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ORIGINAL ARTICLE

Changes in the relationship between sea temperature and recruitment of cod, haddock and herring in the Barents Sea

BJARTE BOGSTAD*, GJERT ENDRE DINGSØR, RANDI B. INGVALDSEN & HARALD GJØSÆTER

Institute of Marine Research, Nordnes, Bergen, Norway

Abstract
Cod, haddock and herring in the Barents Sea have strongly variable recruitment. For these three stocks, earlier studies have suggested a high correlation between their recruitment and a positive relationship between high temperatures and good recruitment. These hypotheses were revisited using stock assessment and temperature data for the period 1913–present. The cod–haddock and herring–haddock recruitment correlations were both significant and positive in some periods, but became insignificant towards the end of the period. Cod and herring recruitment was not significantly correlated. Recruitment variability was found to decline towards the end of the period for all species, in particular for cod. For all three stocks there is a significant positive relationship between recruitment and temperature; this relationship is strongest for haddock and weakest for herring. Recruitment was found to be low at low temperatures and variable at medium/high temperatures during the first year of life for all three species. Temperature during the first winter of life correlates positively with haddock and cod recruitment residuals. This correlation is weakened towards the end of the period for cod, but stays high for haddock. Temperature during the first summer of life correlates positively with herring recruitment during some parts of the period, but also this correlation is weakened towards the end of the period.

Key words: *Barents Sea, recruitment, cod, haddock, herring, temperature*

Introduction

The Barents Sea (BS) is an ecosystem which is strongly influenced by the inflow of warm Atlantic and Coastal Water (e.g. Loeng 1991; Figure 1). With the inflowing water, heat, zooplankton and fish eggs and larvae are brought into the Barents Sea from the Norwegian Sea (e.g. Sundby 2000; Dalpadado et al. 2012 and references therein). Recruitment of northeast Arctic cod *Gadus morhua* Linnaeus, 1758, northeast Arctic haddock *Melanogrammus aeglefinus* (Linnaeus, 1758), and Norwegian spring-spawning herring *Clupea harengus* Linnaeus, 1758 has previously been found to be strongly variable and positively correlated with each other as well as with temperature (e.g. Ottersen & Loeng 2000; Toresen & Østvedt 2000; Dingsør et al. 2007). A visual inspection of recruitment and temperature data (Figure 2) indicates that the correlations and variability have changed in recent years. It was thus decided to revisit this issue by using a longer time series than have previously been available.

In addition to the spawning stock biomass, there are many processes that affect recruitment to fish stocks, e.g. size/age composition of the spawning stock, spawning area and time, prey availability at various life stages, predator presence and oceanographic conditions such as temperature, turbulence and drift.

The processes governing survival between spawning and age 6 months (when cod and haddock settle to the bottom) are probably quite different from those affecting survival from age 6 months to 3 years. Mukhina et al. (2003) found that residual variation in the egg/recruitment relationship for cod was not correlated with average temperatures for either the pelagic or demersal stages. However, they also found that residual variation in the stage abundance/recruitment relationships for larval and juvenile stages were significantly correlated with temperatures during the post-settlement period.

Cod is an important predator on young age groups of cod, haddock and herring (Johansen et al. 2004; Yaragina et al. 2009; ICES 2011a); thus, another

*Correspondence: Bjarte Bogstad, Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway. E-mail: bjarte.bogstad@imr.no

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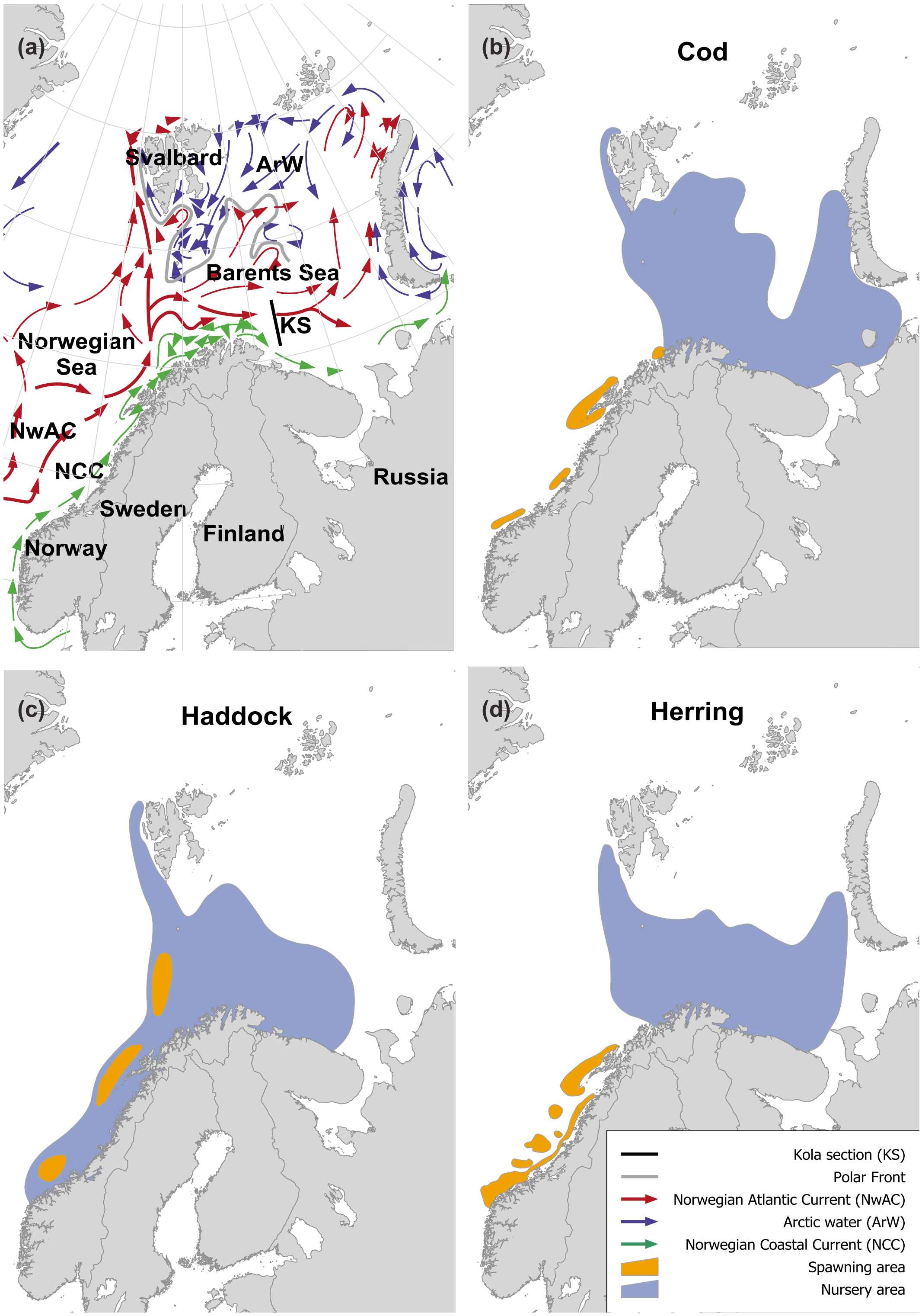

Figure 1. (a) Simplified current system in the Norwegian Sea and Barents Sea. NwAC, Norwegian Atlantic Current; NCC, Norwegian Coastal Current; ArW, Arctic Water; KS, Kola section. (b–d) Spawning and nursery areas for cod, haddock and herring.

process at play is the predation by cod on these pre-recruits (0-group to age 3). Cod as prey for cod (cod cannibalism) was discussed in detail by Yaragina et al. (2009). However, a question that remains open is whether the predation from cod on the young age groups of these species varies with a varying climate. The growth rate of the three species is fairly similar during the first two years of life; thus, a cohort of cod is not likely to affect the abundance of the same cohort of herring and haddock through predation.

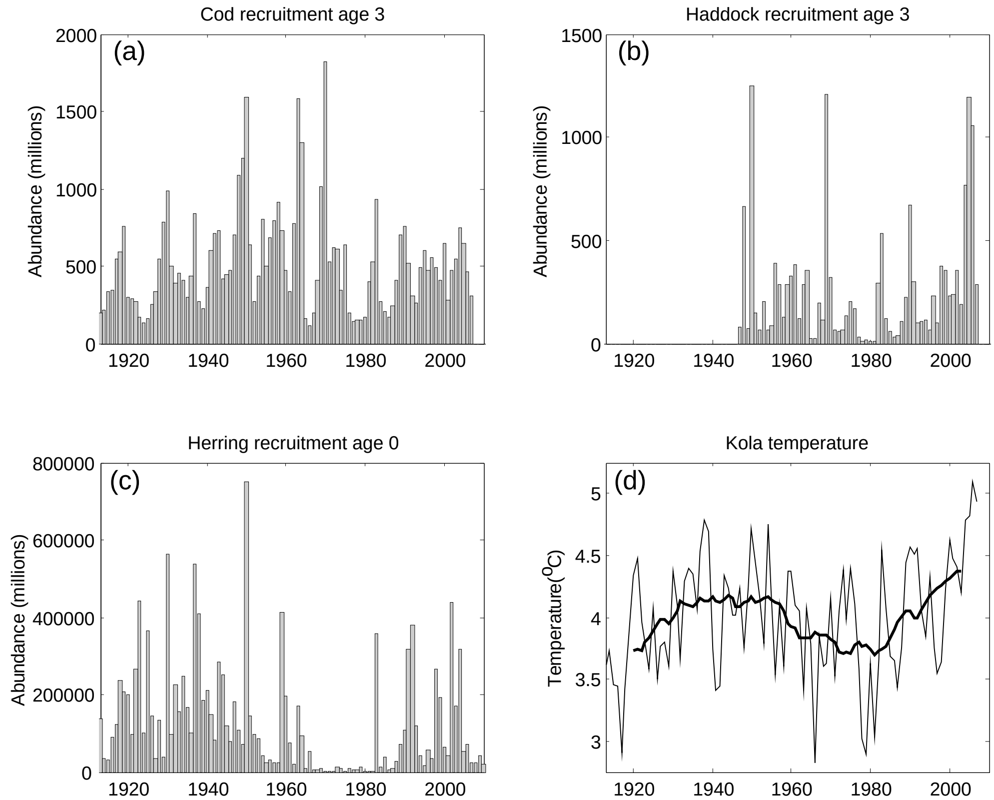

Figure 2. (a) Cod recruitment at age 3, (b) haddock recruitment at age 3, (c) herring recruitment at age 0, (d) Kola temperature (annual mean, bold line shows 15-year running mean).

Temperature influences metabolic processes and is, along with prey availability, the single most important factor that determines growth rates in fish (Brett 1979), and a positive relationship between temperature, growth and the availability of food has been shown for the juvenile fish in the Barents Sea (e.g. Suthers & Sundby 1993; Folkvord 2005; Kristiansen et al. 2011).

Ottersen et al. (2006) found that the temperature–cod recruitment correlation increases with decreasing mean age and length in the spawning stock. As mean age and length as well as diversity in size and age for spawning cod has declined with time (Ottersen et al. 2006, 2010), changes in the relation between temperature and cod recruitment over time might be expected. However, the time series of survey data describing these processes in detail are limited and often short. Thus, detailed studies of the biological processes involved are not possible. However, it is possible to reveal whether there is an overall relationship between ocean temperature and recruitment of the species, which is valid at all temperatures and therefore important when modelling recruitment patterns.

The main purpose of this article is to investigate temperature–recruitment relationships for these stocks as a foundation for the use of such relationships in single- and multispecies population models which are relevant for management. Investigating how such relationships are linked to various biological processes is not addressed in this article.

Use of stock-recruitment relationships in population models

Stock-recruitment relationships are needed both in single- and multispecies models when making prognostic runs. The inclusion of relationships between recruitment and temperature, as well as the recruitment pattern (variability, periodicity, etc.) is highly relevant for single-species models, some of which have been used for testing harvest control rules for the stocks studied here (e.g. Kovalev & Bogstad 2005 for cod). Thus, the modelling of recruitment patterns may have a direct impact on the choice of harvesting strategy. For multispecies models, the recruitment correlation between stocks is, together with predation, probably the main factor governing the behaviour of the modeled system. Some multispecies models for the Barents Sea (e.g. Schweder et al. 2000; Hamre 2003; Howell et al. 2013) have assumed cod and/or herring recruitment to be positively correlated with temperature.

Questions addressed

Our investigation will address whether these assumptions should be revised when considering the long time series from 1913 to 2007. More specifically, we will address the following questions: (1) is there a relation between sea temperature in the first year of life and recruitment for these species, (2) is there a co-variability in the recruitment of the three species, and (3) is there a relation between temperature and recruitment variability?

Cod, haddock and herring life history

Northeast Arctic cod spend most of their life in the Barents Sea. Spawning takes place in March–April in Norwegian coastal areas between 62 and 70°N, with the main concentrations usually found in the Lofoten area, i.e. around 68°N (Yaragina et al. 2011). The pelagic eggs and the larvae drift with the current from the spawning grounds northwards and eastwards and in autumn can be found over most of the Barents Sea. In September–October the 0-group switches from a pelagic to a demersal phase.

Northeast Arctic haddock also spend most of their life in the Barents Sea. Spawning takes place in March–April along the slope between the continental shelf and the Norwegian Sea from about 62 to 70°N (Russkikh & Dingsør 2011). The eggs are pelagic and eggs and larvae are transported and dispersed by currents to the southern Barents Sea as far east as East Murman and as far north as Svalbard. In August–September, 0-group fish are distributed in the southwestern and central Barents Sea, and in September–October the 0-group switches from a pelagic to a demersal phase.

The Norwegian spring-spawning herring spawn in February–March on the Norwegian coastal banks and the eggs are deposited on the bottom (Krysov & Røttingen 2011). After hatching, larvae appear in the upper water layers and drift with the current along the slope of the continental shelf. In August–September 0-group herring are found in the southern Barents Sea and also to a certain extent in the North Norwegian fjords. Some year-classes are also found in the open Norwegian Sea at this stage. At an age of 3–5 years the herring migrate westward into the Norwegian Sea, where they unite with the adult stock. They do not return to the Barents Sea as adults; the Barents Sea thus serves only as a nursery area for the Norwegian spring-spawning herring. Both the migration pattern and the overwintering and spawning areas of this stock have changed considerably during the period considered in our study (Dragesund et al. 1997; Krysov & Røttingen 2011).

Oceanographic conditions

The ocean circulation is dominated by the Norwegian Atlantic Current bringing warm and salty Atlantic Water into the area from the south. Atlantic Water extends over the western and central parts of the Barents Sea, while cold and fresher Arctic Water dominates in the northern part. The borderline between the two main water masses is called the Polar Front, which is fairly sharp in the western parts of the BS. Also, smaller branches of subducted Atlantic Water enter the Arctic areas both below the front and from the north around Svalbard (Loeng 1991). In the eastern BS, the Polar Front is variable and tends to be strong in cold years and weak in warm years.

Material and methods

Fish data

For cod, haddock and herring, we used Virtual Population Analysis (VPA) estimates of spawning stock biomass (SSB) and recruitment from official ICES stock assessments, as well as VPAs for cod and herring extending backwards beyond the period used in the official assessment. For cod, haddock and herring, data from ICES stock assessments on spawning stock and recruitment at age 3 are available back to 1946, 1950 and 1950, respectively (ICES 2007, 2011a, 2011b). For cod, Hylen (2002) extended the VPA back to 1913, while for herring, Toresen & Østvedt (2000) extended the VPA back to 1907. The biological sampling and the age-reading methodology may not be comparable throughout such long periods; thus, such extensions should be used with care. However, they do provide useful information about long-term historical stock trends, and have been used for studies of temperature–recruitment relationships for cod and herring (Toresen & Østvedt 2000; Ottersen et al. 2010).

We therefore decided to perform analyses for two time periods: cohorts 1913–2007 and 1950–2007, respectively. For the 1913–2007 period data are available for cod, herring and temperature, while for 1950–2007 data are available for cod, haddock, herring and temperature.

For cod, we used the age 3 numbers from the VPA without cannibalism (table 3.26 in ICES 2011a), in order to get a consistent time series. However, for the 2006 and 2007 year-classes the difference between the recruitment at age 3 in the runs with and without cannibalism (tables 3.25 and 3.26) is much larger than the cannibalism mortality (table 3.19 in ICES 2011a) indicates. This is due to differences in numbers at age for young age groups in the last year of a VPA caused by the tuning process, which includes data down to age 1. Thus, for these two cohorts we used the recruitment values from the VPA with cannibalism reduced by the cannibalism mortality given in table 3.19 in ICES (2011a). For haddock, we used the VPA given in table 4.18 in ICES (2011a).

For herring, estimates of spawning stock and recruitment are available for both age 0 and 3 (Toresen & Østvedt 2000 for the period before 1950; ICES 2007 for the period 1950–1987; ICES 2011b for 1988–present) and we chose to use the age 0 estimates in order to take into account the considerable fishery on age 0–2 herring in the 1950s and 1960s (Dragesund et al. 1997; ICES 2011b).

The time series of cod and haddock recruitment at age 3 and herring recruitment at age 0 are shown in Figure 2a–c. We did not attempt to use survey estimates of abundance at various life stages because such series are available for relatively short periods (max. 30 years) only.

Sea temperature data

The Russian Kola section is a commonly used time series representing the variability in the large-scale climate in the Barents Sea (Tereshchenko 1996). This series dates back to 1900, and is the only time series spanning the study period. Measurements were taken at quarterly intervals from 1900 to 1921; thereafter at monthly intervals. The series used here is mean temperature in the 0–200 m depth layer between 70°30′ and 72°30′N along 33°30′E. We use annual mean temperatures, with mean temperatures during summer (May–September) at the year of spawning, and mean temperatures during the first winter of life (November–March). The annual mean temperatures and the 15-year running mean temperature are shown in Figure 2d.

Analysis methods

We fitted three different stock-recruitment relationships – segmented regression (hockey-stick), Beverton–Holt, and Ricker – for each stock assuming lognormal error structure using the Fisheries library in R (FLCore 3.0, Kell et al. 2007). We selected the relationship which gave the best overall fit based on the Akaike Information Criterion. The residuals on the log scale (ln(observed/modelled)) were then used further. For cod and herring we fitted stock-recruitment relationships both for the periods 1913–2007 and 1950–2007. The residuals for the period 1950–2007 were rather similar in both cases, so we only used the residuals calculated for the period 1913–2007 for cod and herring in the further analysis.

To account for temporal changes in the time series and the relations, relative standard deviation and correlation coefficients were calculated using centred sliding windows over 15 years. This means that the relative standard deviations/sliding window correlation coefficients for year n were calculated from the time series starting at year ($n-7$) and ending at year (n+7). The 15-year time span was found the most appropriate due to a tradeoff between reducing the cutoff at the start and end of the time series and still having sufficient length of the time to produce reliable standard deviation/correlation coefficients. Increasing the time span would have given less information on the last decade.

To adjust for autocorrelation in the series, the effective number of degrees of freedom n^* was calculated for each sliding window correlation in accordance with Pyper & Peterman (1998): $\frac{1}{n^*} = \frac{1}{n} + \frac{2}{n} \sum_{j=1}^{n/5} r_{xx}(j) r_{yy}(j)$ where $n = 15$ is the sample, and $r_{xx}(j)$ and $r_{yy}(j)$ are the autocorrelations of the time series X and Y, at lag j. Following the recommendation of Pyper & Peterman (1998) a maximum of $n/5$ lags were included in the calculation of n^*. The statistical significance of the linear correlation coefficients was calculated using the derived effective number of degrees of freedom. All time series were normalized (means extracted and divided by the standard deviation) before correlation analysis was performed. The time series showing a statistically significant linear trend had the trend removed before correlation analysis.

In this study we have applied linear relationships between ocean temperature and recruitment, although the processes involved are likely to be non-linear. However, because the relationships are unknown and likely to vary among the processes, we find starting out with simple linear relationships to be the most appropriate approach. Other, more complicated, relationships could be considered in subsequent studies.

Results

The 1930s–1950s were warm compared with the long-term mean, while the 1960s–1970s were cold. Thereafter, there has been a long-term temperature increase of almost 1.5°C. All the years 2004–2007 had higher annual mean sea temperatures than during the last maximum, and 2006 was the warmest year ever observed (Figure 2d).

All fitted stock recruitment models were very similar (Figure 3a–c) and the choice of model will not affect our results or conclusions. However, segmented regression stock-recruitment relationships turned out to give the overall best fit for cod and herring, based on the Akaike Information

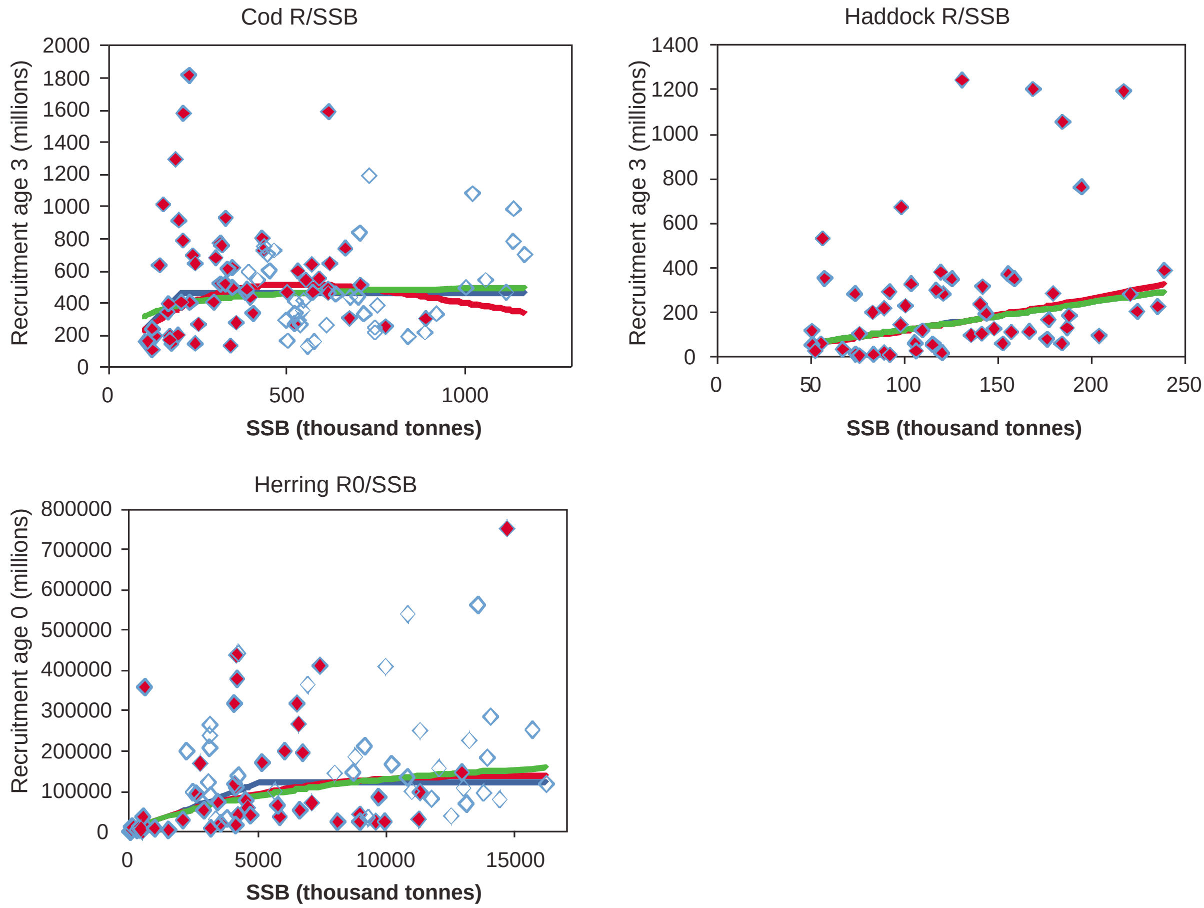

Figure 3. (a) Cod stock-recruitment plot for cohorts 1913–2007 with fitted stock-recruitment functions. (b) Haddock stock-recruitment plot for cohorts 1950–2007 with fitted stock-recruitment functions. (c) Herring stock-recruitment relationship for cohorts 1913–2007 with fitted stock-recruitment functions. Segmented (blue), Ricker (red) and Beverton–Holt (green) stock-recruitment relationships. Open symbols: cohorts 1913–1949, filled symbols: cohorts 1950–2007.

Criterion (Table I). All models gave equal fit for haddock, but to be consistent we selected segmented regression for this stock as well, although a break point was not found. The recruitment is quite variable for the whole range of stock sizes (Figure 3a–c) for all three species, and a large part of the variation is not accounted for by the segmented regressions fitted to the data.

Temporal changes in recruitment variability are evident in Figures 2a–c and 4a–c. Cod and herring had low temporal variability in the 1940s. Cod showed high recruitment variability in the 1960s and 1970s, while haddock and herring showed high recruitment variability in the 1970s and 1980s. Since the 1990s, cod and haddock have had lower recruitment variability than ever observed earlier.

Table I. Akaike Information Criterion for different stock-recruitment models.

Stock	Ricker	Beverton–Holt	Segmented regression
NEA cod	−42.3	−45.6	−53.4
NEA haddock	43.7	43.9	43.9
NSS herring	67.5	67.6	66.7

There are also temporal changes in the recruitment correlation between the species (Figure 5a–c). Cod and haddock recruitment are positively correlated in the 1960s and 1970s, and in a short period in the 1980s (Figure 5a). There is no statistically significant recruitment correlation between cod and herring, but there is a positive recruitment correlation between haddock and herring in the 1960s and the 1980s. Since the 1990s there is no statistically significant recruitment correlation between the three species.

The correlation between the cod/haddock recruitment and temperature show that the temperatures during the first winter of life are more important than the summer temperatures (Figure 6a–c). The haddock recruitment had strong and relatively invariant correlation to the winter temperature over the period 1950 to present, while cod recruitment varied in synchrony with the winter temperatures only from the 1960s to the 1980s. The herring variability seems to be more correlated to the summer temperatures than

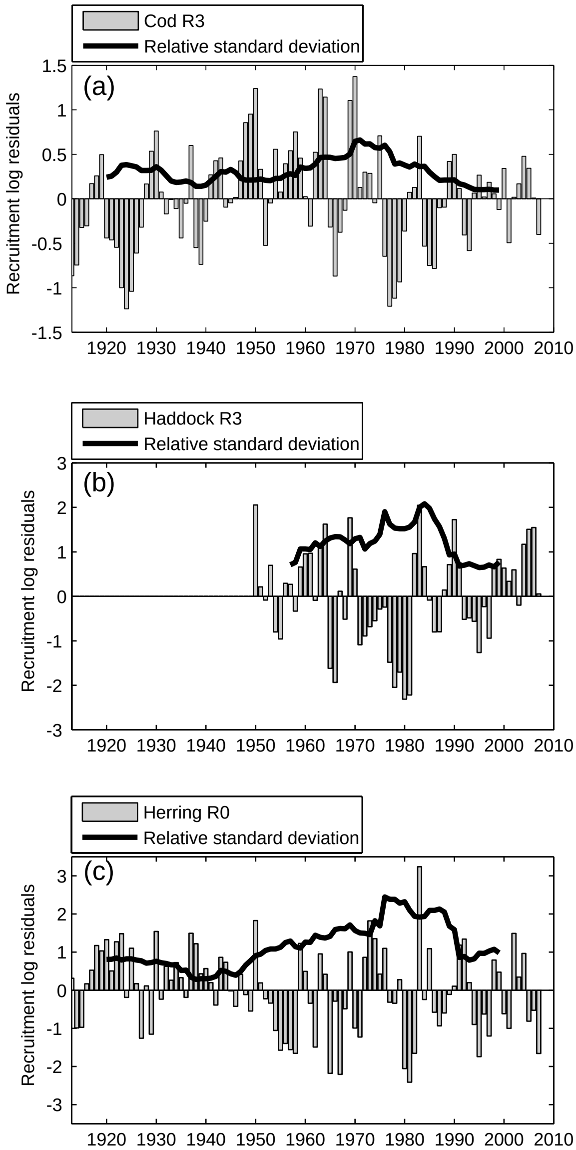

Figure 4. (a–c) Recruitment residuals and relative standard deviation (15-year centred sliding window) for cod, haddock and herring. Note different scales on *y*-axis.

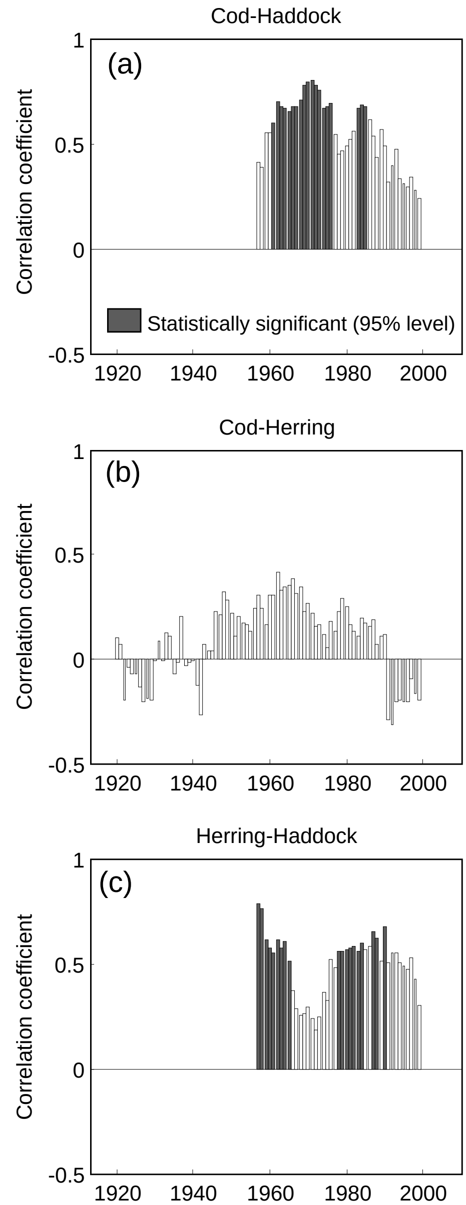

Figure 5. (a–c) Correlation (15-years sliding centred windows) between cod, haddock and herring recruitment residuals. The correlations which are statistically significant at the 95% confidence level are marked with grey.

to the winter temperatures, although this relation is evident only in some time periods.

The recruitment log-residuals show a positive relationship with temperature for the three species (Fig. 7a), although a weak relationship for herring. Figure 7b indicates that the recruitment variability declines as temperature increases; however, due to autocorrelation between the data points, caused by sliding windows, inferences from these plots should be treated cautiously. Temperature also seems to affect the cod–haddock covariability (Figure 7c).

Discussion

In this study we have used annual mean sea temperatures as a proxy for the climatic conditions in the Barents Sea. Earlier studies have shown that high temperatures are associated with increasing areas of the warm Atlantic part of the Barents Sea (Dalpadado et al. 2012), as well as with larger areas having a temperature in the range preferred by 0-group cod, haddock and herring (Eriksen et al. 2012). Additionally, at high temperatures higher zooplankton biomass has been observed in the Barents Sea (Dalpadado et al. 2003; Orlova et al. 2005), presumably due to higher inflow of *Calanus finmarchicus* with the Atlantic and coastal water from the Norwegian Sea to the Barents Sea (e.g. Sundby 2000; Dalpadado et al. 2012 and references therein).

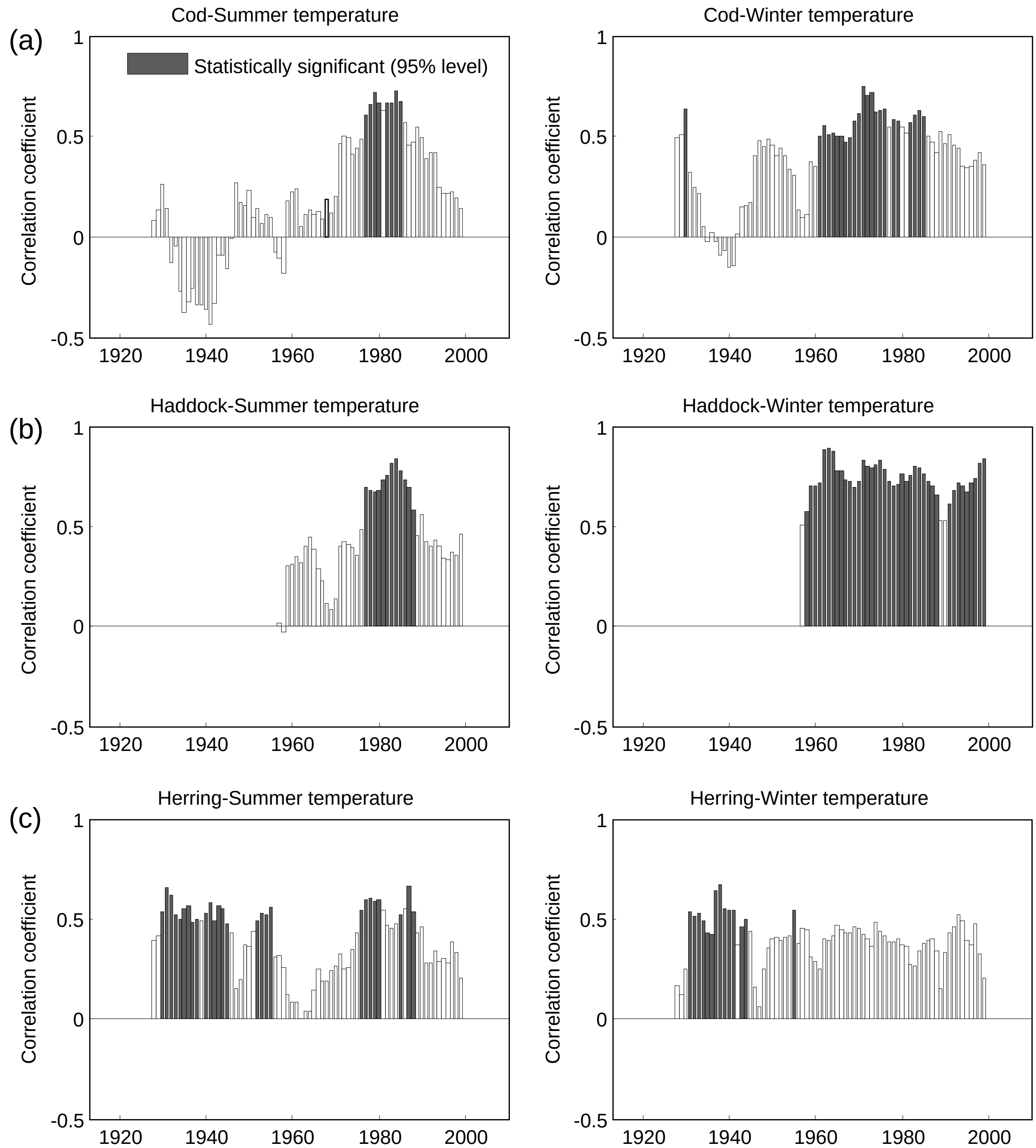

Figure 6. (a–c) Correlation (15-years sliding centred windows) between recruitment residuals and summer (May–September) and winter (November–March) temperatures in the Kola section in the first year of life for cod, haddock and herring. The correlations which are statistically significant at the 95% confidence level are marked with grey.

A positive relationship between temperature, growth and the availability of food has also been shown for the juvenile fish in the Barents Sea (e.g. Suthers & Sundby 1993). Kristiansen et al. (2011) estimated that the cumulative effect of higher growth rates and survival through the entire spawning season in warm years increased the survival of cod larvae spawned in the Lofoten area by 175%. Thus, high temperature is a proxy for larger areas having suitable temperatures for the recruits, higher food supply, and better growth conditions. This study does not distinguish between the direct and indirect effects.

Ottersen & Loeng (2000) found synchrony in year-class strength for cod, haddock and herring in the Barents Sea and explained this as a common response to temperature fluctuations. By extending the time series and adjusting for spawning stock biomass, we show that such a synchrony is only true for certain periods (Figure 5), and that the strength of the relationship to temperature varies through the studied period (Figure 6). It should be noted that previous authors addressing recruitment correlations for these three stocks have not used recruitment residuals in their analyses; also, analyses of

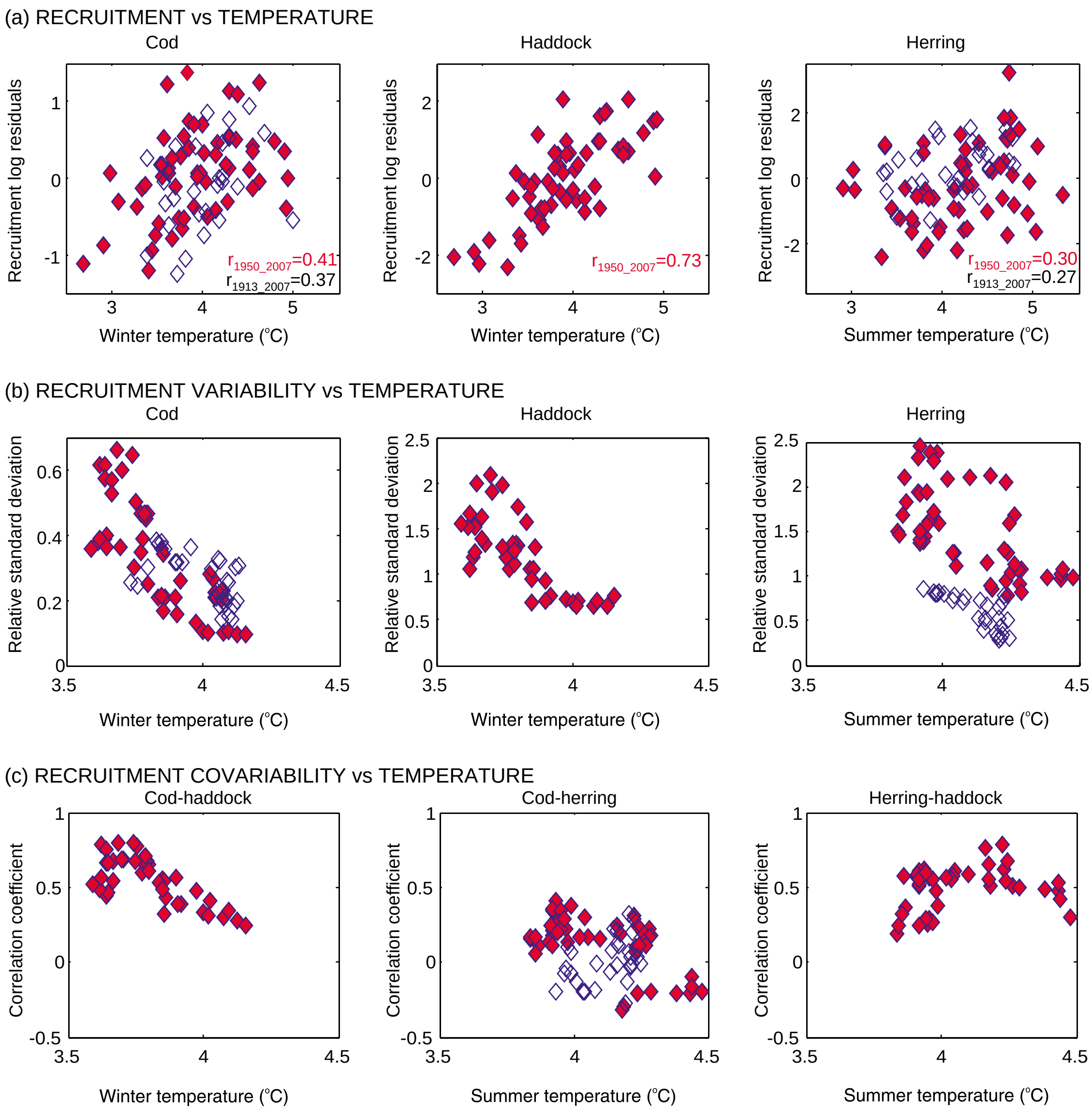

Figure 7. (a) Annual values of recruitment log residuals (Figure 3) versus temperature (winter temperatures for cod and haddock and summer temperature for herring). Open symbols: cohorts 1913–1949, filled symbols: cohorts 1950–2007. (b) Relative standard deviation (15-year centred sliding window, Figure 4) versus average temperatures over the same 15-year period. (c) Correlation coefficients (15-year centred sliding window, Figure 5) versus average temperatures over the same 15-year period. Open symbols denote points where the middle year in the sliding window is before 1950, while filled-in symbols denote points where the middle year in the sliding window is 1950 and later.

cod–herring correlations using the long time series back to 1913 have not been performed previously.

In the following sections we will discuss more closely the temperature–recruitment relationship for the three species as well as recruitment variability and co-variability.

Cod recruitment and temperature

Ottersen et al. (2006) found that the climate–cod recruitment correlation increases with decreasing mean age and length in the spawning stock. The low correlation found during the last part of the period, when the spawning stock has been high and mean age and length have therefore increased, is consistent with their findings.

The stock-recruitment plot for cod (Figure 3a) indicates that the recruitment is less variable when the spawning stock biomass is high. This may be caused by the combination of wider spatial and temporal distribution of spawning, which reduces the occurrences of poor year-classes and density-dependent mechanisms, which dampen the strongest year-classes (Fogarty et al. 2001).

The link between climate and cod recruitment has been reviewed by Ottersen et al. (2010). Sundby (2000) suggested that temperature is a proxy for inflow of *Calanus finmarchicus* and increased survival of cod larvae. Like earlier results (Dippner & Ottersen 2001; Dingsør et al. 2007), we found that not only temperatures during the months after spawning are important, but also temperatures during the months of cod juvenile's first winter. Increasing temperatures in the southern BS are equivalent to larger areas of warmer water (Dalpadado et al. 2012) and consequently a wider distribution of the cod juveniles. This might in turn increase the survival due to less overlap with older predatory conspecifics. The same process was hypothesized by Ciannelli et al. (2007), who found that in years with a strong eastward flow into the Barents Sea, juvenile cod had a better survival in the eastern part of the Barents Sea. Ponomarenko (1984) also found the survival of cod from age 0 to 2, as calculated using indices from a Russian survey in late autumn, to be positively related with the temperature during the first and second winter of life. Ottersen et al. (2006) used a sliding 21-year time window and found that the correlation between cod recruitment at age 3 and Kola temperature in December–March in the spawning year was generally very low in the period from 1913 until about 1970, which is in line with our results.

The relationship between winter temperature and cod recruitment is not very strong, but nevertheless, the recruitment is never very high at low temperatures or very low at high temperatures (Figure 7a). The highest recruitment occurs at medium temperatures. For winter temperatures above 4.6°C, high cod recruitment has not been observed, but there are too few observations in this range to draw conclusions about recruitment levels here. Although earlier studies (e.g. Sætersdal & Loeng 1987; Ottersen & Sundby 1995; Ottersen & Stenseth 2001) have shown that the cod recruitment in the Barents Sea increases at higher temperatures, it has also been found that the recruitment of cod stocks in warmer areas might decrease with temperature (Planque & Frédou 1999; Drinkwater 2005). Several studies of 0-group/juvenile cod abundance and growth in the Barents Sea show that maximum abundance and length occur at medium temperatures (Dingsør et al. 2007; Eriksen et al. 2012). Most of the data points from warm years belong to the recent period. Our results may indicate that the temperatures in the Barents Sea are now close to the optimum value for cod recruitment.

Our results also indicate a relationship between the cod recruitment variability and temperatures (Figure 7b), indicating that the cod recruitment variability has a declining trend with increasing temperatures. Such a trend implies that the recruitment can still be substantially higher or lower than the average at high temperatures, but the overall recruitment variability will be reduced.

Haddock recruitment and temperature

The haddock recruitment shows a strong positive relationship to temperatures throughout the observed temperature range (Figure 7a), confirming earlier findings (Ottersen & Loeng 2000; Dingsør et al. 2007). This might be because 0-group/juvenile haddock are distributed in warmer water than 0-group/juvenile cod (Eriksen et al. 2012) and warming of the Barents Sea leads to a larger thermal habitat for juvenile haddock. The recruitment variability for haddock seems to decline with increasing temperature. Figure 4b shows that this decline is related to a series of positive residuals towards the end of the studied period. This is a period where not only has the temperature been high, but the spawning stock has also been at fairly high levels (ICES 2011a) and the reduced recruitment variability may be an effect of both factors.

Herring recruitment and temperature

For herring, the linear relationship between recruitment and temperature is weak (although significant, Figure 7a) and there is no clear trend in recruitment variability with temperature (Figure 7b). This is in contrast to the results of Toresen & Østvedt (2000), who essentially analysed the same data, but with a shorter time series, with different approaches for adjusting for spawning stock biomass and with different use of temperature data from the Kola section time series. However, our results are in line with the findings of Fiksen & Slotte (2002), who found that temperature has relatively low explanatory power of recruitment variability, although we are using a different stock-recruitment model from theirs. It is also consistent with Vikebø et al. (2010), who showed that a rapid displacement to the main nursery area in the Barents Sea was more important for larval survival than ambient temperature. They suggested that the effect was due to reduced overlap with predators and/or higher prey densities, although the casual processes involved remain to be investigated.

Considering recruitment variability, the data set show an interesting difference between before and after 1950 (Figure 7b). The points from the period prior to 1950 (open symbols) seem to cluster in the lower part of Figure 7b, indicating that the recruitment variability for that period was lower, regardless of temperature. We do not know the reason for this, but we know that the herring stock has gone through large changes in migration and spawning areas, and through a stock collapse (Dragesund et al. 1997). All of these factors may have influenced the stock-recruitment relationship.

Recruitment variability and co-variability

However, we also see that in the relatively cold period 1960–1980, the three species show increasing relative standard deviation in recruitment, while in the warming period after the early 1980s they show decreasing variation in recruitment (Figure 4). In about the same period (ca. 1965–1990), the spawning stock biomass was low for both cod and herring. Cod and herring also show low variability in the relatively warm period in the 1930s and 1940s, but this was also a period when the two stocks were relatively large. It is therefore difficult to determine to what extent the recruitment variability is influenced by temperature, SSB, or both.

The cod–haddock recruitment correlation (covariability) seems to be highest at low temperatures, while the herring–haddock recruitment correlation seems to be highest at medium temperatures (Figure 7c). This might also be linked to the different thermal responses for the species. Of the three species, cod juveniles stay in water with the lowest temperatures, while haddock stays in water with the highest temperatures (Eriksen et al. 2012). At low temperatures (such as the 1960s and 1970s), cod and haddock respond similarly, but at high temperatures (as the 1990s and thereafter), they do not.

Conclusions

Our main results can be summarized as follows.

1. Recruitment variability declined towards the end of the period 1950–present for all species, in particular for cod. The reasons are not clear, but are probably a combined effect of enhanced management (leading to a large spawning stock consisting of a wide spectrum of age and size groups) and higher and thus more favorable temperatures (which are thought to stabilize the survival of young stages and indirectly support the effects of management, increasing the spawning stock size).
2. Temperature during the first winter of life correlates positively with haddock and cod recruitment residuals. This correlation is weakened towards the end of the period for cod, but stays high for haddock. Temperature during the first summer of life correlates positively with herring recruitment for some parts of the period, but also this correlation is weakened towards the end of the period. The differences among the species might be caused by different thermal adaptations, but different spawning areas, different drift routes for eggs and larvae or other differences in life histories might also play a role.
3. The relationship between temperatures and the recruitment of cod, haddock and herring in the Barents Sea, as well as the correlation between the recruitment of these three species, varies over the temperature range. At low temperatures, the recruitment of cod and haddock has large variability, varies in synchrony and increases with increasing temperature, but at high temperatures they do not. The herring–haddock correlation is significant or close to that during the entire period 1950–2007, and does not seem to be markedly affected by the temperature.

The relationships found here could be included in single- and multi-species models for use in the investigation of harvest control rules and climatic effects in a management context.

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