R_t were estimated from September to October acoustic surveys (Table 1). L_t was constructed by combining an index based on data collected by PINRO for 1959 to 1990 (Mukhina 1992, Mukhina et al. 2003; here denoted $L_{t\text{-Rus}}$) and an index based on Norwegian surveys for 1981 to 2009 (ICES 2010; here denoted $L_{t\text{-Nor}}$). For 1981 to 2009, we used $L_t = L_{t\text{-Nor}}$, for 1959 to 1980, we used $\ln(L_t) = 28.3 + 0.547 \ln(L_{t\text{-Rus}} + 0.01)$, the conversion equation calculated by least-squares regression for the 10 overlapping years ($R^2 = 0.69$). $N0_t$ was constructed similarly to above, by linking the $N0_{t\text{-new}}$ for 1980 to 2009 (Table 1.2 in ICES 2010) with the other index available for capelin, the so-called 'area-index' (here denoted $N0_{t\text{-old}}$), which covers 1965 to 2004 (ICES 2007), using the following conversion equation: $\ln(N0_{t\text{-new}}) = 15.9 + 1.679 \ln(N0_{t\text{-old}})$ ($R^2 = 0.87$, $n = 27$ overlapping years).

Submitted: April 27, 2012; Accepted: January 2, 2013

Proofs received from author(s): March 22, 2013

Vol. 480: 263–275, 2013
doi: 10.3354/meps10315

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 22

Contribution to the Theme Section 'Harvested fish stocks in a changing environment'

Spatial analysis of North Sea cod recruitment: concurrent effects of changes in spawning stock biomass, temperature and herring abundance

Dag Ø. Hjermann[1,*], Jonathan A. D. Fisher[2], Tristan Rouyer[1], Kenneth T. Frank[3], Nils C. Stenseth[1,4]

[1]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway

[2]Centre for Fisheries Ecosystems Research, Fisheries and Marine Institute of Memorial University of Newfoundland, PO Box 4920 St. John's, Newfoundland A1C 5R3, Canada

[3]Fisheries & Oceans Canada, Bedford Institute of Oceanography, Ocean Sciences Division, Dartmouth, Nova Scotia B2Y 4A2, Canada

[4]Institute of Marine Research, Department of Coastal Zone Studies, Flødevigen Research Station, 4817 His, Norway

---

ABSTRACT: The decline of the North Sea cod *Gadus morhua* has been attributed to both overfishing and ocean warming. However, another hypothesis is that overfishing of piscivorous cod has caused an increased abundance of formerly predatory-controlled pelagic fish including herring *Clupea harengus*, which in turn has suppressed the recruitment of cod through predation on the early life stages of cod. Here we analyze 40 yr of trawl survey data in order to explore how the abundance of young herring affects cod recruitment, and how cod biomass affects the abundance of herring. In both cases we also take into account the effects of spawner biomass (of cod and herring, respectively) and sea temperature. We take a novel, explicitly spatial, approach by analyzing these effects on a local (185 × 167 km) scale. Our results indicate large spatial variability in ecological mechanisms. In the German Bight, high cod recruitment is associated with low herring abundance, low temperatures and high overall cod spawner biomass. This area used to contain a large portion of the cod recruits, and there is a strong correlation between the fraction of cod recruits found in this area and overall recruitment. In this area, herring recruitment is also negatively associated with the abundance of large cod. Thus, for this part of the North Sea, our findings are consistent with a reversal of dominance between cod and herring; however, herring may affect the cod by competition rather than by predation.

KEY WORDS: Interspecific interaction · Ecosystem dynamics · Cultivation effect · Predator-prey reversal · Spatial heterogeneity · Warming

INTRODUCTION

The complex interplay between the species in an ecosystem creates the potential for complex behaviour, including multiple stable states (May 1977). One typical mechanism for such a situation is that per-capita recruitment declines when the population becomes small, known as the demographic Allee effect (Courchamp et al. 2008). As large adults, predatory fish like cod *Gadus morhua* eat small pelagic fish like herring *Clupea harengus*, but in turn, pelagic fish may also prey upon and compete with the smaller, early life stages of their predators. A high biomass of adult predators keeps down species that may be predators/competitors of its eggs and larvae in size-structured ecosystems; this has been termed the 'cultivation effect' (Swain & Sinclair 2000, Walters & Kitchell 2001). When harvesting reduces the abundance of predators, natural mortality of its young life stages may increase, leading to a feedback

---

*Email: d.o.hjermann@bio.uio.no

loop that may hamper or delay recovery of fish stocks after overfishing (de Roos et al. 2003, Frank et al. 2011, Richardson et al. 2011).

While ecosystem models often disregard space, ocean ecosystems are spatially heterogeneous, both because of spatially varying conditions (depth, temperature, bottom habitat, etc.) and because of the movements of organisms (e.g. fish typically have particular spawning, nursery and feeding areas). Therefore, we expect that the interactions among species change spatially. The most obvious case is that predators and prey will only interact when and where they overlap, but other spatially varying factors may also affect predator–prey overlap: the availability of alternative prey, competition among predators, and the size of predators and prey during the season when they overlap. The North Sea (NS) is an example of a spatially heterogeneous ocean, with spatially varying bottom depths, temperatures and fish communities. Overall, the abundance of cod, both spawners and recruits, has declined steadily in the NS since the 1960s. Two reasons for this decline are commonly regarded as plausible (Fig. 1). First, overfishing has depleted the adult (spawning) stock of cod (Cook et al. 1997, Horwood et al. 2006). Secondly, the NS has warmed substantially in recent decades, and high temperatures are associated with low recruitment of NS cod (e.g. Planque & Frédou 1999, Olsen et al. 2011). One mechanism for the negative effect of temperature could be the associated change in species composition and seasonality of zooplankton, which may have led to decreased survival of cod larvae (Beaugrand et al. 2003, Durant et al. 2005, Olsen et al. 2011). The 2 hypotheses of NS cod decline — overfishing and increased temperatures — are not mutually exclusive (Fig. 1; Durant et al. 2005, Olsen et al. 2011); on the contrary, there is some evidence that they may even exacerbate each other's effects (Brander 2005, Kirby et al. 2009). The possible generality of such synergistic effects has been scrutinized by Ottersen et al. (2013, this volume). A third mechanism may be that herring play a crucial role in limiting the recruitment of cod, through predation on, or competition with, cod eggs and larvae (Minto & Worm 2012). The predation mechanism has been discussed since the 1970s, as a period of exceptionally high recruitment years of cod and other gadoids (the 'gadoid outburst'), which started at approximately the same time that the stock of NS herring began to decline (Cushing 1980). Recently, both Fauchald (2010) and Speirs et al. (2010) have argued in favour of this mechanism. Furthermore, the former author suggested that intensive harvesting of cod has released herring from predator control, the result being a positive feedback loop resulting in hysteresis (Scheffer et al. 2001, Beisner et al. 2003), but that the continued harvesting of herring might prevent the system from changing completely into a pelagic-fish-dominated state.

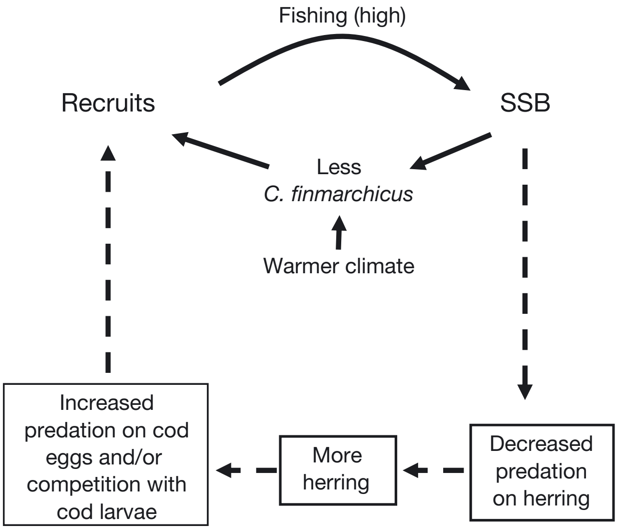

Fig. 1. Proposed mechanisms for the decline of North Sea cod *Gadus morhua* since the 1960s. Relatively direct mechanisms (solid lines) include the negative effect of high fishing mortality on the spawning stock biomass (SSB) and the negative effect of a warmer climate, via a decrease in the young cod's key prey *Calanus finmarchicus*, on recruitment. A more indirect mechanism involves the interactions between cod and herring *Clupea harengus* (dashed lines)

Ecosystem changes following strong reductions in predatory fish have been suggested for other marine areas. In the Baltic Sea, Köster & Möllmann (2000) found, from stomach samples, that herring and sprat *Sprattus sprattus* eat large amounts of cod eggs. In the Baltic, there is a large temporal overlap between cod spawning and herring and sprat feeding, and cod eggs are found concentrated in a narrow depth range. Sprat dominated total consumption, but mostly due to their much larger biomass (the per-capita consumption of herring is about one-third lower than that of sprat). Another cascading effect of predator–prey control may also be in action in the Baltic: as cod has decreased, sprat numbers have increased as a result of lower predation pressure, which has contributed to a reduced abundance of *Pseudocalanus acuspes*, a key prey for larval cod (Möllmann et al. 2008). Additionally, on the eastern Scotian shelf, a former cod-dominated ecosystem, overfishing of cod and other benthic fishes triggered a trophic cascade by releasing zooplanktivorous fish from predatory control, leading to a system characterized by a large abundance of pelagic fish and macroinvertebrates (including crabs and shrimp) and poor productivity of cod and other benthic fishes (Frank et al. 2005). However, recently, the ecosystem appears to be returning to a benthic fish-dominated state (Frank et al. 2011). The Black Sea is another case in which the removal of predatory fish has been suggested to cause large system changes; analyses by Llope et al. (2011) suggested that the overfishing of predatory fish eventually pushed the food chain into an alternative state with a large abundance of ctenophores and a low abundance of zooplankton. In both the Baltic and Black Seas, however, substantial changes in environmental conditions, including water temperature, salinity and phosphorous levels have also had significant effects on the system, interacting with trophodynamic factors (Möllmann et al. 2008, Llope et al. 2011); only in the case of the eastern Scotian shelf does the effect of environmental changes appear to have been relatively small (Frank et al. 2011).

In this paper, we analyzed the concurrent effects of stock size, temperature and herring abundance on cod recruitment on smaller spatial scales (rectangles of approximately 185 × 167 km) than have been considered in previous analyses. NS cod is a spatially structured population (Wright et al. 2006, Heath et al. 2008), making it paramount to take into account the spatial aspects of ecosystem processes (Ciannelli et al. 2013, this volume). Also, in order to investigate whether hysteresis is at play, we explored factors that may affect local herring recruitment, including the possible top-down effect of cod on herring. With this approach, we were better able to pinpoint how environmental and trophodynamic effects vary throughout the NS ecosystem, which may be an important step towards a more complete understanding of the ecosystem. Migration of adults and drift of eggs and larvae were not explicitly incorporated in the analyses, as these patterns may vary substantially between years (e.g. Bartsch et al. 1989); however, the results are interpreted in light of existing knowledge of these patterns.

MATERIALS AND METHODS

Database

The basis for our analysis were data on fish abundance from the International Bottom Trawl Survey (IBTS), Quarter 1 (i.e. January to March), downloaded from http://datras.ices.dk. We used data for each haul but analyzed them using the IBTS grid, which consists of rectangles of 1° longitude (53 to 70 km, increasing towards the south) by 0.5° latitude (56 km), hereafter denoted 'grid cells' (ICES 2010) across the North Sea (mean grid cell area: 3435 km^2, total grid cell area: 663 000 km^2). We used data from 1971 to 2010, as age determination of sampled cod started in 1971. The IBTS started out as a young herring survey using herring gear, but gradually changed to using more multipurpose gear (ICES 2010). Standard gear has been used since 1984, while 10 additional gear types were used before this time. Data from the 6 least common gear types were ignored. For the other 4 non-standard gears, we calculated the catch ratio between hauls of non-standard and standard gear in the same year located <200 km apart, and applied linear regression to log(catch ratio) as a function of distance (in km) and number of days between hauls. In the cases where the intercept of these regressions tended to systematically be <1 or >1, we used the intercept estimates to adjust fish abundance (for details, see Supplement 1 at www.int-res.com/articles/suppl/m480p263_supp.pdf). The data were tabulated both by age and length. The biomass of mature fish was calculated as the fish abundance × mean fraction mature × mean weight for each age, summed over all ages (data on maturity and weight are from ICES 2011a,b). Sea surface temperature (SST) was retrieved from the COADS database with 1° × 1° spatial resolution and monthly temporal resolution (NOAA 2011). From these data we used the mean spring temperature (March to May, i.e. egg and larval stages of cod; Heath et al. 2008) using linear interpolation to quantify the temperature of the centre of each grid cell.

Spatially resolved regression analyses

We made 2 sets of analyses of abundance variations on a local scale, which we defined to be areas of 3 × 3 IBTS grid cells, hereafter denoted 'subareas' (mean size: 185 × 167 km): (1) variations in local cod recruitment as a function of the biomass of cod spawners, SST and the abundance of young herring and (2) variations in local herring recruitment as a function of the biomass of herring spawners, SST and the abundance of large cod. We analysed subareas centred on every grid cell in the dataset (subareas were thus overlapping). When parts of the 3 × 3 grid were on land or outside the study area, these parts were simply disregarded. We used only subareas with at least 4 grid cells of data, and where at least 15 yr of data were available.

Analyses of local cod recruitment

For every subarea *a* we performed 3 regression analyses with the subarea's median cod recruitment (Age 1 cod: *CodAge1*) as the response variable. In the first analyses, we let the predictor variables be the biomass of cod spawners (cod >50 cm: *CodMature*), SST and the abundance of herring that could be predators of cod eggs and larvae or competitors of cod juveniles. For herring as a predator on cod eggs, the literature is equivocal on which size or age group of the herring eats the most cod eggs. Last (1989) found the predation of herring to generally peak in the 15 to 19 cm interval in spring, largely corresponding to Age 1 herring. As this also is the age group that would be expected to compete most with the cod larvae and juveniles later in the season (they both feed on small zooplankton), we chose the abundance of Age 1 herring in the cod's spawning year as a potential explanatory variable. We used the mean over the subarea for all predictor variables, and all abundance variables were log-transformed.

Cod recruitment was modelled using generalized additive models (GAM). This is a kind of regression model similar to multiple linear regression, except that it allows the effects of each explanatory variable on the response variable to be either linear or non-linear (Wood 2011). We used the mgcv library of R, which utilizes the generalized cross validation (GCV) criterion to decide whether each effect is linear or not and, in the latter case, the smoothness of the non-linear effect.

In the first analysis, we assumed that recruitment (the number of Age 1 cod in a given year) was dependent on the local biomass of cod spawners, the temperature and herring abundance in the cod's spawning year (i.e. in the year before):

$$CodAge1_{a,t+1} = \mathrm{s}(CodMature_{a,t}) + \mathrm{s}(SST_{a,t}) + \mathrm{s}(HerrAge1_{a,t}) + \varepsilon_{a,t} \quad (1)$$

where *a* is a single subarea and *t* denotes years (all years with available data), *HerrAge1* is the abundance of Age 1 herring, and ε is a normally distributed error term (as mentioned, abundance data were log-transformed). 's(X)' denotes a non-linear spline function of X, or a linear function of X, in which case $\mathrm{s}(X) = \text{slope} \times X$. To avoid overfitting we constrained each spline function to have a maximum of 2 degrees of freedom (i.e. $k = 3$; Wood 2011). The second regression analysis was similar, except that we replaced the local biomass of cod spawners ($CodMature_{a,t}$) with the biomass of cod spawners in the entire NS ($CodMatureTot_t$):

$$CodAge1_{a,t+1} = \mathrm{s}(CodMatureTot_t) + \mathrm{s}(SST_{a,t}) + \mathrm{s}(HerrAge1_{a,t}) + \varepsilon_{a,t} \quad (2)$$

The motivation for this is that cod eggs and larvae drift for a period, so recruitment does not depend on biomass of spawners in a larger area, while we still expected the effect of temperature and predation from herring to be local. In the third regression analysis, we wanted to specifically analyse short-term variation. This analysis was similar to the second one, except that all variables were detrended to remove the effect of long-term trends in the data series:

$$CodAge1D_{a,t+1} = \mathrm{s}(CodMatureTotD_t) + \mathrm{s}(SSTD_{a,t}) + \mathrm{s}(HerrAgeD1_{a,t}) + \varepsilon_{a,t} \quad (3)$$

where the *D* at the end of the variable names indicates that the variable was detrended, i.e. replaced with the residual after a linear regression between the original variable and year. Detecting effects in the short-term variation would also constitute quite strong evidence, but as detrending removes much of the variation in both predictor and response variables, the power of the analysis decreases substantially (i.e. it is more likely that p-values are >0.05 even though there is a real causal relationship).

In all 3 cases, we performed a model selection procedure independently for each subarea, choosing the model (i.e. the subset of the 3 explanatory variables) with the lowest corrected Akaike's information criterion (AIC_c) that also showed $p \leq 0.05$ for all variables.

Analyses of local herring recruitment

The analyses of herring recruitment were almost a mirror image of the analyses of cod recruitment: in Eqs. (1) to (3) we replaced cod recruitment and spawning stock biomass (SSB) with herring recruitment (abundance of Age 1 herring: *HerrAge1*) and biomass of mature herring (*HerrMature*), respectively. While we expected cod recruitment to be affected by young herring, we expected the abundance of young herring to be influenced mostly by the abundance of large, piscivorous cod, i.e. mature cod. We ran 3 regression analyses equivalent to the analyses of cod recruitment: local effects of all variables, local effects of temperature and predators but effects of total spawner abundance, and analysis of detrended variables:

$$HerrAge1_{a,t+1} = s(HerrMature_{a,t}) + s(SST_{a,t}) + s(CodMature_{a,t}) + \varepsilon_{a,t} \quad (4)$$

$$HerrAge1_{a,t+1} = a + s(HerrMatureTot_{t}) + s(SST_{a,t}) + s(CodMature_{a,t}) + \varepsilon_{a,t} \quad (5)$$

$$HerrAge1D_{a,t+1} = s(HerrMatureTotD_{t}) + s(SSTD_{a,t}) + s(CodMatureD_{a,t}) + \varepsilon_{a,t} \quad (6)$$

Again, all abundance variables were log-transformed prior to analysis, and the effect of each variable in each subarea was calculated as explained in the cod recruitment section.

RESULTS

The biomass of mature cod *Gadus morhua* decreased greatly in the entire NS during the period from 1971 to 2009 (Fig. 2a), with the exception of the north-easterly areas close to the Norwegian Trench and in the English Channel (Fig. 2f). The decrease was, however, somewhat less in the Central North Sea (northwards from the Dogger Bank) and close to Denmark (Fig. 2f). The recruitment of cod in the southern NS has also decreased substantially (Fig. 2b), and the decrease was strongest close to the Danish, German and Dutch coasts (Fig. 2g). A relatively small part of the NS, the German Bight area, contained around 80% of the Age 1 cod in some years of the survey, but, since 1993, has usually contained <5% of them (Fig. 3). The fraction of Age 1 cod that was found within this area was strongly correlated with the recruitment of cod ($R^2 = 0.48$, $t = 5.84$, $p < 0.0001$; Fig. 3). This relationship remained significant ($t = 2.68$, $p = 0.011$) if the general decrease in both variables over time was taken into account by using year as a covariate. In contrast, the biomass of mature herring *Clupea harengus* has generally increased since 1980,

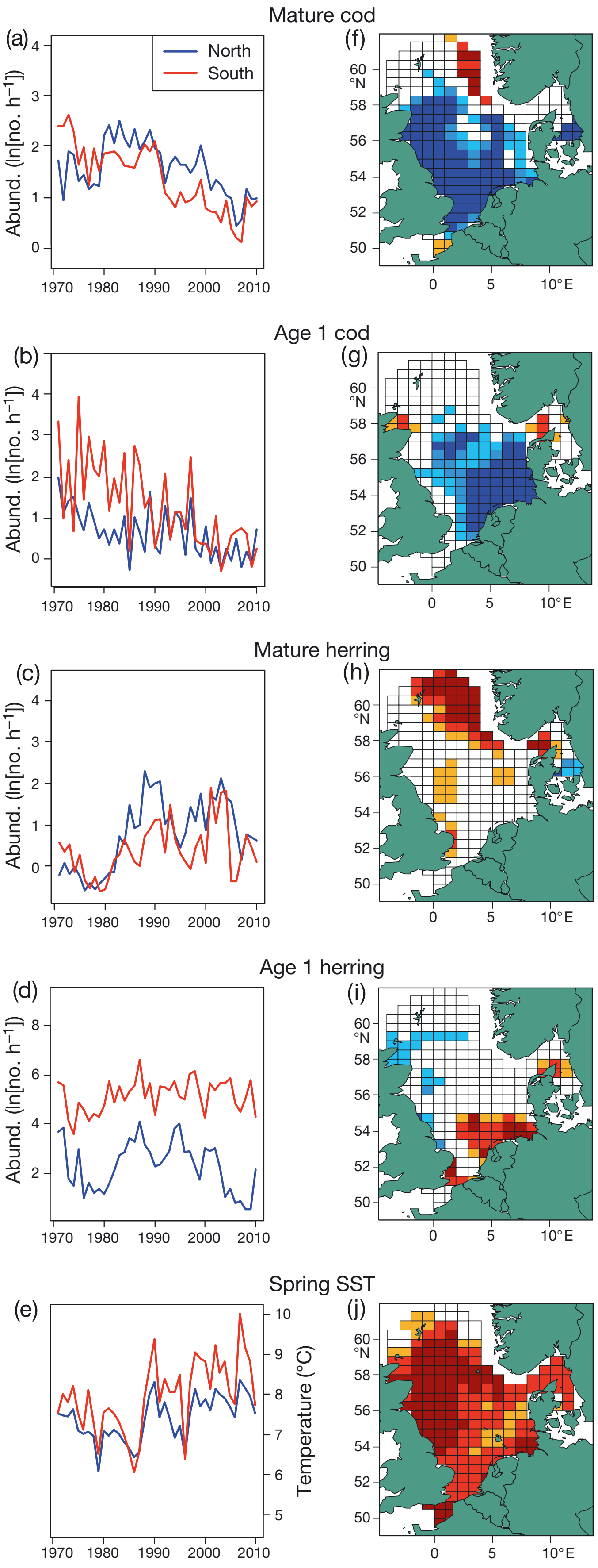

Fig. 2. *Gadus morhua* and *Clupea harengus*. Time series and spatial variation in fish abundances from (a–d, f–i) trawl surveys and (e,j) sea surface temperature (SST). (a–e) Abundance (as log-transformed numbers of fish per hour trawling) in the northern (blue lines) and southern (red lines) North Sea, using 55° N as the dividing line. The Skagerrak/Kattegat area (east of 8° E) was excluded. (f–j) Spatial patterns of the relative linear time trends of the variables (the abundance variables were log-transformed). Shades of blue indicate a significant ($p < 0.05$) decrease over time; shades of orange indicate a significant increase. Slopes were estimated for subareas (3° × 3° grid cell areas). The statistical significance of the time trend is shown by the colour of the central grid cell—dark shading (dark orange or dark blue): $p < 0.001$; medium shading: $0.001 < p < 0.01$; light shading: $0.01 < p < 0.05$

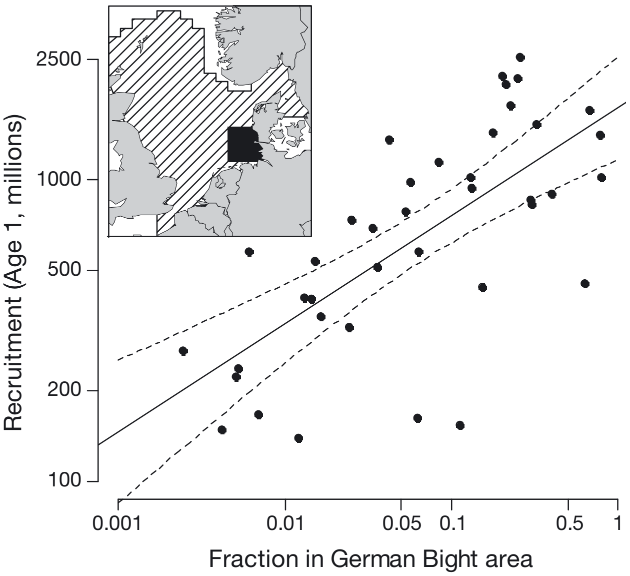

Fig. 3. *Gadus morhua*. Relationship between recruitment of North Sea cod (measured as number of Age 1 cod) and the fraction of all Age 1 cod found in the German Bight area (east of 6° E, south of 55° 45′ N) in the International Bottom Trawl Survey (IBTS). The estimates of Age 1 cod abundance are from a previous cod assessment (ICES 2011c). The lines show the result of linear regression between the log-transformed variables, with a 95 % confidence interval ($R^2 = 0.48$, $t = 5.84$, $p < 0.0001$). The inset shows the German Bight area (black rectangle), as well as the entire area covered by the IBTS (hatched area)

in particular in the northern areas (Fig. 2c,d,h). The abundance of Age 1 herring increased in the southeast but decreased in the northwest (Fig. 2i). The SST has increased basically everywhere (Fig. 2e,j)

The optimal model for cod recruitment varied spatially (Fig. 4; Fig. S3a,c,e in Supplement 2 at www.int-res.com/articles/suppl/m480p263_supp.pdf). Cod recruitment was positively associated with the local cod spawning stock abundance in only parts of the area, and with total cod spawning stock abundance in the German Bight and north of Scotland (Fig. 4a,b; see also Fig. S4a,b in Supplement 2). Cod recruitment was negatively associated with local SST in the entire southern NS and with the local abundance of young herring in large parts of the southeastern NS (Fig. 4a,b). When removing long-term trends (i.e. examining only short-term trends), the significant association with temperature persisted in the southernmost areas, while the association with herring abundance remained significant in only a limited part of the area (Fig. 4c). However, when examining the model estimates of the full model (before model selection), it was clear that a tendency still existed for negative effects of both herring and temperature in the German Bight area, but for a large part, they were not statistically significant (Fig. S5c in Supplement 2).

The optimal model for herring recruitment was also highly variable spatially (Fig. 5; Fig. S3b,d,f). Herring recruitment was positively related to local spawner abundance in a few areas of the NS (Fig. 5a; see also Fig. S6a in Supplement 2, but was associated with total spawner biomass in most of the southern NS (Fig. 5b). Local SST had a negative effect on recruitment in the western NS and a non-linearly positive effect in some areas on the southern shores (Fig. 5a,b; Fig. S6a,b). The association between herring recruitment and cod abundance was positive in the central NS and negative in some areas, including the German Bight (Fig. 5b). In contrast to the analysis of cod recruitment, each factor's effect on herring recruitment had roughly the same spatial pattern when long-term trends were removed, although temperature drops out of the model in some areas (Fig. 5c; Fig. S7c in Supplement 2).

DISCUSSION

Our study adds important spatial dimensions and nuances to both the generally accepted hypotheses of declining NS cod *Gadus morhua* recruitment (decreased spawning stock and higher temperatures; Cook et al. 1997, Beaugrand et al. 2003) and to the newly proposed mechanism of ecosystem hysteresis through predation by herring *Clupea harengus* (Fauchald 2010). Regarding the latter hypothesis, we indeed found that the decrease in cod recruitment in a smaller area, the German Bight, was consistent with the hypothesis of strong effects of reciprocal predation between cod and herring. Although this area is small, it has in many years contained a large proportion, or even most, of the cod recruits (Daan et al. 1990). Moreover, we found that high recruitment in this area appears to be related to good cod recruitment in the entire NS, indicating that this is a key nursery area for cod. Our results indicate that the decrease in cod recruitment in this area is not the result of 1 factor alone, but of 3 simultaneous ones: decreased biomass of mature cod, increasing temperatures and increasing abundance of herring (Fig. 4). Furthermore, the increase in herring in this area cannot be fully explained by the increasing total biomass of herring spawners; there appears to be an additional effect of the local abundance of cod spawners, who are important predators of herring.

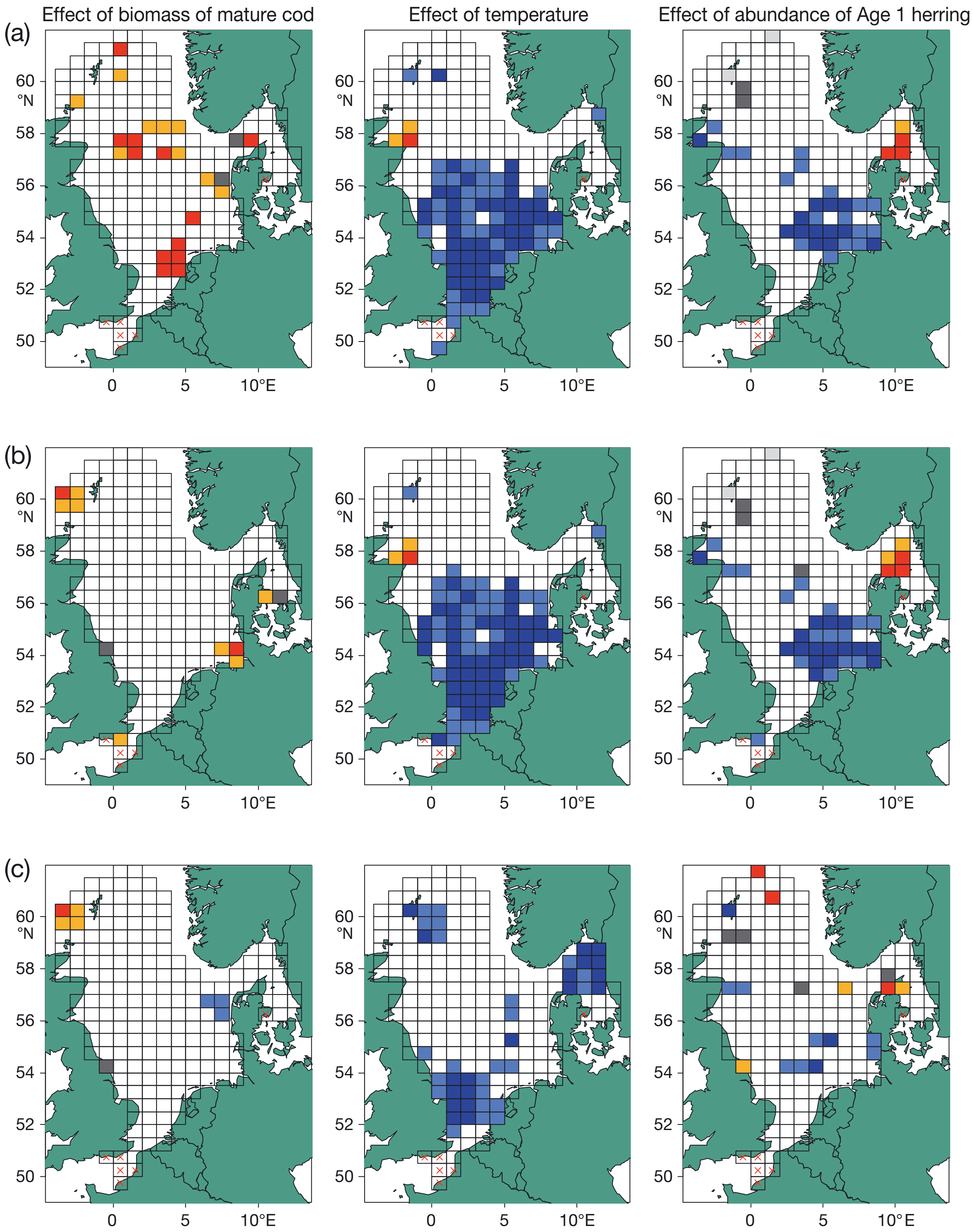

Fig. 4. *Gadus morhua*. Effect of each predictor variable on cod recruitment. Each row of graphs represents one model: (a) Eq. (1), (b) Eq. (2) and (c) Eq. (3). Dark and light blue indicate predominantly negative effects; dark and light orange indicate predominantly positive effects; and dark and light grey indicate non-effects. Darker shading indicates $p < 0.01$, while lighter shading indicates $0.01 < p < 0.05$. Red crosses: subareas that were not analysed due to too few years of data. The conditions for classifying effects as 'predominantly negative', 'predominantly positive', or 'non-monotonic' are given in Supplement 3 at www.int-res.com/articles/suppl/m480p263_suppl.pdf; the actual shapes of the effects are given in Supplement 2 (Fig. S4)

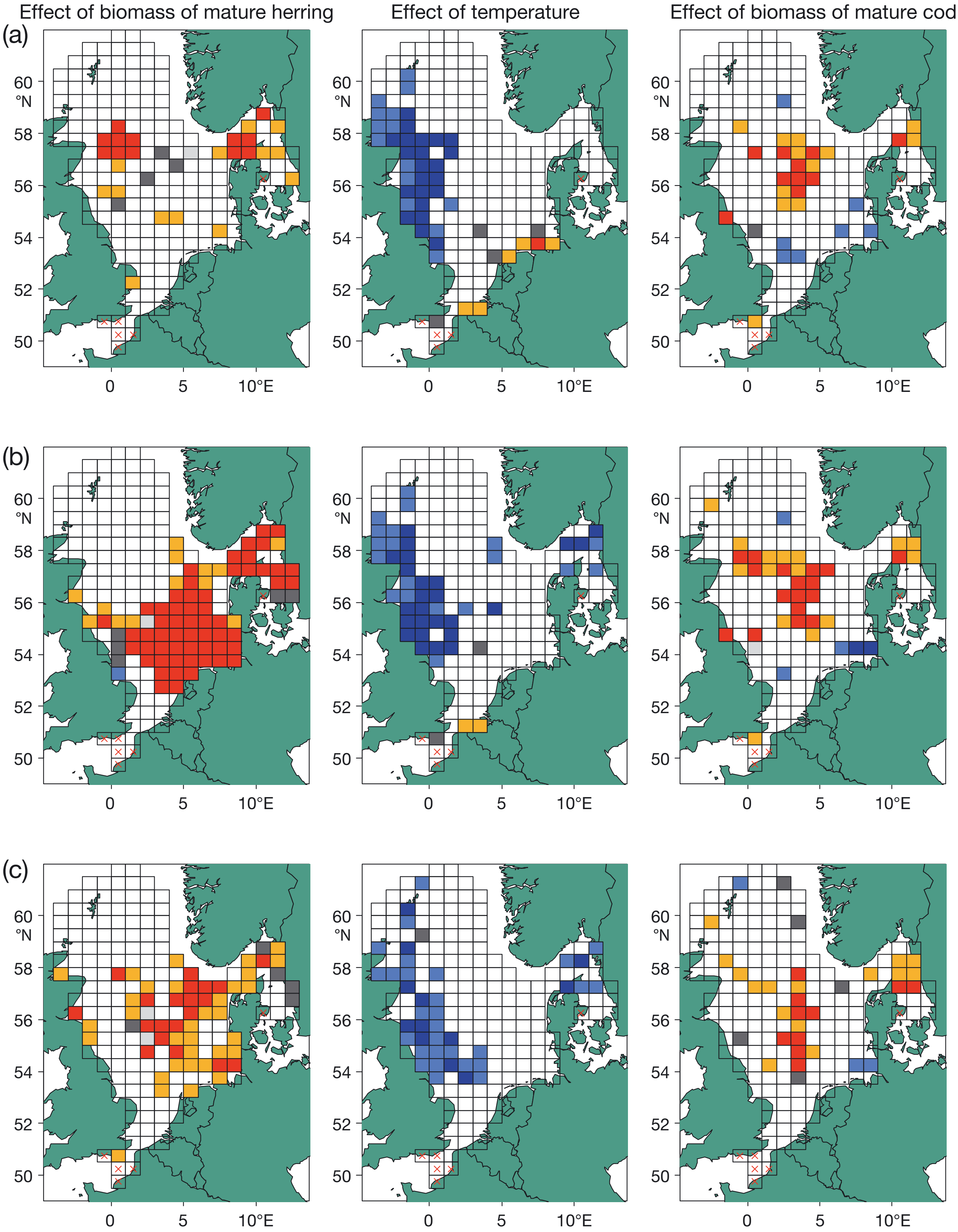

Fig. 5. *Clupea harengus*. Effect of each predictor variable on the abundance of young herring. Each row of graphs represents one model: (a) Eq. (4), (b) Eq. (5) and (c) Eq. (6). Colours and symbols as in Fig. 4. The actual shapes of the effects are given in Supplement 2 (Fig. S6)

Our analysis, however, does not explicitly take into account the migrations of adult fish or the drift of eggs and larvae. To investigate the sensitivity of the results to this limitation, we assumed either that spawners contribute only to recruitment in their own subarea, or that they contribute to recruitment anywhere in the NS. These 2 alternative assumptions are extreme end-points: Both cod and herring have eggs and larvae that drift passively with the currents for some time, and, in both cases, the spawning grounds are separate from nursery areas. However, the young are not spread by random all over the NS (e.g. Heath et al. 2008, Gröger et al. 2010).

Both NS cod and NS herring have been found to have substantial spatial structure. In the case of cod, it spawns in several locations in the NS, mostly in the western and southern parts, and the present consensus is that NS cod is likely to be 'composed of a complex of more or less isolated sub-stocks' (ICES 2011c). Based on microsatellite DNA markers, Hutchinson et al. (2001) found 4 genetically distinct groups. Advection patterns indicate that cod in the southern NS (the German Bight, the Dogger Bank and the Southern Bight) are quite isolated from cod in the remaining NS (Heath et al. 2008). Also, the elemental signature of the otoliths indicates that most adults originate from local nursery areas, and that there does not appear to be detectable exchange between spawning areas >200 km apart (Wright et al. 2006). Thus, Wright et al. (2006) argued that the NS cod forms a metapopulation, and we would expect cod recruitment to depend on the abundance of spawners in an upstream area. In the case of NS herring, it has 3 or 4 spawning components in separate locations on the west side of the NS; spawning starts in the north in August and ends in January in the south (Daan et al. 1990, Gröger et al. 2010). The herring juveniles of several stocks mix (Ruzzante et al. 2006, Gröger et al. 2010), and as they grow, they gradually move into deeper water; by Age 1 they are spread over the entire southern NS. Thus, for herring, it seems that the most correct assumption is that spawners contribute to recruitment anywhere in the NS (i.e. Fig. 5b). However, herring are more geographically structured than previously believed, as Ruzzante et al. (2006) found clear and temporally stable genetic and morphologic differences between fish from 3 areas (NS, Skagerrak and Kattegat/western Baltic), in spite of the mixing of these 3 stocks in the nursery, feeding and overwintering aggregations. In the cases of both cod and herring, we found the effects of temperature and interspecific predation to be robust to the choice of assumptions.

The relationship between cod and herring has been the subject of much discussion (Cushing 1980, Hislop 1996). It is striking that the papers that suggest a substantial effect of herring predation on cod are based on modelling or statistical analyses (Andersen & Ursin 1977, Fauchald 2010, Speirs et al. 2010, Minto & Worm 2012, present paper). In contrast, earlier work based on herring stomach samples (Daan et al. 1985, Last 1989) concluded that herring predates on an insignificant amount of cod eggs. However, recent analyses have revealed that predation on eggs and larvae may be highly localized in space and time (Segers et al. 2007, Temming et al. 2007, Pliru et al. 2012), and stomach samples collected during single seasons may simply miss these important bouts. For the Barents Sea, time-series studies indicating that capelin are heavily affected by herring predation (Hamre 1994, Gjøsæter & Bogstad 1998, Hjermann et al. 2004) were published several years before field studies were actually able to confirm substantial predation (Hallfredsson & Pederson 2009). NS herring, being an effective zooplankton feeder, may also be a significant competitor with larval and juvenile cod for food (Cushing 1980, Hislop 1996). For the Norwegian Sea, the most recent studies estimate that herring consumes as much as 50 million tonnes of zooplankton annually and can reduce other species' consumption of the key zooplankton *Calanus finmarchicus* by >50% (Utne et al. 2012). Our analysis suggests that predation and/or competition from herring may—together with high temperatures—explain some of the decline in NS cod, namely the recruitment failure of the southernmost component of NS cod. Hislop (1996) also pointed to spatial patterns when he argued that the mid-1960s 'gadoid outburst' of cod, whiting and haddock could not have been caused by the reduction of herring: namely, the 1950s to 1960s decline of herring occurred first in the southern NS and later in the northern NS, but the recruitment of the northern-spawning haddock did not increase earlier than that of cod or whiting, which spawn in the south NS as well. Also, Huse et al. (2008) have suggested a similar effect of herring on Norway pout in the NS; they found that the stock–recruitment relationship for this species improved substantially when one considered only the part of the Norway pout SSB not overlapping with herring.

The importance of quantifying predator–prey spatial overlap is increasingly being recognized in analyses of recruitment variation and in the development of recruitment models in the NS. For example, using IBTS data at smaller spatial scales, Temming et al. (2007) illustrated that dense local aggregations of juvenile cod could be eliminated by predation, while Kempf et al. (2009) considered the roles of other predators, spatial overlap and temperature to interact in constraining cod recruitment. In a management context, the roles of spatial overlap are increasingly being considered in the development of multispecies NS assessment models (e.g. Kempf et al. 2010), although our analyses extend beyond the species-specific to include life stage/size-specific interactions involving both adults and early life stages.

The consequences and implications of the life stage-specific interactions that we have quantified between species extend beyond the NS. In the Northwest Atlantic, consistent with the hypothesis of role reversals, the cod recruitment rate was inversely related to pelagic fish biomass in the southern Gulf of St. Lawrence (Swain & Sinclair 2000). On the eastern Scotian Shelf, the combined recruitment of several large-bodied benthic fishes increased only after the biomass of small pelagic fishes declined, suggesting a predator–prey reversal and an explanation for the lagged recovery of benthic fishes following almost 2 decades of fishing moratoria (Frank et al. 2011). Swain & Mohn (2012) reported that for cod alone, recruitment rate (annual recruitment divided by Age 5+ biomass) was unrelated to forage fish biomass on the eastern Scotian Shelf. However, a meaningful determination of recruitment rates is critically dependent on knowing the annual reproductive potential of the parent stock, which cannot be properly evaluated when significant changes in age and size at maturity, sex ratio, condition factors, or the potential for skipped spawning seasons have occurred (Rideout et al. 2006, Mohn & Rowe 2012) and been ignored (Marshall et al. 2006, Marshall 2009). Complex interactions between life stages, however, are not unique to pelagic fish preying upon the pelagic early life stages of benthic fishes, as the opposite interactions between benthic and pelagic fishes have also recently been documented, with implications for population management. In the Northwest Atlantic, the dominant benthic fish, haddock *Melanogrammus aeglefinus*, has been implicated in the decline of Atlantic herring recruitment, due to its overlapping with, and preying upon, benthic herring eggs (Richardson et al. 2011). These complex interactions in other areas serve to highlight the need to consider spatial and stage-specific interactions, and the consequences of pelagic × benthic interactions influencing population dynamics via more than a single life stage.

Several studies have indicated that temperature has a negative effect on NS cod through lower larval survival due to changes in the plankton community (Beaugrand 2003). This is supported by our study, which also clearly indicates that these negative effects are limited to the southern NS. It has also been suggested that temperatures in the NS are currently so high that they could have a direct negative effect on adult cod via physiological mechanisms (Drinkwater 2005, Pörtner & Knust 2007). However, Righton et al. (2010) found that southern NS cod do not avoid high temperatures and they have the highest growth rates of all studied stocks, despite experiencing temperatures that have been shown to be very stressful in laboratory experiments. However, during the spawning season (when the survey used in our study was conducted), they found a much narrower temperature range for cod, with a preferred temperature of 5 to 10°C across widely separated cod stocks.

When we detrended the data, i.e. removed long-term changes, much of the effects became weaker and were no longer statistically significant. This would be expected if a variable not included in the analysis, and which has a strong trend, was the actual cause of recruitment change. However, it is hard to think of any such effects that are unrelated to the included variables (e.g. fishing effort would mainly decrease recruitment by decreasing SSB). The weakening of the effects can also expected as a purely statistical effect, as much of the variability in the data is removed, decreasing the statistical power of the analysis. Thus, the statistical power might not be sufficient to detect the signal through the noise. A high level of noise (i.e. high variability on small spatial and temporal scales) is unavoidable in analyses of survey data, due to the inherent patchiness of marine fish populations.

It should be noted that the survey method, bottom trawling in winter, is designed to catch young herring as well as demersal fish like cod. Therefore, the method considerably underestimates adult herring, which live more pelagically. However, the abundance patterns seen in the survey are quite consistent with the assessment estimates (Fig. S8b in Supplement 2), which is not surprising, as the catchability in this survey was also used in the assessment of cod and herring biomass (so-called tuning). This suggests that our analyses and interpretations are not biased by the quality of the survey data.

Finally, we note that predation/competition may interact with temperature and spawning stock size. We chose to assume additive effects of the 3 predictor variables, as allowing for interactions would result in too many spurious effects. One may argue that our finding that recruitment is driven by different factors in different locations may be a result of this assumption. Thus, the reason that variable *x* has a significant effect in one place but not in another, may not be the locations per se, but because the range of variable *x* differs between the sites, or because it interacts with another variable *y*. For instance, Kempf et al. (2009) found that mean SST during the second quarter had a negative effect on recruitment up to a level of 9°C but not above this threshold. This result, however, appears to conflict with the fact that cod in the NS already live near the warmest edge of their distributional range in the eastern Atlantic, so we would expect rather the opposite, i.e. that the negative effects of temperature would be aggravated at high temperatures (Drinkwater 2005). This expectation is, however, not supported by the results of Ottersen et al. (2013); while they substantiated that NS cod are affected by temperature, they found no significant changes in recruitment dynamics over the period from 1963 to 2007.

In conclusion, this study quantified spatial variance in the leading mechanisms proposed to affect the variations in important ecosystem components such as cod and herring. Our results support the interpretation that recruitment is affected by a combination of spawning stock abundance and sea temperatures (as suggested by, e.g. Durant et al. 2005, Kempf et al. 2009, Olsen et al. 2011). However, a large, temperate area like the NS can hardly be viewed as a single ecosystem; rather it is a collection of ecosystems the heterogeneous climatic conditions, habitats and species compositions of which differ quite strongly, although their borders are diffuse and unstable and migration among them may be high. While taking this into account obviously makes studies of ecosystem processes more difficult, changes in the spatial structure of marine populations is important, as they can affect the resilience and recovery potential of populations (Ciannelli et al. 2013). The present results support the view that a good understanding of NS cod dynamics is impossible if spatial variability is not taken into account. Although there is no field evidence of substantial predation on cod eggs in the NS, our findings are consistent with the hypothesis that herring have a negative impact on cod recruitment in the German Bight, an area formerly known as a key area for cod recruits (Daan et al. 1990), either through egg predation or competition. However, the direction of causal relationships is inherently difficult to confirm based on time-series data only, despite our efforts to quantify levels of uncertainty and compare multiple models. The existence of hysteresis, or other mechanisms leading to Allee effects in exploited fish, has important implications for management. Thus, it is important to continue developing and refining methods that are able to take into account spatial variability in a parsimonious manner and to incorporate spatially variable ecosystem processes into management models (Kempf et al. 2010).

Acknowledgements. We thank the Research Council of Norway (RCN) for funding the workshop Tropharct through the MICO project (No. 186310, Match/Mismatch and Ecosystem). This work is associated with the IMBER regional program, Ecosystem Studies of Sub-Arctic Seas (ESSAS). D.O.H. was funded by the RCN (No. 200497, ADMAR). The SST data were provided by the Data Support Section of the Computational and Information Systems Laboratory at the National Center for Atmospheric Research. NCAR is financed by grants from the National Science Foundation. We are grateful to Per Fauchald, Marcos Llope and 3 anonymous reviewers for commenting on an earlier version of the paper.

LITERATURE CITED

Andersen KP, Ursin E (1977) A multi species extension to the Beverton and Holt theory of fishing with accounts of phosphorus circulation and primary production. Medd Kom Dan Fisk Havunders Fisk 7:319–436

➤ Bartsch J, Brander K, Heath M, Munk P, Richardson K, Svendsen E (1989) Modeling the advection of herring larvae in the North Sea. Nature 340:632–636

➤ Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. Fish Oceanogr 12:270–283

➤ Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–664

➤ Beisner BE, Haydon DT, Cuddington K (2003) Alternative stable states in ecology. Front Ecol Environ 1:376–382

➤ Brander KM (2005) Cod recruitment is strongly affected by climate when stock biomass is low. ICES J Mar Sci 62: 339–343

Ciannelli L, Fisher JAD, Skern-Mauritzen M, Hunsicker ME, Hidalgo M, Frank KT, Bailey KM (2013) Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. Mar Ecol Prog Ser 480:227–243

➤ Cook RM, Sinclair A, Stefansson G (1997) Potential collapse of North Sea cod stocks. Nature 385:521–522

Courchamp F, Berec L, Gascoigne J (2008) Allee effects in ecology and conservation. Oxford University Press, Oxford

➤ Cushing DH (1980) The decline of the herring stocks and the gadoid outburst. J Cons Int Explor Mer 39:70–81

➤ Daan N, Rijnsdorp AD, Vanoverbeeke GR (1985) Predation by North Sea herring *Clupea harengus* on eggs of plaice *Pleuronectes platessa* and cod *Gadus morhua.* Trans Am Fish Soc 114:499–506

➤ Daan N, Bromley PJ, Hislop JRG, Nielsen NA (1990) Ecology of North Sea fish. Neth J Sea Res 26:343–386

➤ de Roos AM, Persson L, Thieme HR (2003) Emergent Allee effects in top predators feeding on structured prey populations. Proc Biol Sci 270:611–618

Drinkwater K (2005) The response of Atlantic cod (*Gadus morhua*) to future climate change. ICES J Mar Sci 62: 1327–1337

Durant JM, Hjermann DO, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelli N, Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecol Lett 8:952–958

Fauchald P (2010) Predator–prey reversal: a possible mechanism for ecosystem hysteresis in the North Sea? Ecology 91:2191–2197

Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. Science 308:1621–1623

Frank KT, Petrie B, Fisher JAD, Leggett WC (2011) Transient dynamics of an altered large marine ecosystem. Nature 477:86–89

Gjøsæter H, Bogstad B (1998) Effects of the presence of herring (*Clupea harengus*) on the stock–recruitment relationship of Barents Sea capelin (*Mallotus villosus*). Fish Res 38:57–71

Gröger JP, Kruse GH, Rohlf N (2010) Slave to the rhythm: how large-scale climate cycles trigger herring (*Clupea harengus*) regeneration in the North Sea. ICES J Mar Sci 67:454–465

Hallfredsson EH, Pedersen T (2009) Effects of predation from juvenile herring (*Clupea harengus*) on mortality rates of capelin (*Mallotus villosus*) larvae. Can J Fish Aquat Sci 66:1693–1706

Hamre J (1994) Biodiversity and exploitation of the main fish stocks in the Norwegian Sea–Barents Sea ecosystem. Biodivers Conserv 3:473–492

Heath MR, Kunzlik PA, Gallego A, Holmes S, Wright PJ (2008) A model of meta-population dynamics for North Sea and West of Scotland cod—the dynamic consequences of natal fidelity. Fish Res 93:92–116

Hislop JRG (1996) Changes in North Sea gadoid stocks. ICES J Mar Sci 53:1146–1156

Hjermann DØ, Stenseth NC, Ottersen G (2004) Indirect climatic forcing of the Barents Sea capelin: a cohort effect. Mar Ecol Prog Ser 273:229–238

Horwood J, O'Brien C, Darby C (2006) North sea cod recovery? ICES J Mar Sci 63:961–968

Huse G, Salthaug A, Skogen MD (2008) Indications of a negative impact of herring on recruitment of Norway pout. ICES J Mar Sci 65:906–911

Hutchinson WF, Carvalho GR, Rogers SI (2001) Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. Mar Ecol Prog Ser 223:251–260

ICES (International Council for the Explorations of the Sea) (2010) Manual for the international bottom trawl surveys, Revision VIII. Addendum to report of the International Bottom Trawl Survey Working Group. ICES CM 2010/SSGESST:06

ICES (International Council for the Explorations of the Sea) (2011a) Report of the Working Group on the Assessment of demersal stocks in the North Sea and Skagerrak (WGNSSK). ICES CM 2011/ACOM:13

ICES (International Council for the Explorations of the Sea) (2011b) Report of the Herring Assessment Working Group for the area south of 62° N (HAWG). ICES CM 2011/ACOM:06

ICES (International Council for the Explorations of the Sea) (2011c) Report of the ICES Advisory Committee 2011. ICES Advice, 2011, Book 6. ICES, Copenhagen

Kempf A, Floeter J, Temming A (2009) Recruitment of North Sea cod (*Gadus morhua*) and Norway pout (*Trisopterus esmarkii*) between 1992 and 2006: the interplay between climate influence and predation. Can J Fish Aquat Sci 66:633–648

Kempf A, Dingsor GE, Huse G, Vinther M, Floeter J, Temming A (2010) The importance of predator–prey overlap: predicting North Sea cod recovery with a multispecies assessment model. ICES J Mar Sci 67:1989–1997

Kirby RR, Beaugrand G, Lindley JA (2009) Synergistic effects of climate and fishing in a marine ecosystem. Ecosystems 12:548–561

Köster FW, Möllmann C (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES J Mar Sci 57:310–323

Last JM (1989) The food of herring, *Clupea harengus*, in the North Sea, 1983–1986. J Fish Biol 34:489–501

Llope M, Daskalov GM, Rouyer TA, Mihneva V, Chan KS, Grishin AN, Stenseth NC (2011) Overfishing of top predators eroded the resilience of the Black Sea system regardless of the climate and anthropogenic conditions. Glob Change Biol 17:1251–1265

Marshall CT (2009) Implementing information on stock reproductive potential in fisheries management: the motivation, challenges and opportunities. In: Jakobsen T, Fogarty MJ, Megrey BA, Moksness E (eds) Fish reproductive biology: implications for assessment and management. Blackwell Publishing, Chichester, p 395–420

Marshall CT, Needle CL, Thorsen A, Kjesbu OS, Yaragina NA (2006) Systematic bias in estimates of reproductive potential of Atlantic cod (*Gadus morhua*) stock: implications for stock-recruit theory and management. Can J Fish Aquat Sci 63:980–994

May RM (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471–477

Minto C, Worm B (2012) Interactions between small pelagic fish and young cod across the North Atlantic. Ecology 93:2139–2154

Mohn RK, Rowe S (2012) Recovery potential assessment for the Laurentian south designatable unit of Atlantic cod (*Gadus morhua*): the eastern Scotian Shelf cod stock (NAFO Div. 4VsW). DFO Can Sci Advis Sec Res Doc 2011/138. Department of Fisheries and Oceans, Ottawa

Möllmann C, Mueller-Karulis B, Kornilovs G, St John MA (2008) Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback coops in a simple ecosystem. ICES J Mar Sci 65:302–310

NOAA (National Oceanic and Atmospheric Administration) (2011) ICOADS 1 degree. Available at: www.esrl.noaa.gov/psd/data/gridded/data.coads.1deg.html (accessed 1 May 2011)

Olsen EM, Ottersen G, Llope M, Chan KS, Beaugrand G, Stenseth NC (2011) Spawning stock and recruitment in North Sea cod shaped by food and climate. Proc Biol Sci 278:504–510

Ottersen G, Stige LC, Durant JM, Chan KS, Rouyer TA, Drinkwater KF, Stenseth NC (2013) Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. Mar Ecol Prog Ser 480:205–225

Planque B, Frédou T (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 56:2069–2077

Pliru A, van der Kooij J, Engelhard GH, Fox CJ, Milligan SP, Hunter E (2012) Sprat feeding behaviour, selective predation, and impact on plaice egg mortality. ICES J Mar Sci 69:1019–1029

Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315:95–97

Richardson DE, Hare JA, Fogarty MJ, Link JS (2011) Role of egg predation by haddock in the decline of an Atlantic herring population. Proc Natl Acad Sci USA 108: 13606–13611

Rideout RM, Morgan MJ, Lilly GR (2006) Variation in the frequency of skipped spawning in Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador. ICES J Mar Sci 63:1101–1110

Righton DA, Andersen KH, Neat F, Thorsteinsson V and others (2010) Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. Mar Ecol Prog Ser 420:1–13

Ruzzante DE, Mariani S, Bekkevold D, Andre C and others (2006) Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. Proc Biol Sci 273:1459–1464

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Segers FHID, Dickey-Collas M, Rijnsdorp AD (2007) Prey selection by North Sea herring (*Clupea harengus*), with special reference to fish eggs. ICES J Mar Sci 64:60–68

Speirs DC, Guirey EJ, Gurney WSC, Heath MR (2010) A length-structured partial ecosystem model for cod in the North Sea. Fish Res 106:474–494

Swain DP, Mohn RK (2012) Forage fish and the factors governing recovery of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf. Can J Fish Aquat Sci 69:997–1001

Swain DP, Sinclair AF (2000) Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Can J Fish Aquat Sci 57:1321–1325

Temming A, Floeter J, Ehrich S (2007) Predation hot spots: large scale impact of local aggregations. Ecosystems 10:865–876

Utne KV, Hjøllo SS, Huse G, Sogen M (2012) Estimating the consumption of *Calanus finmarchicus* by planktivorous fish in the Norwegian Sea using a fully coupled 3D model system. Mar Biol Res 8:527–547

Walters C, Kitchell JF (2001) Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Can J Fish Aquat Sci 58:39–50

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R Stat Soc, B 73:3–36

Wright PJ, Neat FC, Gibb FM, Gibb IM, Thordarson H (2006) Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. J Fish Biol 69(Suppl C):181–199

Submitted: June 13, 2012; Accepted: February 26, 2013

Proofs received from author(s): April 3, 2013

Vol. 480: 277–287, 2013
doi: 10.3354/meps10308

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 22

Contribution to the Theme Section 'Harvested fish stocks in a changing environment'

Population growth across heterogeneous environments: effects of harvesting and age structure

Joël M. Durant[1,*], Manuel Hidalgo[1,5], Tristan Rouyer[1,6], Dag Ø. Hjermann[1,7], Lorenzo Ciannelli[2], Anne Maria Eikeset[1], Natalia Yaragina[3], N. C. Stenseth[1,4]

[1]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway
[2]College of Earth, Ocean and Atmospheric Sciences, Oregon State University, 104 COAS Administration Building, Corvallis, Oregon 97331-5503, USA
[3]Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), 6 Knipovich Street, Murmansk 183038, Russia
[4]Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway

[5]*Present address:* Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Moll de Ponent s/n, 07015 Palma, Spain
[6]*Present address:* Laboratoire Ressources Halieutiques de Sète, Ifremer, Station de Sète, Av. Jean Monnet, BP 171 – 34203 Sète Cedex, France
[7]*Present address:* Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, 0349 Oslo, Norway

ABSTRACT: Population growth is affected by several factors such as climate, species interaction and harvesting pressure. However, additional complexity can arise if fishing increases the sensitivity to environmental variability. To predict the effects of fisheries and climate on marine populations, there is a need for improved understanding of how they affect key ecological processes such as population growth. In this study, we used a comparative approach investigating commercially fished species across different ecosystems: the Norwegian Sea–Barents Sea (Northeast Arctic cod), the North Sea (North Sea cod), the Atlantic Ocean (European hake), the Mediterranean Sea (European hake), and the Gulf of Alaska and Bering Sea (walleye pollock). Our objective was to compare the effects of commercial fisheries, age structure and environmental variability on population growth rate. We show that although all stocks experienced a decline in abundance, only 3 of them showed a concomitant decreasing trend in generation time (South Atlantic hake, North Atlantic hake and Northeast Arctic cod), suggesting a fishing-induced erosion in their age structure. Intra-specific analysis shows that changes in generation time triggered an increase in the relative contribution of recruitment to population growth. Furthermore, the contribution from recruitment to population growth changes due to large-scale climate indices or regional-scale environmental covariates, such as sea temperature. This study illustrates how and where the interaction between large-scale ecological patterns and regional/short-scale processes are important for designing management regulations.

KEY WORDS: Barents Sea · Mediterranean Sea · Bering Sea · Cod · *Gadus morhua* · European hake · *Merluccius merluccius* · Pollock · *Theragra chalcogramma* · Leslie matrix · Fisheries

INTRODUCTION

Population dynamics in general and population growth in particular is affected by several factors such as climate, species interactions and harvesting pressure. Harvesting pressure has been proposed as a possible pathway for an increasing sensitivity of marine fish populations to climate (e.g. Rouyer et al. 2011, but see Ottersen et al. 2013, this Theme Section). Thus, in addition to the obvious consequences of high and often size-selective mortality from commercial fishing (loss of older and larger individuals), interacting effects between exploitation and environment influence fish stock production (Hsieh et al. 2010).

*Email: joel.durant@bio.uio.no

These complex interactions may also depend on the life cycle characteristics of the species studied. The life cycles of many fish species in high-latitude seas have adapted to a strong pulse of primary productivity in spring, short summers, and partial ice cover during parts of the year. Also, food resources and suitable habitat for young are often spatially clustered. For these fish species, evolutionary pressure pushes towards developing adaptive strategies for the timing of life cycle events (e.g. reproduction), the length of spawning and feeding migrations, and the use of environmental cues (e.g. photoperiod and temperature). Analogously, some oligotrophic systems, such as the Mediterranean Sea, may display similar adaptive life history strategies to match the favourable environmental conditions occurring at small spatial and temporal scales (Hidalgo et al. 2009).

Specific strategies, such as greater longevity and bet-hedging, allow species inhabiting high latitudes to survive until encountering favourable conditions for reproduction within a particular temporal window, whereas more temperate/tropical species typically have more opportunistic reproduction strategies (Murphy 1968, Fromentin & Fonteneau 2001) with faster traits (earlier maturation, faster growth, reduced age structure). For instance, cod stocks display a broad range of life history traits related to the mean temperature of their environment (Brander 1995). Since high-latitude species are more sensitive to environmental variability than temperate/tropical species and can display broad age distributions, which are potentially affected by exploitation (Miller et al. 1991, Brunel & Boucher 2006, Rouyer et al. 2011), comparing different species inhabiting across the latitudinal gradient will provide insight into important aspects of such strategies.

Fisheries management challenges are increased by climate change (Le Maho & Durant 2011). Indeed, when looking at the effect of harvesting on fish stocks (e.g. reduction of abundance, distribution, biodiversity or genetic diversity; age truncation; juvenescence) fisheries have also to take into account the effect of climate change on the fish population dynamics and trophic interactions (Cury et al. 2008). However, separating the environmental effects on marine fish stock dynamics from those of exploitation has been a long-term challenge. In this study we investigated how climate, fishing and internal population properties such as age structure operate across different ecosystems. Specifically, we explored how external forcing (climate and fishing) and recruitment modulate the population dynamics of fish within different environments. To do so, we calculated the population growth based on yearly Leslie matrices and its elasticity to recruitment of 7 commercially exploited stocks: the European hake *Merluccius merluccius* in the Northeast Atlantic Ocean (Southern and Northern) and the Mediterranean Sea, the cod *Gadus morhua* in the North Sea and Barents Sea, and the pollock *Theragra chalcogramma* in the Bering Sea and the Gulf of Alaska. The elasticity is the percentage change in output for a certain percentage change in input; it illustrates the changes in population growth as a ratio of changes in either survival or recruitment. This tells us where the population is more sensitive to modification of its vital rates. Modeling the elasticities for different stocks is expected to give new insights into how recruitment that is affected by climate, age structure, or fishing pressure in turn affects the population growth rate. Our aim is to explore the differences produced by external and internal drivers contributing to the variability in population growth rate across different ecosystems. To do so, we compared stocks with different fishing pressure (from fished to overfished) and from different latitudes (high to intermediate latitudes).

MATERIALS AND METHODS

The fish data used (age-specific abundance, fishing mortality, and maturity ogives) were extracted from assessments made using virtual population analyses (VPA; i.e. based on commercial catch data, Lassen & Medley 2001 and references therein for methods) tuned to the survey data. From these data we calculated the average fishing mortality (F) for each year. Table 1 summarizes the data used. Fig. 1 displays the general geographical localisation of each stock.

European hake *Merluccius merluccius*

The European hake (here called hake) (Fig. S1 in the Supplement at www-int-res.com/articles/suppl/m480p277_supp.pdf) is a groundfish species inhabiting the North Atlantic European coast (from north of Norway to the Mauritanian waters) and the entire Mediterranean Sea. Three areas (Fig. 1) for which age-structured information on hake was available are considered in this study (FAO-GFCM 2009, ICES 2009): 2 in the Atlantic Ocean referred to (for management purposes) as North Atlantic stock (NA hake) and South Atlantic stock (SA hake), and one in the Mediterranean Sea around the Balearic Islands

Table 1. Data description of the stocks considered. NEA: Northeast Arctic; NS: North Sea; EBS: Eastern Bering Sea; GOA: Gulf of Alaska; NA: Northern Atlantic; SA: Southern Atlantic; BI: Balearic Islands; VPA: virtual population analysis; NAO: North Atlantic Oscillation; GULF: annual mean values of the Gulf Stream; PDO: Pacific Decadal Oscillation; UI: upwelling index; IDEA: hydro-climatic index based on the air-sea heat fluxes in the Gulf of Lions during winter. +: data used; –: no data

	NEA cod	NS cod	EBS pollock	GOA pollock	NA hake	SA hake	BI hake
VPA years[a]	1946–2010	1963–2011	1964–2010	1961–2010	1978–2008	1982–2008	1980–2008
Years used	1946–2000	1963–2007	1982–2004	1983–2002	1979–2003	1983–2003	1981–2004
Population life history variables							
Age range assessed (yr)	3–12+	1–7+	1–10+	2–10+	0–8+	0–8+	0–5+
Maturity ogives	Annual	Mean	Mean	Mean	Annual	Annual	Mean
Recruits number	+	+	+	+	+	+	+
Elasticity	+	+	+	+	+	+	+
Environmental variables							
Temperature (°C)	+	+	+	+	+	+	+
NAO	+	+	–	–	+	+	+
GULF	–	–	–	–	+	+	–
PDO	–	–	+	+	–	–	–
UI	–	–	–	–	–	+	–
IDEA	–	–	–	–	–	–	+
Fishing mortality (F)	+	+	+	+	+	+	+

[a] VPA data were not reliable in the later years, so we used a shorter time series than available

(BI hake). Hake is regarded as overharvested in all 3 areas (ICES 2009). For each stock, F over age was calculated for the most harvested age classes of each area (based on the F at age profile): $F_{2–5}$ for SA hake, $F_{2–6}$ for NA hake and $F_{2–4}$ for BI hake (the subscripts indicate the ages used in yr).

Cod *Gadus morhua* of the Lofoten-Barents Sea and North Sea systems

The Northeast Arctic (NEA) cod population inhabiting the Barents Sea is at present the world's largest stock of Atlantic cod (Worm & Myers 2003) (Fig. S2 in the Supplement). NEA cod spawns along the Norwegian coast. The North Sea (NS) cod is another cod population whose abundance has declined steadily since the 1960s (ICES 2011b, Hjermann et al. 2013, this Theme Section). Age-structured information on NEA cod is available from 1946 (ICES 2011a) and for NS cod from 1963 (ICES 2011b). For NS cod, proportion of mature individuals per age was given as a mean per age class. Average fishing mortality was calculated for age groups 5–10 ($F_{5–10}$) for NEA cod and age groups 2–4 ($F_{2–4}$) for NS cod.

Walleye pollock *Theragra chalcogramma* of the Bering Sea and Gulf of Alaska systems

Walleye pollock (Fig. S2 in the Supplement) currently constitutes the second largest single-species fishery in the world. Information on Eastern Bering Sea (EBS) pollock and Gulf of Alaska (GOA) pollock year-class strength is available back to 1964 (Ianelli et al. 2009, Dorn et al. 2010). However, since catch data are uncertain prior to 1982, we used data only from 1982 onwards for EBS pollock and 1983 onwards for GOA pollock. For EBS pollock, the proportion of matures per age was given as a mean per age class. For GOA pollock, annual estimates of the age-specific proportion of mature individuals was available from 1983 onward. Fishing mortality is given by $F_{6–10}$ and $F_{5–8}$ for EBS and GOA pollock, respectively.

Environmental data

Climate indices and regional-scale hydroclimatic variables were used as potential environmental drivers. Climate indices capture complex spatio-temporal variability into a simple metric and integrate larger-scale climate processes and their variability (Hallett et al. 2004). They have been shown to be good predictors for biological processes because they reduce complex space and time climatic variability into simple measures (Stenseth et al. 2003). We selected a relevant large-scale climate index for each studied stock. For the NA hake stock, we used annual mean values of the Gulf Stream index (GULF; http://web.pml.ac.uk/gulfstream/data.htm), which is the first principal component of the position of the North Wall of the Gulf Stream (Taylor 1995). For the SA hake stock we used an upwelling index (UI) obtained from

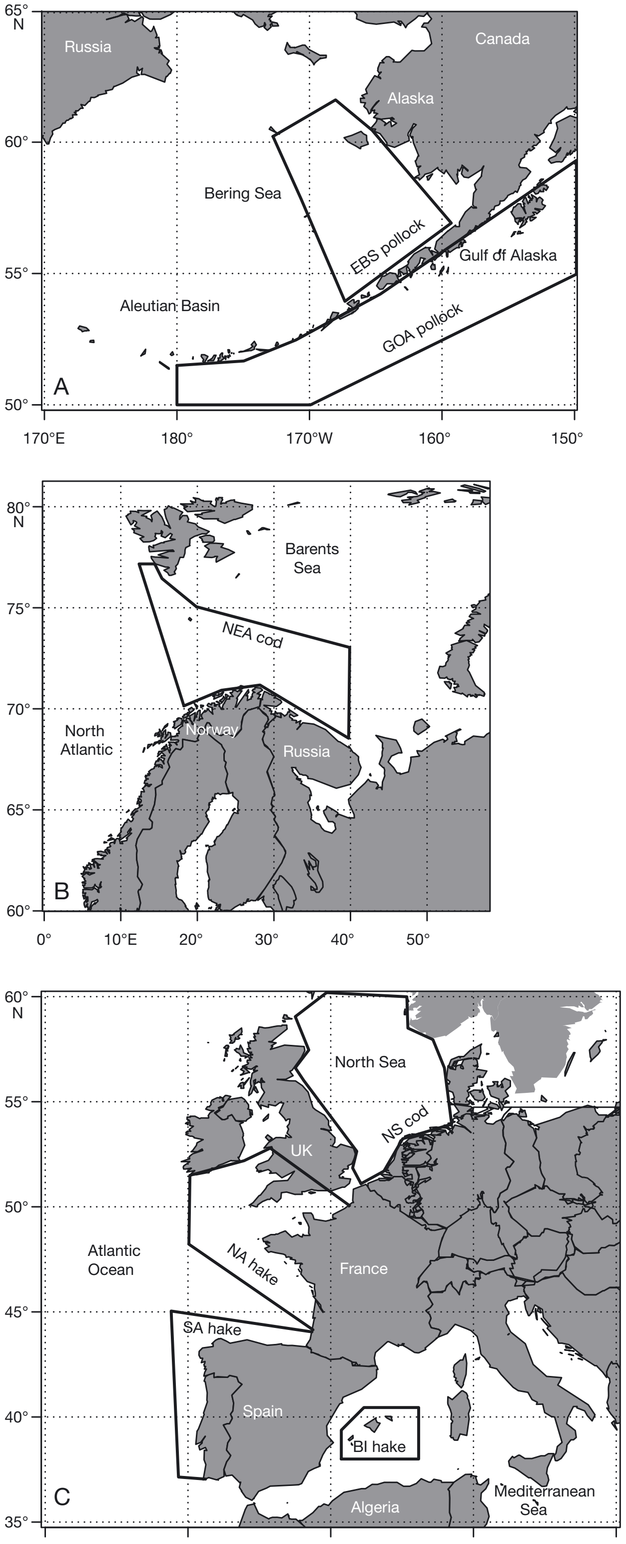

Fig. 1. Geographic location of the 7 stocks analysed. (A) Eastern Bering Sea (EBS) and Gulf of Alaska (GOA) pollock stocks. (B) Northeast Arctic (NEA) cod stock. (C) Northern Atlantic (NA), Southern Atlantic (SA) and Balearic Islands (BI) hake stocks

the monthly mean of daily offshore Ekman transport values ($-Q_x$; m^3 s^{-1} km^{-1}) offshore of the NW Spanish peninsula (see 'Methods' in Lavín et al. 1991). For the BI hake we used the IDEA index, a mesoscale (regional) hydro-climatic index based on the air-sea heat fluxes in the Gulf of Lions during winter (Massutí et al. 2008, Monserrat et al. 2008). For the NEA and NS cod, we used the North Atlantic Oscillation calculated for winter months (wNAO) (Hurrell & Deser 2009). For the EBS and GOA pollock we used the Pacific Decadal Oscillation calculated for winter months (wPDO).

Temperature was also used as a regional hydro-climatic variable potentially affecting the survival of early life stages of demersal species before settlement to the bottom. The temperature variables used have been reported to explain the dynamics for NA, SA and BI hake (Hidalgo et al. 2012), NEA (Hjermann et al. 2004) and NS cod (Hjermann et al. 2013), and GOA (Ciannelli et al. 2004) and EBS pollock (Mueter et al. 2011). Sea surface temperature (SST) for hake were obtained from the Climate Diagnostics Center (NCEP/NCAR) reanalysis fields (Kalnay et al. 1996) on a 1 × 1 degree grid and averaged over the area of each studied stock. Seasonal averages were calculated for each stock in winter (from December to February) and spring (from March to May) over each study area covering from early life stages survival to recruitment. For the Barents Sea we used yearly average sea temperature measured monthly at 0–200 m depth (ST) on the Russian Kola meridian transect (33° 30′ E, 70° 30′ N to 72° 30′ N) (see references in Hjermann et al. 2004). Time series of temperature for the NS cod and pollock stocks have been extracted over the distribution area of each stock from the extended reconstructed SST (NOAA_ERSST_V3) data set provided by the Physical Sciences Division of the NOAA Earth System Research Laboratory (www.esrl.noaa.gov/psd/). Data are available from 1960 to 2007 with 1 × 1 degree grid resolution for the cod from 1880 to 2009 and with 2 × 2 degree grid resolution for the pollock (based on the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) Sea Surface Temperature data). The data were averaged as follows: North Sea, Long 51.5° to 55.5°/Lat 0.5° to 4.5° for March to May ($\text{SST}_{\text{spring}}$; Hjermann et al. 2013); Bering Sea, Long −174° to −166°/Lat 56° to 60° for April to July. For the Gulf of Alaska, we extracted summer temperature (SST_{sum1}, Long −164° to −162°/Lat 50° to 54° for June–July–August) and winter temperature ($\text{SST}_{\text{wint2}}$, Long −164° to −160°/Lat 56° to 60° for December–January–February).

Calculation of population growth and elasticity

One way to reduce the complexity of age-structured population dynamics is to approach the question of population persistence through the use of Leslie matrix models (Leslie 1945, Caswell 2001, Hastings & Botsford 2006). Leslie matrix models are age-structured population models that use estimates of demographic rates for different age or size classes to project population dynamics (Caswell 2001). Vital rates are summarized in an annual transition matrix **A**, which defines the population sizes in the following year (n_{t+1}) as the product of the matrix **A** and the current year's population size (n_t), where the n_t values are vectors defined by the number of individuals within each age class. The long-term (asymptotic) population growth rate, *r*, is given by the logarithm of the dominant eigenvalue λ of **A** (Caswell 2001).

Here we compiled annual Leslie matrices $\mathbf{A}_t$ for each population studied. Note that $\mathbf{A}_t$ is compiled for the age structure measured in year *t* (hence valid only for the time frame year *t* to year *t* +1) as is the resulting yearly realized population growth rate, r_t.

For a given year, the transition matrix $\mathbf{A}_t$ is defined as follows:

$$A_t = \begin{pmatrix} \mathrm{RS}_{0,t} & \mathrm{RS}_{1,t} & \mathrm{RS}_{2,t} & \dots & \mathrm{RS}_{i\max,t} \\ S_{1-0,t} & 0 & 0 & \dots & 0 \\ 0 & S_{2-1,t} & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & S_{i\max-(i\max-1),t} & 0 \end{pmatrix}$$

where $S_{i-(i-1),t}$ is the survival between age class *i* at year *t* and age class *i*–1 at year *t*–1, and $\mathrm{RS}_{i,t}$ is the recruitment success of year class *i* at year *t*. $\mathrm{RS}_{i,t}$ is function of 2 components: the maturity rates and the proportion of survived recruits per age class.

An advantage of the Leslie matrix approach is the well-established derivation of elasticities of *r* to the vital rates in **A** (Caswell 2001). The elasticity matrix (**E**) describes the proportional response of *r* (through the first eigenvalue) to a proportional perturbation in the vital rates; in other words, it provides information on the relative contribution of vital rate(s) to the variations in r_t (details can be found in Caswell 2001). However, **A** gives the asymptotic population growth rate (i.e. the first eigenvalue of **A**), that is, the rate of growth of the population if the population has reached the stable age structure and if present environmental conditions were maintained indefinitely. Consequently, the asymptotic population growth can be biased at a short time scale for populations with no stable age structure due to environmental variations (e.g. large year-to-year variations in recruitment). In order to evaluate how recruitment affects spawning stock biomass and population numbers, we performed a transient elasticity (hereafter called elasticity, $\boldsymbol{e}_t$) analysis following the principles found in Caswell (2007). We used numerical methods based on simulating the population from year *t* to year *t*+*X*. If we do such a simulation using the year-specific transition matrices $\mathbf{A}_t$, the simulated population time series will be exactly equal to the input data. We calculated elasticity by increasing recruitment (i.e. the respective elements of the Leslie matrix) by 1% in a single year *t* and evaluated the effect of the perturbation on numbers of fish in the age classes exploited by fishing (*N*) in year *t*+*X*. This was repeated for every year *t* of the time series (except those that are less than *X* years from the end of the time series). In order to compare species, we selected *X* to be approximately equal to the specific generation time μ_t (the mean age of the parents of the offspring produced by a cohort over its lifetime; Caswell 2001). Thus, changes in recruitment at time *t* will have time to be reflected in the mature population at time *t*+*X*. μ_t is calculated from $\mathbf{A}_t$ and is itself changing every year (Figs. S1 & S2 in the Supplement).

Thus, the results of the perturbation depends not only on the year-specific transition matrices $\mathbf{A}_t$, but also on the age structure at the time of the perturbation, and the results differ from analyses of the elasticity of asymptotic growth rate (i.e. the first eigenvalue of $\mathbf{A}_t$).

Thereafter, elasticity is the sum of the elasticities due to recruitment for each year. For the generalized additive model (GAM) and generalized additive mixed model (GAMM) analyses, $\boldsymbol{e}_t$ was logit transformed: $\log(\boldsymbol{e}_t/(1-\boldsymbol{e}_t))$.

Note that in order to test whether the assumption of homogeneous fecundity can affect our results on population growth we have also calculated the population growth for each stock replacing abundance by biomass, without finding any significant differences in the results. We have therefore decided to keep the $\boldsymbol{e}_t$ obtained from abundance.

Statistical analysis

To investigate the effect of climate, anthropogenic pressure and the intrinsic demography in shaping stocks' elasticity to recruitment, we combined stock-specific analyses with meta-analyses across all stocks. We related the temporal variability in each stock's elasticity to recruitment, $\boldsymbol{e}_t$, to demographic variables such as fishing mortality and mean age of the spawning stock, as well as to each stock's specific environmental variables (both regional and large-scale climate indices) using GAM formulations as implemented in the mgcv library of R 2.11.1 (Wood & Augustin 2002). The rationale for also looking at the effect of environmental variables, which only indirectly affect $\boldsymbol{e}_t$, is that these variables may influence several demographic variables simultaneously, including natural mortality, which is unknown in our study. To smooth the resulting relationship, we set the maximum degrees of freedom for each smooth term to 2 (i.e. $k = 3$). We applied a backward selection strategy of GAM regressions based on minimisation of the generalized cross-validation criterion (GCV), and a measure of the proportion of variance explained (using unbiased estimators), R^2. A covariate was retained if its removal decreased GCV without affecting R^2 (Green & Silverman 1994). To model $\boldsymbol{e}_t$ for all the stocks in one model ,we used a GAMM formulation (GAMM in the mgcv library). As explanatory variables we used μ, F and SST (SST and ST alike). We thus added to the GAM formulation (fixed effects) as described above a random effect (stock names, years) to take into account the specific effect of the stocks and of the years data were sampled. Akaike's information criterion (AIC) values were used to select the best model instead of GCV because the latter does not account properly for the random effect. We found no auto-correlation (using the ACF function) in the residuals of the selected models. No significant correlation was found between covariates.

RESULTS

Time series of fish abundance, generation time μ, fishing mortality F, per-capita population growth rate and transient elasticity $\boldsymbol{e}_t$ for hake, cod and pollock stocks are presented in the supplementary material (Figs. S1 & S2). All the stocks showed a general temporal decrease in population numbers within the study period; this was more pronounced for NA hake, SA hake, NS cod and GOA pollock. The SA hake, NA hake and NEA cod stocks showed a decrease in μ, indicating a progressive and directional change in their age structure. These 3 stocks displayed an increase in the transient elasticity to recruitment with time, and indicated an increasing contribution of recruitment success to the population growth rate.

Elasticity analysis of recruitment changes

Table 2 displays the best stock-specific GAMs selected based on the minimisation of the GCV values (see Table S1 in the Supplement). The explained variance ranged from 16.6% NS cod to 68.8% for SA hake (Table 2, see Figs. S3 & S4 in the supplement; www.int-res.com/articles/suppl/m480p277_supp.pdf). We note that a decrease in the μ of the stock led to an increase in the elasticity to recruitment for the hake (3 stocks considered to be over-harvested), the NEA cod stock and the GOA pollock stock. Likewise, an increase in the fishing mortality led to an increase in the elasticity to recruitment for the EBS pollock stock as well as for the 2 cod stocks.

For all stocks, the elasticity to recruitment $\boldsymbol{e}_t$ was affected by the local environmental covariates, i.e. sea temperature. However, the shape and direction of the effect of sea temperature varied among stocks (Figs. S3 & S4 in the Supplement, Table 2). The regional hydroclimatic conditions such as UI influenced the SA hake stock, while large-scale climatic phenomena such as wPDO and wNAO influenced the 2 pollock stocks and the NS cod stock, respectively.

Table 2 also displays the best GAMM selected based on the minimisation of the AIC values (see Table S1 in the Supplement). The best GAMM showed that a decrease of the generation time μ of the stock led to an increase in the elasticity to recruitment (Fig. 2A) as did a decrease of the fishing mortality, albeit to a lesser extent (Fig. 2B). Looking at average values per stock, elasticity to recruitment was negatively related to the generation time of the stock (μ averaged over time) (Fig. 2C). The stocks displaying smaller averaged μ also displayed a greater mean elasticity to recruitment (linear model, F-statistic $F_{1,5} = 35.12$, $p < 0.002$, $R^2 = 0.88$), as growth rate depends more on recruitment for stocks with less mature age classes. The elasticity to recruitment was positively related to the mean fishing mortality (Fig. 2D). This relationship that was not significant (linear model, logit transformed $\boldsymbol{e}_t = -2.08 + 0.64F$, F-statistic $F_{1,5} = 0.53$, $p = 0.50$, $R^2 = 0.10$) and remained so when removing NEA cod, although the relationship was much improved (linear model, logit transformed $\boldsymbol{e}_t = -2.08 + 0.99F$, F-statistic $F_{1,4} = 4.88$, $p = 0.09$, $R^2 = 0.55$). Note that the relationship shown in Fig. 2D is inverse to the one shown in Fig. 2B (GAMM result on yearly data). Mean generation time was negatively related to mean fishing mortality when NEA cod was not taken into account (Fig. 2E). This relationship, which was not significant (linear

Table 2. Results of generalized additive models (GAMs) on transient elasticity of the population growth to recruitment change. $s(X,\mathrm{edf} = y)$ is the smoothing term, where X represents the explanatory variable and y is the estimated degrees of freedom (edf) of the smoothing term. When edf is 1, the relationship is linear. The general sense of the relationship is indicated with (+) and (–), (+,–) or (–,+) for quadratic relationships. p-values for each variable are indicated ($^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\ddagger}p < 0.1$). Dev: proportion of the null deviance explained by the model. NEA: Northeast Arctic; NS: North Sea; EBS: Eastern Bering Sea; GOA: Gulf of Alaska; NA: Northern Atlantic; SA: Southern Atlantic; BI: Balearic Islands; μ: mean age of the parents of the offspring produced by a cohort over its lifetime (generation time); F: fishing mortality for different age range as indicated; wPDO: winter Pacific Decadal Oscillation; UI: upwelling index, a regional hydro-climatic index; SST: sea surface temperature (°C) with 'wint' for winter and for GOA 'sum1' for summer at Location 1 and 'wint2' for winter at Location 2; ST: sea temperature at 0–200 m depth

Stock	Intercept	Generation time	Fishing mortality	Climate index	Sea temperature 1	Sea temperature 2	Dev (%)
SA hake	–1.45 ± 0.04***	μ^{***} edf=1 (–)		UI edf=1.72 (+,–)	$\mathrm{SST}_{\mathrm{wint}}$ edf=1 (+)		68.8
NA hake	–1.59 ± 0.03***	μ edf=1 (–)			$\mathrm{SST}_{\mathrm{wint}}^{\ddagger}$ edf=1 (–)	$\mathrm{SST}_{\mathrm{spring}}^{*}$ edf=1 (+)	51.6
BI hake	–1.44 ± 0.06***	μ^{*} edf=1.77 (–,+)			$\mathrm{SST}_{\mathrm{wint}}$ edf=1.56 (–,+)		39.1
NEA cod	–2.75 ± 0.08***	μ^{*} edf=1 (–)	$F_{5-10}^{\ddagger}$ edf=1.66 (+)		ST^{*} edf=1.17 (+)		41.4
NS cod	–1.17 ± 0.09***		$F_{2-4}^{\ddagger}$ edf=1 (+)	wNAO edf=1.65 (–,+)	$\mathrm{SST}_{\mathrm{spring}}$ edf=1 (–)		16.6
EBS pollock	–1.60 ± 0.12***		F_{6-10} edf=1 (+)	wPDO^{*} edf=1 (–)	SST edf=1 (–)		37.0
GOA pollock	–2.35 ± 0.22***	μ edf=1 (–)		wPDO edf=1.81 (–,+)	$\mathrm{SST}_{\mathrm{wint2}}^{*}$ edf=1 (–)	$\mathrm{SST}_{\mathrm{sum1}}$ edf=1.78 (+)	45.0
All stocks[a]	–1.81 ± 0.04***	μ^{***} edf=1.64 (–)	F^{**} edf=1 (–)				

[a] Results of generalized additive mixed model (GAMM) of elasticity for all stocks with years and stock as random variables

model, F-statistic $F_{1,5} = 2.56$, p = 0.227), became highly significant when removing the NEA cod stock (linear model, $\mu = 7.11 - 4.42F$, F-statistic $F_{1,4} = 39.06$, $p < 0.01$, $R^2 = 0.90$). It showed that the more exploited stocks have shorter generation times, which may be linked to a narrower age structure, suggesting an effect of exploitation on the demographic characteristics of the stock, with the noticeable exception of NEA cod.

DISCUSSION

In this comparative study on 7 gadoid stocks, we showed spatial similarities and dissimilarities of the effect of climate, fishing and demographic structure on the elasticity of the population growth rate to recruitment. In other words, the ecological mechanisms shaping the contribution of recruitment to the growth rate differ across systems, while common general patterns have been identified.

Effects of harvesting

The 7 stocks studied displayed differences in the elasticity of the population growth to recruitment that were linked to the level of exploitation, though the strength and direction of the relationship varied with the level of the hierarchy and the scale of the analyses performed. On an intra-stock basis, the northern species (2 cod and 1 pollock stock) showed a significant positive effect of fishing on the elasticity to recruitment (Table 2), whereas the 3 hake stocks, which are all considered to be overharvested (ICES 2009), did not. The overall analyses showed that the

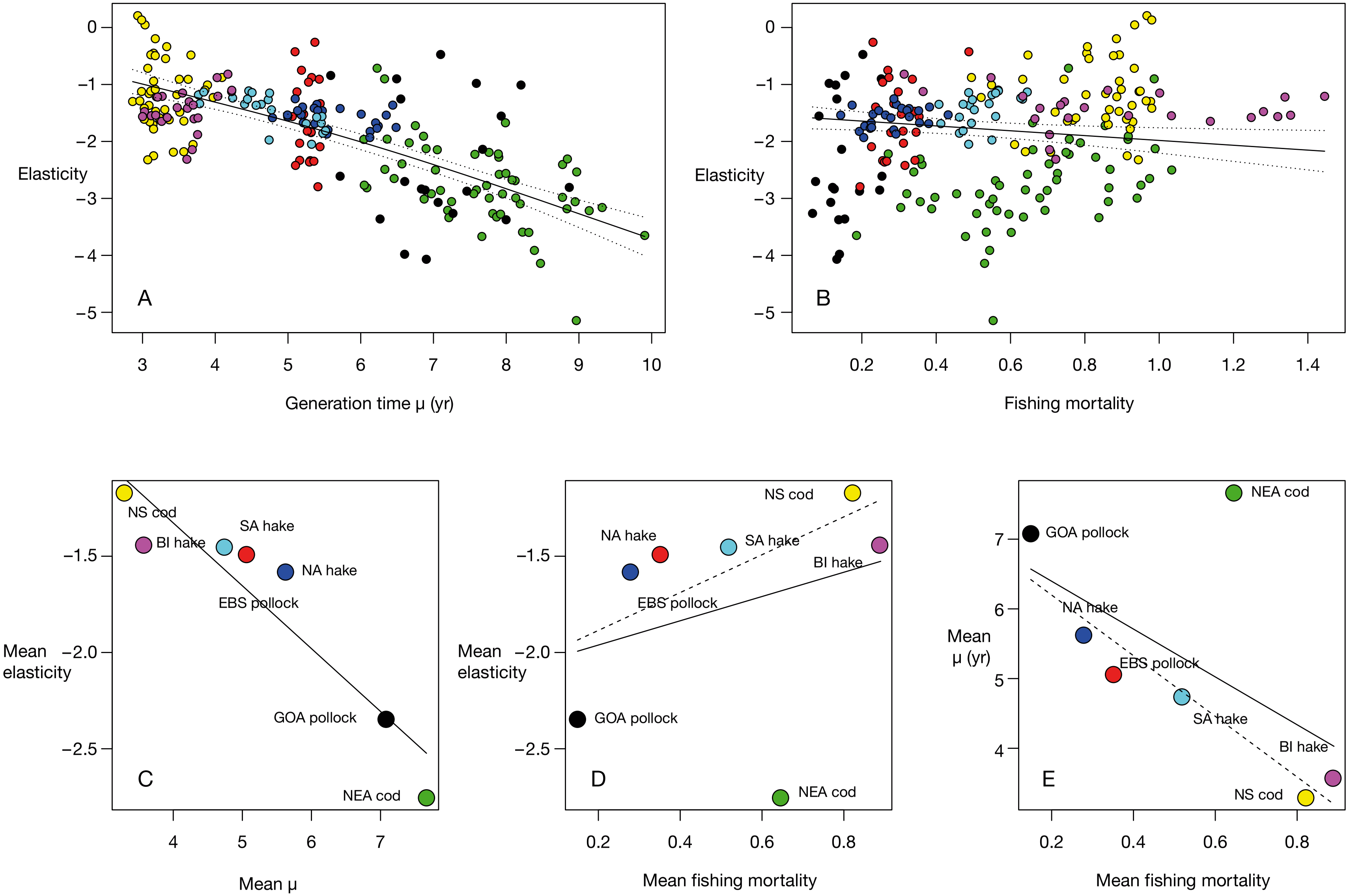

Fig. 2. (A) Relationship between mean age of the parents of the offspring produced by a cohort over its lifetime generation time (μ) and the contribution of recruitment to population growth rate (logit-transformed transient elasticity to recruitment $\boldsymbol{e}_t$). Line represents the relationship found by the generalized additive mixed model (GAMM) (Table 2). Dotted lines delimit the confidence intervals. See (C–E) for colour-coded stock names. Abbreviations as in Table 1. (B) Relationships between fishing mortality and the logit-transformed $\boldsymbol{e}_t$. Line represents the relationship found by the GAMM (Table 2). Dotted lines delimit the confidence interval. (C) Relationship between mean μ and mean logit-transformed $\boldsymbol{e}_t$ for each stock (slope = −0.33 ± 0.06, $p < 0.01$). (D) Relationship between mean fishing mortality and mean logit-transformed $\boldsymbol{e}_t$ for each stock with NEA cod included (0.63 ± 0.84, p = not significant) and without NEA cod (dashed line, slope = 0.98 ± 0.42, $p = 0.08$). (E) Relationships between mean fishing mortality and mean μ for each stock with NEA cod included (slope = −3.43 ± 2.07, p = not significant) and without NEA cod (dashed line, slope = −4.35 ± 0.71, $p < 0.01$)

within-stock effect of fishing mortality *F* was weakly negative (Fig. 2B) whereas the between-stock effect of mean *F* appeared to be generally quite strongly positive, with NEA cod being a notable exception (Fig. 2D). Thus, among stocks and within 2 of the species (cod and hake), an increase in elasticity with *F* was found, in agreement with theory, whereas the reverse pattern observed in the global model (Fig. 2B) seemed counterintuitive. We suggest that historically heavily exploited stocks with low μ have a lower capacity to change their productivity and hence their growth rate compared with stocks that are historically less exploited (e.g. GOA pollock) or that have retained a broader demographic structure in spite of exploitation (e.g. NEA cod and NA hake). In other words, the long-term effect of fishing may affect how the fish respond to short-term variations changes in *F*. These results highlight the importance of measuring these types of patterns at several scales in order to make the correct inference about the effects of management on stock demography.

Effects of generation time and combined effects with harvesting

While all stocks have been exploited for a long time, geographical differences were found, with a general tendency to higher mean μ for the northern stocks of the same species (Fig. 2C).

Overall, the elasticity to recruitment was mainly shaped by changes in μ; the longer the generation time, the lower the elasticity to recruitment (Fig. 2A,C). On an intra-stock basis, the temporal variations in the elasticity to recruitment did not always appear to be related to those in μ (Table 2). Indeed, whereas a strong negative effect of μ on the elasticity was found for the SA hake and NEA cod stocks, these effects were weak for the NA hake and GOA pollock stocks and were not present for the EBS pollock and NS cod stocks. Note that for the BI hake stock the effect of μ on the elasticity to recruitment was non-linearly positive.

Our results suggest that changes in μ likely had a larger effect on the elasticity to recruitment for the more exploited stocks (Fig. 2E), which may have been induced by a long-lasting demographic truncation and fishery-induced evolutionary change (Olsen et al. 2004). In this respect, the NEA cod seemed to be a counter example with a strong effect of μ on the elasticity to recruitment, despite being considered to be quite healthy (ICES 2011a). However, the NEA cod stock shows as much of an effect of μ on elasticity as the hake stocks that are thought to be overexploited (ICES 2009). Note that the effect of μ on the elasticity might be reduced if we were to use same time-series length for NEA cod as we used for hakes, only 2 to 3 decades. This suggests that age truncation and over-exploitation are not concomitant patterns, though they are often linked.

Effects of the environment and geographic location of the stocks

Several studies have demonstrated that stocks located at the limits of a species' geographical distribution are more sensitive to environmental variability (Brunel & Boucher 2006) and that these limits are moving with climate change. The reduction in both the spatial heterogeneity and spatial distribution of spawning stocks has been suggested to decrease population stability (Hsieh et al. 2008, Hsieh et al. 2010, Ciannelli et al. 2013, this Theme Section). In this study, 2 stocks at the northern limit of the species' geographical distribution (EBS pollock and NEA cod) were studied over 3 decades, and both displayed an effect of temperature, albeit inversed. The positive effect of temperature on the NEA cod stock elasticity occurred concomitantly to the long-term change in age structure (Ottersen et al. 2006, Rouyer et al. 2011) and in spatial distribution (Opdal 2010). Note that although the NEA cod stock displayed a 50 yr decrease in μ and in abundance, it is still considered to be in good health (ICES 2011a) due to improved management and strong and stable recruitment since the 90s). However, the negative effect of temperature on the elasticity of EBS pollock may constitute a more direct and short-term influence of the complex mesoscale processes that favour the success of the recruitment in the Bering Sea (see review by Hunt et al. 2011). This may explain the strong negative effect of PDO on this stock elasticity (Table 2). In other words, during low PDO years (i.e. when it is cold), the pollock stock is more linked to recruitment variability rather than to population survival. There was only one stock at the southern limit of the species' geographical distribution (NS cod) that was studied over 4 decades. In contrast to NEA cod, the NS cod stock displayed a negative effect of temperature on recruitment (e.g. Hjermann et al. 2013). A positive effect of SST on NA and SA hake elasticity was shown in increased larval survival, which thus favoured recruitment success (Goikoetxea 2011, Hidalgo et al. 2012). Similar to Hidalgo et al. (2012), we found evidence for environmental effects on the elasticity to recruitment for SA hake (upwelling during summer and winter temperature) (Domínguez-Petit et al. 2008) and (winter SST) for BI hake (Hidalgo et al. 2011)

The 2 studied pollock stocks displayed opposite effects of SST on the elasticity to recruitment (Table 2) that can be explained by the much lower temperature in the Bering Sea (SST May to July) compared with the Gulf of Alaska (SST_{sum1} June to August). In those areas, the climate effects could also trigger changes in trophic interactions, such as the recruitment of competitive species, or changes in spatial distribution (Bailey 2000, Ciannelli et al. 2005). For example, in the Gulf of Alaska it is well accepted that the decline in pollock recruits is driven by increased predation on small pollock by arrowtooth flounder *Atheresthes stomias*, which is now dominant in terms of biomass in that system (A'mar et al. 2010). In the Bering Sea, changes in pollock recruitment could be also be driven by changes in arrowtooth flounder distribution, but to a lesser extent since in the Bering Sea, pollock, skates and sharks all prey on arrowtooth flounder (Ianelli et al. 2009).

In conclusion, our comparative study on gadoid stocks across ecosystems illustrates how extrinsic variables shape the specific strategies used by the different species and their response to a decrease in generation. Our findings emphasise how the elasticity to recruitment can be affected by a long-term change in age structure of the population (perhaps due to fishing; Hidalgo et al. 2011, 2012, Rouyer et al. 2011, but see Ottersen et al. 2013, this Theme Section), but can also be directly affected by the ongoing fishing intensity. The elasticity of the population growth rate to recruitment cannot thus be solely explained by the age structure or the fishing intensity. To determine the elasticity, both parameters are needed.

Acknowledgements. We thank The Research Council of Norway (RCN) for funding the workshop Tropharct through the MICO project (grant no. 186310, Match/Mismatch and Ecosystem). This work is associated with the IMBER regional program, Ecosystem Studies of Sub-Arctic Seas (ESSAS). We are greatly in debt to all the people who collected the data used in the study and made them available to us. J.M.D., A.M.E. and D.Ø.H. acknowledge the support from the RCN through the ADMAR project (grant no. 200497/130). M.H. received support from Marie Curie Intra-European fellowship (IEF, FP7-PEOPLE-IEF-2008; project No 236549). L.C. acknowledges the support from the National Science Foundation – Research Coordination Network grant no. 1140207. We thank Leif-Christian Stige for comments and advice. We are indebted to Valerio Bartolino and Martin Lindegren and 3 anonymous referees who reviewed an earlier version of this article.

LITERATURE CITED

➤ A'mar ZT, Punt AE, Dorn MW (2010) Incorporating ecosystem forcing through predation into a management strategy evaluation for the Gulf of Alaska walleye pollock (*Theragra chalcogramma*) fishery. Fish Res 102:98–114

➤ Bailey KM (2000) Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. Mar Ecol Prog Ser 198:215–224

➤ Brander KM (1995) The effect of temperature on growth of Atlantic cod (*Gadus morhua* L). ICES J Mar Sci 52:1–10

➤ Brunel T, Boucher J (2006) Pattern of recruitment variability in the geographical range of the exploited northeast Atlantic fish species. J Sea Res 55:156–168

Caswell H (2001) Matrix population models: construction, analysis, and interpretation, 2nd edn. Sinauer Associates, Sunderland, MA

➤ Caswell H (2007) Sensitivity analysis of transient population dynamics. Ecol Lett 10:1–15

➤ Ciannelli L, Chan KS, Bailey KM, Stenseth NC (2004) Nonadditive effects of the environment on the survival of a large marine fish population. Ecology 85:3418–3427

➤ Ciannelli L, Bailey KM, Chan KS, Belgrano A, Stenseth NC (2005) Climate change causing phase transitions of walleye pollock (*Theragra chalcogramma*) recruitment dynamics. Proc Biol Sci 272:1735–1743

➤ Ciannelli L, Fisher JAD, Skern-Mauritzen M, Hunsicker ME, Hidalgo M, Frank KT, Bailey KM (2013) Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. Mar Ecol Prog Ser 480:277–243

➤ Cury PM, Shin YJ, Planque B, Durant JM and others (2008) Ecosystem oceanography for global change in fisheries. Trends Ecol Evol 23:338–346

➤ Domínguez-Petit R, Korta M, Saborido-Rey F, Murua H, Sainza M, Piñeiro C (2008) Changes in size at maturity of European hake Atlantic populations in relation with stock structure and environmental regimes. J Mar Syst 71:260–278

Dorn M, Aydin K, Barbeaux S, Guttormsen M, Spalinger K, Wilkins M (2010) Assessment of the walleye pollock stock in the Gulf of Alaska. NPFMC Gulf of Alaska SAFE:53–156

FAO-GFCM (2009) Report of the eleventh session of the Scientific Advisory Committee. GFCM, Marrakech

➤ Fromentin JM, Fonteneau A (2001) Fishing effects and life history traits: a case study comparing tropical versus temperate tunas. Fish Res 53:133–150

Goikoetxea N (2011) Influence of the northeastern Atlantic oceano-meteorological variability on the northern hake (*Merluccius merluccius*). Analysis of the 1978–2006 period. University of the Basque Country, Bilbao

Green PJ, Silverman BW (1994) Nonparametric regression and generalized linear models: a roughness penalty approach. Chapman & Hall/CRC, London

➤ Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71–75

➤ Hastings A, Botsford LW (2006) A simple persistence condition for structured populations. Ecol Lett 9:846–852

➤ Hidalgo M, Tomas J, Moranta J, Morales-Nin B (2009) Intra-annual recruitment events of a shelf species around an island system in the NW Mediterranean. Estuar Coast Shelf Sci 83:227–238

Hidalgo M, Rouyer T, Molinero JC, Massutí M, Moranta J, Guijarro B, Stenseth NC (2011) Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. Mar Ecol Prog Ser 426:1–12

Hidalgo M, Rouyer T, Bartolino V, Cerviño S and others (2012) Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species. Ecography 35: 637–649

Hjermann DØ, Stenseth NC, Ottersen G (2004) The population dynamics of Northeast Arctic cod (*Gadus morhua*) through two decades: an analysis based on survey data. Can J Fish Aquat Sci 61:1747–1755

Hjermann DØ, Fisher JAD, Rouyer T, Frank KT, Stenseth NC (2013) Spatial analysis of North Sea cod recruitment: concurrent effects of changes in spawning stock biomass, temperature and herring abundance. Mar Ecol Prog Ser 480:263–275

Hsieh CH, Reiss CS, Hewitt RP, Sugihara G (2008) Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. Can J Fish Aquat Sci 65:947–961

Hsieh CH, Yamauchi A, Nakazawa T, Wang WF (2010) Fishing effects on age and spatial structures undermine population stability of fishes. Aquat Sci 72:165–178

Hunt GL, Coyle KO, Eisner LB, Farley EV and others (2011) Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES J Mar Sci 68:1230–1243

Hurrell JW, Deser C (2009) North Atlantic climate variability: the role of the North Atlantic Oscillation. J Mar Syst 78:28–41

Ianelli JN, Barbeaux S, Honkalehto T, Kotwicki S, Aydin K, Williamson N (2009) Assessment of the walleye pollock stock in the Eastern Bering Sea. NPFMC Bering Sea and Aleutian Islands SAFE:49–147

ICES (2009) Report of the Working Group on the Assessment of Southern Shelf Stocks of Hake, Monk, and Megrim [WGHMM], 5–11 May 2009. ICES, Copenhagen, ICES CM 2009/ACOM 08

ICES (2011a) Report of the Arctic Fisheries Working Group (AFWG), 28 April–4 May 2011, Hamburg, Germany. ICES, Copenhagen, ICES CM 2011/ACOM 05

ICES (2011b) Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK), 4–10 May 2011. ICES, Copenhagen, ICES CM 2011/ACOM 13

Kalnay E, Kanamitsua M, Kistlera R, Collins W and others (1996) The NCEP/NCAR 40-year reanalysis project. Bull Am Meteorol Soc 77:437–471

Lassen H, Medley P (2001) Virtual population analysis—a practical manual for stock assessment. FAO Fish Tech Pap 400. FAO, Rome

Lavín A, Díaz del Río G, Cabanas JM, Casas G (1991) Afloramiento en el noroeste de la Península Ibérica. Indices de Afloramiento para el punto 43° N 11° W. Período 1966–1989. Inf Tec Inst Esp Oceanogr 91:1–40

Le Maho Y, Durant JM (2011) Impacts of climate change on marine ecosystems. In: Vidas D, Schei PJ (eds) The world ocean in globalisation: climate change, sustainable fisheries, biodiversity, shipping, regional issues. Brill, Martinus Nijhoff Publishers, Leiden, p 133–146

Leslie PH (1945) On the use of matrices in certain population mathematics. Biometrika 33:183–212

Massutí E, Monserrat S, Oliver P, Moranta J and others (2008) The influence of oceanographic scenarios on the population dynamics of demersal resources in the western Mediterranean: hypotheses for hake and red shrimp off the Balearic Islands. J Mar Syst 71:421–438

Miller JM, Burke JS, Fitzhugh GR (1991) Early life history patterns of Atlantic North American flatfish: likely (and unlikely) factors controlling recruitment. Neth J Sea Res 27:261–275

Monserrat S, Marcos M, López-Jurado J (2008) Interannual variability of Winter Intermediate Water at the Balearic Islands. J Mar Syst 71:413–420

Mueter FJ, Bond NA, Ianelli JN, Hollowed AB (2011) Expected declines in recruitment of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea under future climate change. ICES J Mar Sci 68:1284–1296

Murphy GI (1968) Pattern in life history and the environment. Am Nat 102:391–403

Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428:932–935

Opdal AF (2010) Fisheries change spawning ground distribution of northeast Arctic cod. Biol Lett 6:261–264

Ottersen G, Hjermann DO, Stenseth NC (2006) Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. Fish Oceanogr 15:230–243

Ottersen G, Stige LC, Durant JM, Chan KS, Rouyer TA, Drinkwater KF, Stenseth NC (2013) Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. Mar Ecol Prog Ser 480:205–225

Rouyer T, Ottersen G, Durant JM, Hidalgo M and others (2011) Shifting dynamic forces in fish stock fluctuations triggered by age truncation? Glob Change Biol 17: 3046–3057

Stenseth NC, Ottersen G, Hurrell JW, Mysterud A and others (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proc Biol Sci 270:2087–2096

Taylor AH (1995) North-south shifts of the Gulf Stream and their climatic connection with the abundance of zooplankton in the UK and its surrounding seas. ICES J Mar Sci 52:711–721

Wood SN, Augustin NH (2002) GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecol Model 157:157–177

Worm B, Myers RA (2003) Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology 84:162–173

Submitted: April 27, 2012; Accepted: February 12, 2013

Proofs received from author(s): March 21, 2013