ICES Journal of Marine Science, 2022, **79**, 2430–2441
DOI: 10.1093/icesjms/fsac181
Advance access publication date: 11 October 2022
Original Article

ICES CIEM
International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

Persistent differences in recruitment variability among co-occurring North Atlantic groundfish species

Edda Johannesen [1,*], Dave Keith [2], Michael J. Fogarty [3], Nancy Shackell [2] and Kenneth T. Frank [2]

[1] Institute of Marine Research, P.O. Box 1870, Nordnesgaten 50, Vestland 5005, N5817 Bergen, Norway
[2] Ocean and Ecosystem Sciences Division DFO, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2, Canada
[3] 124 West Falmouth Hwy, Falmouth, MA 02574, USA

[*] *Corresponding author: tel: +47 47026913;* e-mail: edda.johannesen@hi.no.

Knowledge of recruitment and its variability in marine fish populations contributes to sustainable fisheries but a full understanding remains elusive. An earlier study showed that haddock (*Melanogrammus aeglefinus*) stocks exhibited consistently higher variability and lower reproductive rates compared to cod (*Gadus morhua*) stocks in the geographic regions where they co-occurred. Thus, cod may have a higher resilience to overexploitation, whereas haddock stocks may be more likely to be rescued by chance strong recruitments events. Since that initial study, the ecosystems and stocks have experienced large structural and functional changes, as well as changes in management practice and ocean warming. Here, we updated the previous earlier analysis with new data and found that despite large changes in the ecosystems explored, the patterns of recruitment variability have persisted. Recruitment variability remains higher in haddock than in cod, and the maximum annual reproduction rate at low spawning stock biomass (SSB) remains higher in cod than in haddock, although the latter difference is now less pronounced. Despite the economic and ecological importance of cod and haddock, and their long history of scientific scrutiny, the persistent difference in their reproductive biology remains unexplained.

Keywords: over-exploitation, climate change, stock structure, reproductive traits.

Introduction

Patterns of recruitment and its variability are known to differ substantially among marine fish species depending on their life history (e.g. Houde, 2016). Typically, environmental variations (climatic fluctuations, oceanographic conditions, and food web dynamics) are important drivers of recruitment variability, especially among small-bodied, semelparous, short-lived species, whereas intrinsic factors (physiological condition, age diversity, and age/size structure of the spawning stock) are more important for species that are long-lived, iteroparous, and attain large body sizes (discussed in Houde, 2016, see also Longhurst, 2002). Given the demonstrated survival advantage that offspring from older, repeat spawners have over first-time, smaller parents, targeted fishing of larger individuals can have a negative effect on recruitment beyond the effect of biomass removal (Fogarty *et al*., 2001; Marshall, 2016). Also, when causing a truncation of age structure and/or a reduction in stock biomass or body size (Trippel, 1985; Scott *et al*., 2006), exploitation can increase the importance of environmental variation on recruitment among larger-bodied species (Ottersen and Holt, 2022).

Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) are heavily exploited gadoids found in shelf and coastal ecosystems in the western and eastern North Atlantic. When comparing their recruitment variability and reproductive rates, Fogarty *et al*. (2001) found consistent differences between the two species despite many similarities in their life-history and reproductive traits. Among the shared reproductive traits are traits that have been used to classify fish species according to their population dynamics, recruitment variability, and susceptibility to overfishing (Winemiller and Rose, 1992). These include relatively small pelagic eggs, larvae, and early-stage juveniles, high egg production (Lowerre-Barbieri *et al*., 2017), batch spawning (Murua and Saborido-Rey, 2003), as well as similarities in egg size, relative fecundity (number of eggs per unit female body weight), age at first maturity, and median age at maturity (Hislop, 1984). Both species are long-lived, which gives a broad age structure with several reproductive age groups, which, combined with their reproductive traits, serves to buffer against environmental perturbation and, up to a point, against perturbations caused by fishing. However, most stocks of these species have been overexploited historically. During the early 1990s, the cod and haddock fishery in the NW Atlantic collapsed due to overfishing, resulting in landings <10% of their historic maxima (Sinclair and Murawski, 1997).

The decline of cod and haddock stocks motivated Fogarty *et al*. (2001) to study their ability to withstand and recover from overexploitation. The study involved a comparative analysis of sympatric cod and haddock stocks in eight areas across the North Atlantic focusing on reproductive parameters generated from theoretical stock and recruitment relationships. They found that haddock stocks exhibited consistently higher variability and lower reproductive rates compared to cod stocks in all the geographic regions considered. This led the authors to conclude that cod has a stronger ability to withstand overexploitation, but that depleted haddock

Received: April 6, 2022. **Revised:** September 2, 2022. **Accepted:** September 7, 2022

Table 1. Region, species (C=cod, H=haddock), start and end year of time series, minimum and maximum spawning stock biomass in kilotons, with associated year in parenthesis, ratio of Maximum to Minimum SSB (SSB Max:Min), age at recruitment used in the assessment (R), for three stock the age of recruitment was standardised to equal age at recruitment of the stock found in the same area (in paranthesis), ratio of Maximum to Minimum recruitment (R Max:Min), and standard deviation of the log10 transformed recruitment indices (SD R).

Region	Area	Species	Years	Min SSB	Max SSB	SSB Max:Min	*R* age	*R* Max:Min	SD *R*
Northeast	Barents Sea	C	1946–2018	108 (1965)	2 263 (2013)	21	3	22	0.323
		H	1950–2018	49 (1985)	524 (2013)	17	3	143	0.505
	Faroese	C	1959–2019	15 (2007)	122 (1984)	8	1	50	0.332
		H	1957–2019	10 (2011)	94 (2003)	9	1	137	0.485
	Icelandic	C	1955–2018	115 (1993)	726 (1955)	6	3 (2)	5	0.146
		H	1979–2019	35 (1987)	154 (2004)	4	2	36	0.348
	Irish Sea	C	1968–2012	1 (2009)	19 (1982)	19	1	35	0.408
		H	1993–2019	2 (1994)	21 (2018)	11	0 (1)	24	0.332
	North Sea	C	1963–2020	32 (2005)	220 (1971)	7	1	35	0.378
		H	1972–2021	52 (1991)	551 (2002)	11	0 (1)	118	0.613
Northwest	Eastern Georges Bank	C	1978–2014	6 (2005)	60 (1981)	10	1	54	0.416
		H	1969–2014	5 (1974)	126 (2014)	25	1	5 532	0.658
	Eastern Scotian Shelf	C	1970–2009	4 (2003)	156 (1985)	39	3	13	0.323
		H	1970–2000	7 (1974)	84 (1985)	12	3	55	0.505
	Western Scotian Shelf	C	1983–2016	6 (2013)	104 (1991)	17	1	24	0.332
		H	1985–2013	16 (2013)	49 (2004)	3	1	73	0.485

stocks have a higher probability of recovery from depletion through large recruitment events.

Since the earlier analysis by Fogarty *et al.* (2001), the shelf ecosystems in the North Atlantic and the cod and haddock stocks inhabiting them have changed and, in some instances, quite dramatically. These changes could alter the patterns of recruitment variability and resilience to overfishing as reported by Fogarty *et al.* (2001). Here, we analysed model output from the most recent stock assessments of sympatric cod and haddock stocks to determine whether the recruitment variability and reproductive rate differences have persisted since the mid-1990s, the end of the period examined by Fogarty *et al.* (2001).

Changes since the mid-1990s include large-scale environmental warming trends that have occurred in the shelf seas across the North Atlantic, with accelerated warming in the most recent decades (Bindoff *et al.*, 2019; Garcia-Soto *et al.*, 2021; Gonçalves Neto *et al.*, 2021). In the western Atlantic, cod and haddock stocks collapsed in the early 1990s, when fishing moratoria were introduced, but the collapses were accompanied by ecosystem regime shifts and trophic restructuring, which may have prevented recovery of the stocks (Frank, 2005; Swain and Benoit, 2015). In the eastern Atlantic, the fate of the stocks and the changes in the ecosystem have been more varied. The northernmost cod and haddock stocks, residing in the Barents Sea, reached record high biomass levels during the past decade (Landa *et al.*, 2014; Johannesen *et al.*, 2020), whereas in the same period, Irish Sea cod and Faroese haddock declined to historic lows (ICES, 2013, 2020). The Barents Sea stocks increased rapidly and expanded northwards following strong recruitment and reduced fishing pressure. The demographic structure of many cod and haddock stocks has also changed over the last two decades. For instance, the condition and size-at-age of Scotian Shelf cod and haddock have declined since the mid-1990s and have remained low since then (Shackell and Frank, 2007; Shackell *et al.*, 2010). In the North Sea, cod and haddock size and age at maturity have also declined (Baudron *et al.*, 2011; Baudron *et al.*, 2014; Marty *et al.*, 2014), and similar but not as dramatic declines in size and age at maturity have been observed for Icelandic cod (Pardoe and Marteinsdóttir, 2009).

Weel-documented changes to the trophic structure, management regimes, and stock characteristics (spatial distribution, maturity, size, and condition at age) occurring in a warming ocean may all have impacted recruitment of both cod and haddock, but not necessarily to the same extent for both species nor in the same direction throughout their ranges (Fogarty *et al.*, 2008; Mantzouni *et al.*, 2010; Klein *et al.*, 2017). Persistent differences in recruitment patterns between cod and haddock suggest that despite similarities in reproductive traits and life-history, there are some trait differences between the species that are fixed and part of the fundamental biology of the species. We tested for consistency in differences in recruitment patterns by dividing our analysis into two periods—before and after 1993 with the former corresponding to the period studied by Fogarty *et al.* (2001) and the latter associated with the many documented changes already noted.

Methods

Data

We compiled recruitment and SSB estimates for cod and haddock stock pairs from the geographic areas that were evaluated by Fogarty *et al.* (2001) (Table 1). There were, however, three exceptions. We added the western Scotian Shelf and the Irish Sea areas to replace Brown's Bank (part of the western Scotian Shelf) and the west of Scotland areas. The west of Scotland haddock is no longer assessed as a separate stock, but instead is now part of the larger North Sea stock assessment. Fogarty *et al.* (2001) used data from the whole Georges Bank area, but here we used the eastern Georges Bank, since this allowed for a more up-to-date time series. The data we used was model output from recent age-structured assessments of sympatric cod and haddock stocks conducted by the International Exploration of the Seas (ICES), Fisheries and Oceans Canada (DFO), and the Transboundary Resource Assessment Committee (TRAC). Uncertainty in the estimates was not available in these assessment reports and could not be further considered. The compiled data are available as Supplementary S1, and a map over the study region is in Supplementary S2 (Figure S1).

ICES reports with the latest available assessments were the source for the northeast (NE) Atlantic stocks: Barents Sea cod (cod.27.1–2) and haddock (had.27.1–2) (ICES, 2021a), Faroese cod (cod27.5.b.1) and haddock (had.27.5.b) (ICES, 2020), Icelandic cod (cod.27.5.a) and haddock (had.27.5.a) (ICES, 2021b), Irish Sea cod (cod.27.7a) (ICES, 2013) and Irish Sea haddock (had.27.7a) (ICES, 2021c), and North Sea cod (cod.27.47d20) and haddock (had.27.46a2) (ICES, 2021d).

Regional stock and recruitment data for the northwest (NW) Atlantic stocks of cod and haddock were obtained from the following sources: eastern Scotian Shelf: cod Div. 4VsW (Swain and Mohn, 2012) and haddock Div. 4VW (Mohn and Simon, 2002), western Scotian Shelf Div. 4 × 5Y: cod (DFO, 2019) and haddock (Wang *et al.*, 2017), and eastern Georges Bank: cod (Wang *et al.*, 2015) and haddock (Stone *et al.*, 2015).

The estimated age at recruitment varied among stocks in the Irish Sea, the North Sea, and Iceland (Table 1). We standardized age at recruitment to be identical for cod and haddock for these areas (see Supplementary S1 for more details). Icelandic cod recruitment at age 3 ($R3$) was back-calculated to age 2 ($R2$) by assuming an instantaneous natural mortality rate (M) = 0.2 and a fishing mortality rate (F) = 0. Age 0 ($R0$) for North Sea haddock was replaced with abundance at age 1 estimates from the assessment (ICES, 2021d). Age 1 ($R1$) for the Irish Sea haddock was calculated from age 0 ($R0$) by setting $M = 0.2$ and using discard estimates of F for age 0 from the assessment (ICES, 2021c).

Analysis

Recruitment variability was assessed by estimating the standard deviation (*SD*) of the residuals from a Ricker stock and recruitment model fitted to the SSB and recruitment time series for each stock (Fogarty *et al.*, 2001). The *SD* was based on the difference between the observed log(R/SSB) and the log(R/SSB) predicted from log(SSB), which is the remaining recruitment variability after the effect of SSB on recruitment is accounted for. The Ricker model was linearized to

$$\log\left(\frac{R}{\mathrm{SSB}}\right) = \log(a) + b \times \log(\mathrm{SSB}) + \in_{\mathrm{i}}, \tag{1}$$

where R is the number of recruits, SSB is the spawning stock biomass in the birth year of the recruits, log(a) is the intercept of the relationship, b is the slope, and $\in_i$ is a normally distributed error term.

Given the uncertainty of the fitting of theoretical stock and recruitment relationships to data, we also quantified recruitment variability using a more flexible approach using Generalized Additive Models (GAMs), which served to remove trends, potentially resulting from SSB, from the recruitment time series (log transformed) for each stock. The *SD* of the residuals from the GAM approach was used as a second metric of recruitment variability for each stock.

To test for synchronizing effects of the environment on cod and haddock recruitment, we quantified the correlation between cod and haddock log transformed recruitment. A positive correlation may imply that the environment impacts recruitment of sympatric stocks in the same direction.

The parameter log(a) (1) is commonly referred to as the steepness parameter and provides an estimate of the number of recruits produced per unit SSB at low SSB levels (Lowerre-Barbieri *et al.*, 2017; Wiff *et al.*, 2018). In addition, an estimate of reproductive capacity at low SSB was calculated by taking the mean number of recruits per SSB when SSB was <40% of the maximum SSB (see Supplementary S2, Figure S2). We choose 40% as a cut-off since this resulted in a reasonable number of data points for the analysis, and we reference to these estimates as maximum annual reproductive rate (MARR). These parameters are indicators of a stock's ability to recover from collapse/depletion and were standardized to represent an estimate of the number of spawners produced by each spawner at low abundance (Fogarty *et al.*, 2001). The details on the standardization can be found in Myers *et al.* 1999 and were done using the "fishmethods" package in *R*. The *R*-scripts used here can be found at github (https://github.com/dave-keith/haddock).

We separated the analysis into two time-intervals to facilitate a comparison with the results obtained by Fogarty *et al.* (2001) and to assess the possibility that there were differences in the observed patterns during the most recent period. Hence, the updated time series was split into a "*Pre-1993*" (years prior to and including 1992) and a "*Recent*" period (1993 to end of time series). We calculated the change in recruitment variability and reproductive capacity at low SSB for each stock to contrast the two periods.

Results

The time series was generally longer for the NE Atlantic stocks compared to the NW Atlantic stocks (Table 1, Figure 1). Most NW Atlantic stocks are no longer assessed annually, and the eastern Scotian Shelf haddock, once sustaining a substantial fishery, has not been assessed since 2001. The NE stocks, except the Irish Sea cod stock, are regularly assessed. The average time series length for the cod and haddock stocks from the NE Atlantic stocks was 59 years (range: 40–72) and 49 years (range: 26–68), respectively. For the NW Atlantic stocks of cod and haddock, the time series length was 36 years (range: 33–39) and 34 years (range: 28–45), respectively.

Trends in recruitment and SSB

The SSB of all cod stocks reached minimum levels after 2000, except for the two northernmost stocks, Icelandic and Barents Sea cod (1993 and 1965, respectively, Table 1, Figure 1). Maximum SSB was reached as early as 1955 for Icelandic cod and prior to the *Recent* period for all cod stocks except the Barents Sea cod, which peaked in 2013. The average SSB level across cod stocks was 35% lower in the *Recent* period compared to *Pre-1993*. The overall decline was driven by the NW Atlantic stocks, where SSB was on average 72% lower, compared to a 13% reduction for the NE Atlantic stocks (Figure 1). During the *Recent* period, some of the NE Atlantic stocks declined (Irish Sea, North Sea, and Faroese), and some increased (Barents Sea and Iceland) (Figure 1), whereas in the NW Atlantic, the cod stocks either continued to decline or stayed at a low level during the *Recent* period (Figure 1). In contrast to cod, the SSB of all haddock stocks peaked after 2000, except for the eastern Scotian Shelf haddock, which peaked in 1985. Minimum SSB levels were observed in the 1980s for the northernmost haddock stocks (Iceland and Barents Sea), during the 1970s for the eastern Scotian Shelf and the eastern Georges Bank haddock, and more recently for the Faroese and western Scotian Shelf haddock (Table 1). Overall, SSB levels for haddock were 20% higher in the *Recent*

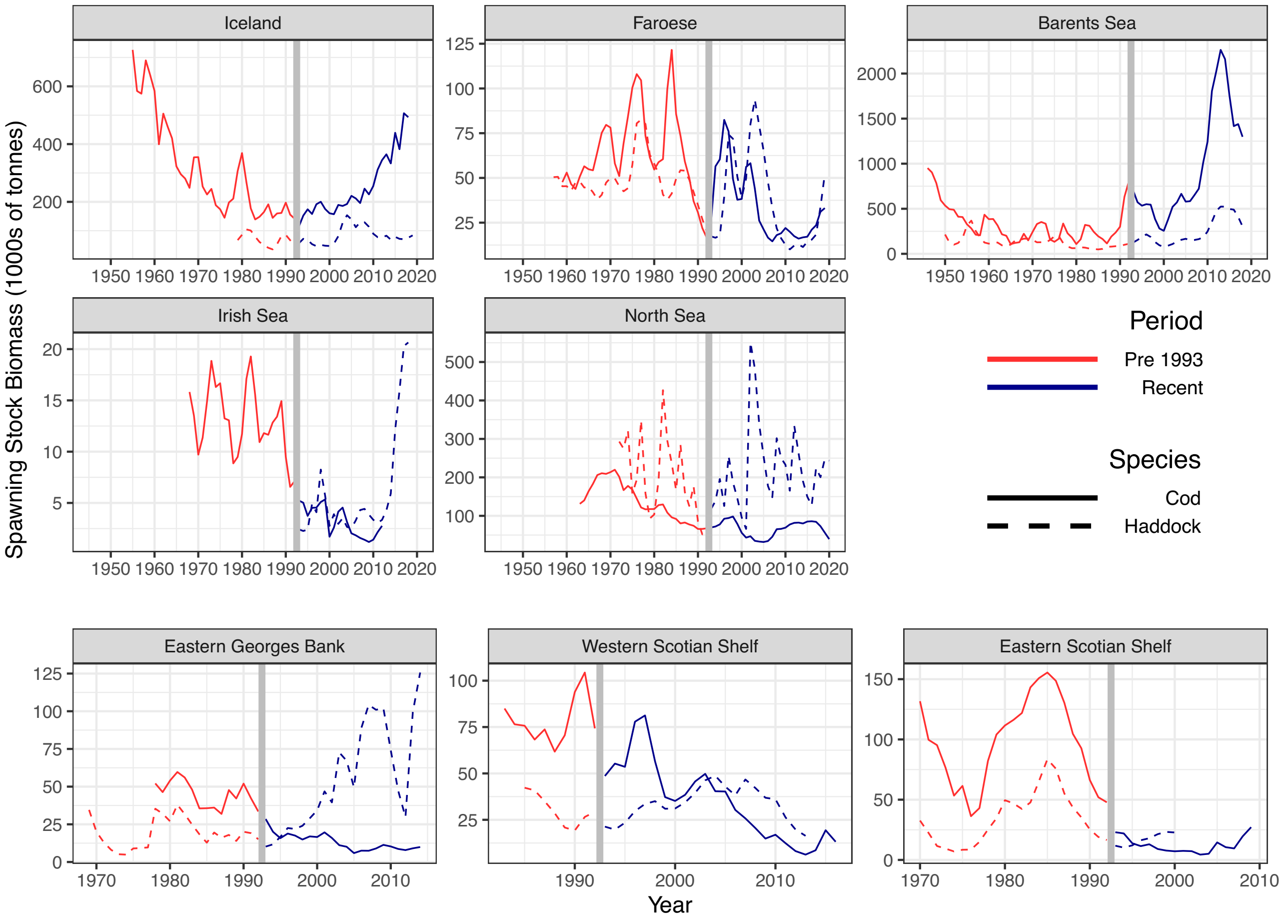

Figure 1. SSB (thousands of tonnes) time series for eight cod (solid line) and haddock (dashed line) stocks in the Atlantic Ocean. The red line indicates data from the *Pre-1993* period, while the blue line is for the *Recent* period. The vertical grey line indicates the division between the two periods.

period, and this was more pronounced for the NW Atlantic stocks (40%) than for the NE Atlantic stocks (10%). Variability in SSB, based on the ratio of the maximum to minimum observed values in the time series, was lowest among the NE Atlantic haddock stocks (range: 4.4–10.7), followed by NE Atlantic cod stocks (range: 6.3–20.9), NW Atlantic haddock stocks (range: 3.1–25.2), and NW cod stocks (range : 10–39).

The average ratio of the maximum to minimum number of recruits was higher for haddock (854) than for cod (30), although the Georges Bank haddock stock is clearly an outlier (Table 1). Removing this stock lowered the average of maximum to minimum recruitment for haddock to 84, which was still nearly three times higher in comparison to cod. Apart from Georges Bank, the haddock stock with the most variable recruitment was the Barents Sea stock (Table 1). For cod across all regions, the recruit numbers in the *Recent* period were on average 58% lower than the *Pre-1993* period, in the NE Atlantic, the decline was 49%, while in the NW Atlantic this decline was much greater averaging 73% (Figure 2). For haddock across all regions, the recruit numbers were 50% higher in the *Recent* period compared to the *Pre-1993* period. In the NE Atlantic, there was no difference in the average recruitment numbers between the two periods, while in the NW Atlantic, the recruit numbers averaged 110% higher in the *Recent* period (Figure 2).

The log of recruits produced per kilogramme of spawning stock biomass [log(R/SSB)] revealed some interesting trends over time (Figure 3). In the Barents Sea, where the stocks have peaked recently, the number of recruits per spawner biomass was lower during the *Recent* period. A similar pattern was evident in the North Sea, but there, cod levels were lower in the *Recent* period. On the eastern Scotian Shelf, the number of recruits per spawner was higher in the *Recent* period compared to *Pre-1993*, but this result was based on only 11 years of data. The Irish Sea haddock was an outlier, and this might be due to the standardization of age at recruitment from $R0$ to $R1$ (see the “Discussion” section).

The correlation between the cod and haddock recruitment time series *Pre-1993* was significantly positive for the North Sea, the Faroese, and Barents Sea, positive but not significant for Iceland, the eastern Scotian Shelf, and the eastern Georges Bank, and nonsignificant but negative for the western Scotian Shelf (Figure 4). The correlation between the cod and haddock recruitment tended to be positive also in the *Recent* period, but for all regions except for the North Sea and the Faroese, the correlation was not significant (Figure 4).

Correlations between recruitment of different stocks of the same species were generally weak, except for between the eastern Georges Bank and western Scotian Shelf, where both cod and haddock had strong positive correlations (Supplementary S2; Table 1).

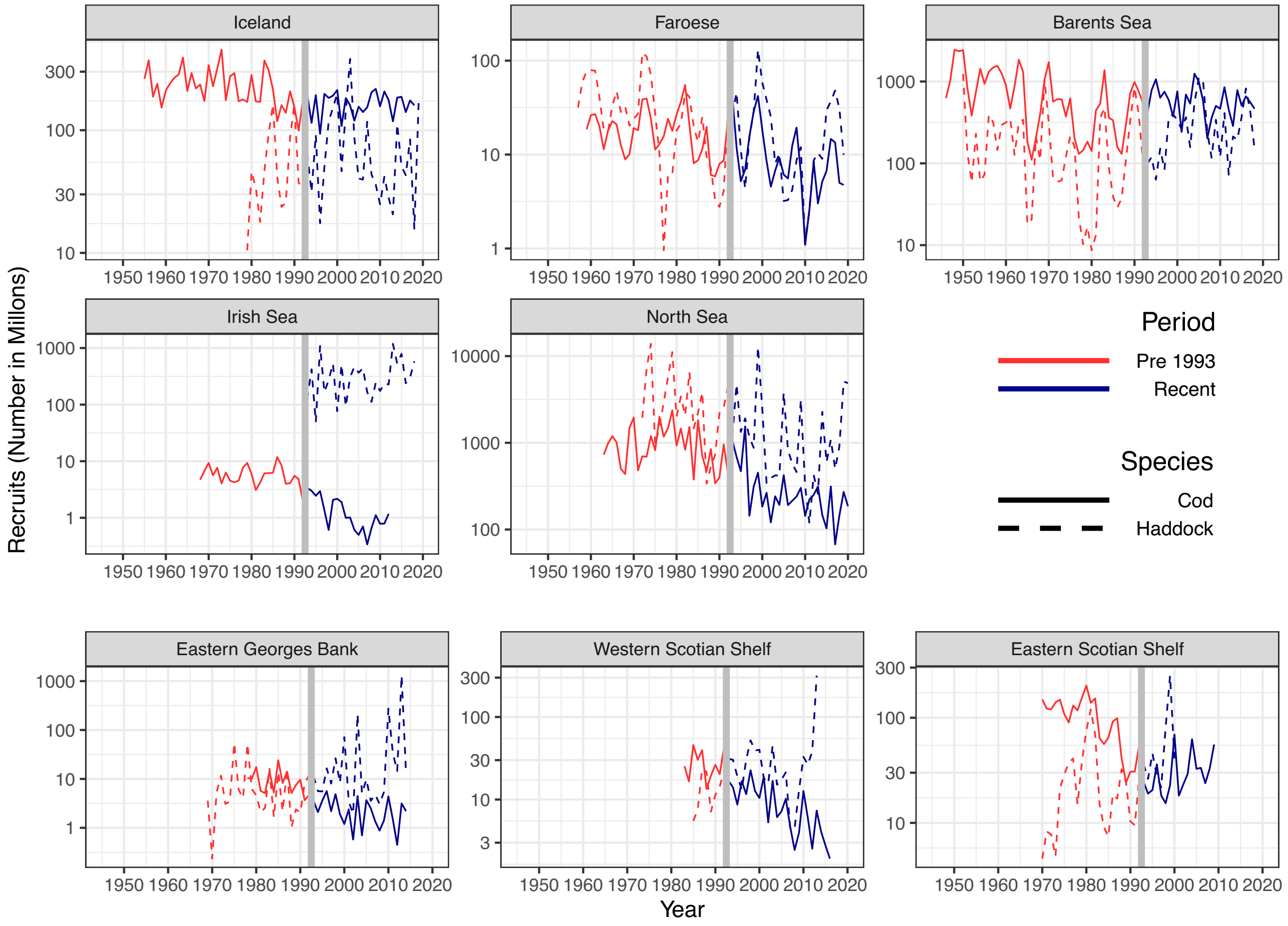

Figure 2. Recruitment (in millions) time series for eight cod (solid line) and haddock (dashed line) stocks in the Atlantic Ocean. The red line indicates data from the *Pre-1993* period, while the blue line is for the *Recent* period. The vertical grey line indicates the division between the two periods.

Recruitment variability

The *SD* of the recruitment residuals from the Ricker model was on average 80% higher for the haddock stocks than for the cod stocks in the *Pre-1993* period (Figure 5a, Table 2). In the *Recent* period, the *SD* of the recruitment residuals was, on average, 70% higher for the haddock stocks in comparison to the cod stocks (Figure 5a, Table 2). Density plots of the residuals from the Ricker model are shown in Supplementary S2 as Figure S3, illustrating the larger recruitment residuals for haddock compared to cod.

Across both species and time intervals, the Ricker models explained on average 27% of the variance between recruits and SSB (Table 2). When averaged across all areas, the stock and recruitment relationship was somewhat stronger for cod (explained variance = 31%) than haddock (23%), whereas for each species, there was little difference between time periods, except for a few stocks. The Barents Sea cod and haddock stocks exhibited much stronger stock and recruitment relationships during the *Recent* period. The Irish Sea cod stock showed a strong *Pre-1993* stock and recruitment relationship, which weakened considerably during the *Recent* period.

Recruitment variability estimated from the GAMs, measured as the *SD* of the recruitment residuals, revealed that recruitment was more variable for haddock compared to cod during both periods (Figure 5b), and thus very similar to the results based on the residuals from the Ricker model (Figure 5a).

The autocorrelation in recruitment residuals from the Ricker and the GAMs by stock and by period was similar (Supplementary S2, Figures S4 and S5).

Reproductive rate at low stock size

In the *Pre-1993* period, the MARR at low SSB [i.e. the standardized log*(a)* parameter in the Ricker model] was higher for cod than for haddock in five of seven areas (no data from the Irish Sea), but this was only significant for three regions (based on non-overlapping *CI* from the 1:1 line for the Barents Sea, North Sea, and eastern Scotian Shelf, Figure 6a). In the *Recent* period, the MARR of the cod was higher for five out of seven areas but was significant only for three (Barents Sea, North Sea, and Iceland, Figure 6a). In addition, during the *Recent* period, the estimated MARR for the NE Atlantic region was higher for cod than haddock for all stocks, while the results from the NW Atlantic were more variable, with the western Scotian Shelf being the only area in which the haddock MARR was significantly higher than for cod (Figure 6).

The MARR, a measure of the reproductive capacity at low SSB, was also calculated by taking the mean number of recruits per SSB when SSB was <40% of the maximum SSB (Supplementary S2, Figure S2).

All SSB values of eastern Georges Bank and the western Scotian Shelf cods were >40% of the maximum values in the *Pre-1993* period, (there were no data for haddock in the Irish Sea

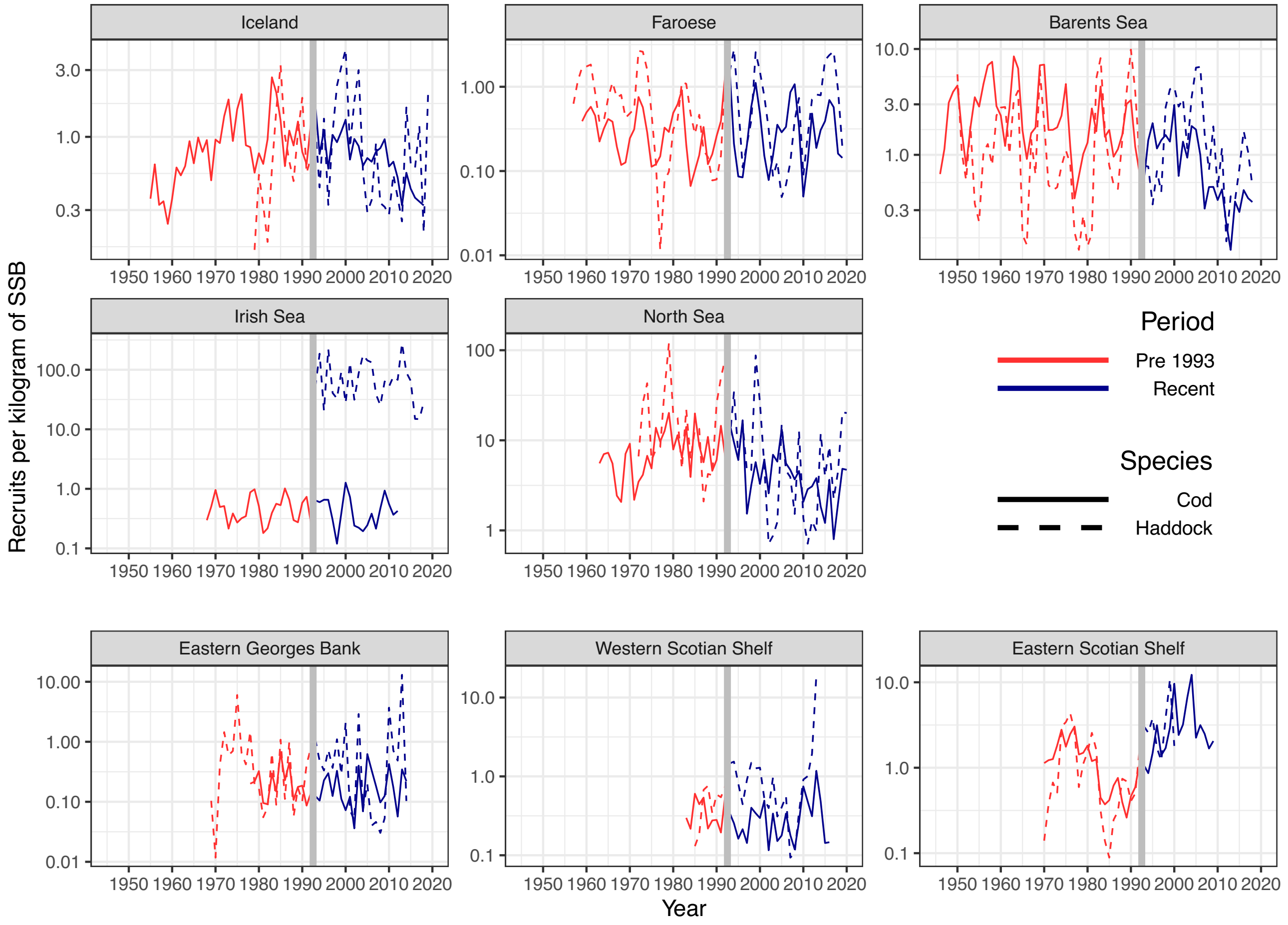

Figure 3. A time series of the number of recruits produced per kilogramme of SSB for eight cod (solid line) and haddock (dashed line) stocks in the Atlantic Ocean. The red line indicates data from the *Pre-1993* period, while the blue line is for the *Recent* period. The vertical grey line indicates the division between the two periods.

in the *Pre-1993* period). The estimate of the MARR produced similar results to the Ricker model results and was higher for cod than for haddock based on those that could be calculated in this manner.

In the *Recent* period, the MARR for all the NW Atlantic stocks was similar or higher for haddock than for cod, while for the NE Atlantic stocks, the MARR was higher for cod (Figure 6b).

Comparing periods

The direct comparison between the *Pre-1993* and *Recent* periods is shown in Figure 7. Recruitment variability increased for all stocks consistently (residuals from both Ricker and GAM), except cod and haddock in the Barents Sea, eastern Scotian Shelf haddock, and Icelandic cod. Overall, the reproductive rates at low stock sizes from the *Pre-1993* to *Recent* period decreased for cod, whereas the change was more variable for haddock but tended to increase (Figure 7c and d).

Harmonizing the length of the time series to 1985–2013 revealed patterns consistent with the analysis on the complete time series (Supplementary S2, Figures S6 and S7).

Discussion

Life-history traits and recruitment variability

Despite substantial and ongoing changes in the environment and fishing exploitation regimes, our results confirm those of Fogarty *et al.* (2001): haddock stocks consistently demonstrate higher recruitment variability in comparison to cod stocks across the North Atlantic. While there is ample information on the temporal coherence of recruitment of sympatric species or stocks per se (e.g. Megrey *et al.*, 2009), there is much less empirical evidence comparing the magnitude of recruitment variability (but see Walsh *et al.*, 2004). A recent empirical study by Thorson *et al.* (2014) evaluated recruitment variability within and among taxonomic orders and found that within-order recruitment variability tended to be higher than among orders (Thorson *et al.*, 2014). This result is consistent with our findings since cod and haddock both belong to the same family, Gadidae. Traits related to recruitment include both fixed and variable traits that are responsive to changes in the environment (Lowerre-Barbieri *et al.*, 2017). The persistent differences in recruitment variability between cod and haddock stocks suggest the existence of fixed species-specific life-history traits between the two species.

But which traits are involved in these persistent differences? Fogarty *et al.* (2001) reported that cod, based on the US stocks, had a more protracted spawning season over a broader spatial extent compared to haddock, and offered this as an explanation for the difference in recruitment variability, since a longer spawning season could act as a bet-hedging strategy to dampen recruitment variability. However, in the Barents Sea, haddock tend to have a longer spawning season in comparison to cod (Bergstad *et al.*, 1987) while exhibiting higher

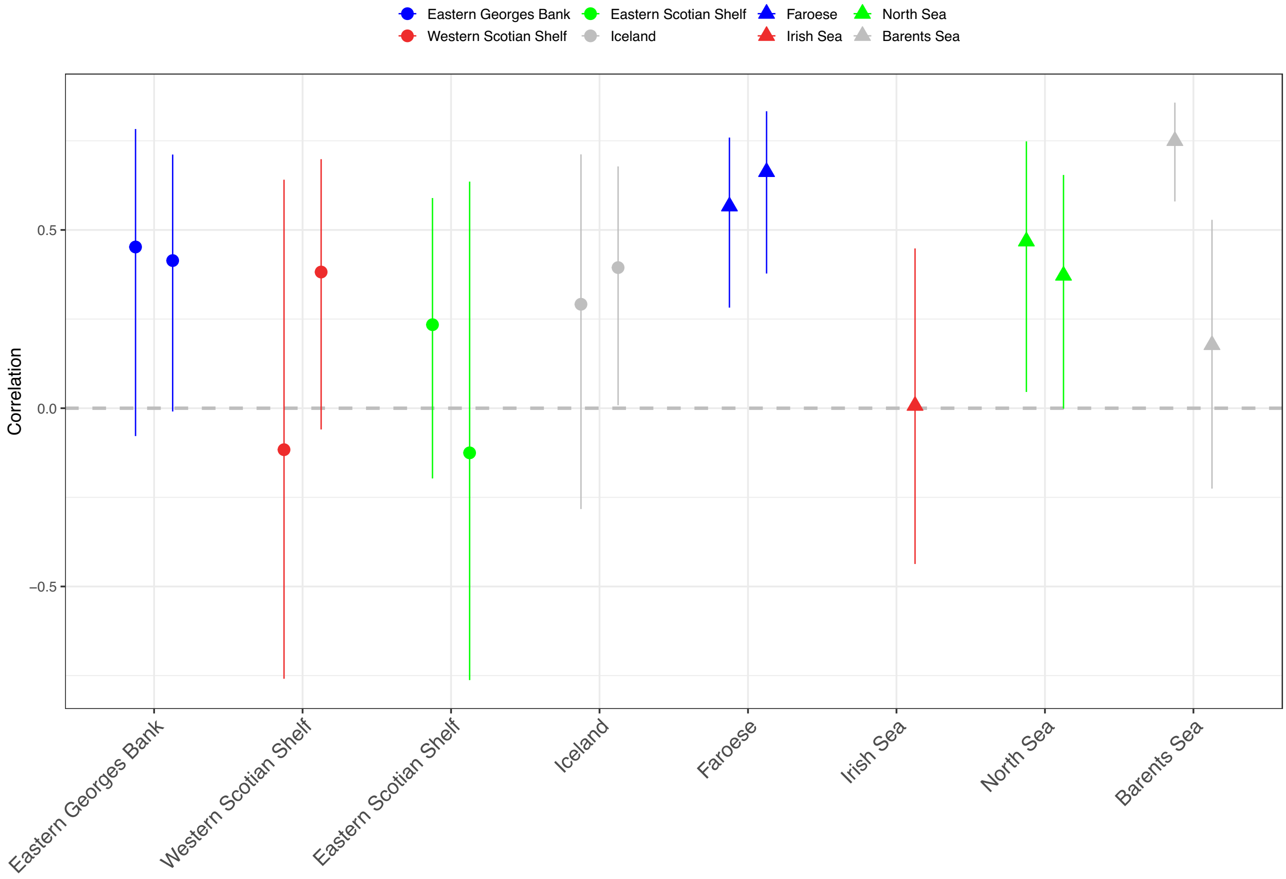

Figure 4. Correlation of the recruitment (log scale) time series between cod and haddock stocks in each region. For each stock, the *Pre-1993* period is shown on the left and the *Recent* period is on the right. The Irish Sea correlation is only available for the *Recent* period. The error bars represent the 95% *CI*.

recruitment variability. Therefore, the length of the spawning season cannot explain the general pattern.

Two traits that appear to be consistently different between the two species across areas are diet and maximum size. Adult haddock can be characterized as benthivores, feeding on invertebrates such as brittle stars and polychaetes (Tam *et al.*, 2016), whereas cod grows bigger and is much more piscivorous, and also prone to eating its own young (Link *et al.*, 2009). The cannibalistic behaviour can result in density dependence, which potentially stabilizes recruitment by dampening the production of strong year classes before they reach a larger (fishable) size. Fogarty *et al.* (2001) were able to assess the relative strength of compensatory responses in four paired pre-recruit cod and haddock populations and found that cod compensation was stronger compared to haddock in three out of four cases. Compensatory processes such as cannibalism may reduce recruitment variability, but note that the degree of cod cannibalism varies substantially among ecosystems (Link *et al.*, 2009), and the effect of cannibalism on recruitment will be less in areas where older, large cod have recently become rare, such as in the NW Atlantic stocks examined herein (e.g. Shackell *et al.*, 2010).

Could the relevant traits be found in differences between the early-life stages of cod and haddock? The haddock eggshell (chorion) is sticky, and this attribute has been used to differentiate between morphologically similar early-stage eggs of cod and haddock (S. Sundby, IMR, personal communication). This chorion characteristic binds oil droplets, enhancing exposure to toxic compounds (Sørhus *et al.*, 2015), but likely has some unknown adaptive significance that may impact recruitment variability, and in some circumstances, increase recruitment success. Haddock larvae develop larger pectoral fins earlier than cod, improving their manoeuvrability (Auditore *et al.*, 1994; Petrik *et al.*, 2009), which might be of benefit in foraging under some instances, but may also infer a cost.

At this stage, the traits responsible for the difference in cod and haddock recruitment variability remain unknown. Despite cod and haddock having large economic, cultural, and ecological importance and over a century of scientific scrutiny, there are many aspects of their basic biology, including their evolutionary history (Malmstrøm *et al.*, 2016; Roa-Varón *et al.*, 2020), which remain poorly understood.

It is important to note that there are a few methodological limitations to our study. First, we standardized age at recruitment for Icelandic cod and Irish Sea haddock to make them comparable to haddock and cod within the same area. We assumed constant natural mortality of $M = 0.2$ for both stocks, but the natural mortality is probably higher and more variable for juveniles. The high $\log(R/\mathrm{SSB})$ for the Irish Sea relative to the other stocks (Figure 3) is most likely a result of the assumed low natural mortality. However, since this standardization was applied only to two stocks, we believe this does not invalidate the overall results. Similar standardization was undertaken by Fogarty *et al.* (2001), but there all the stocks

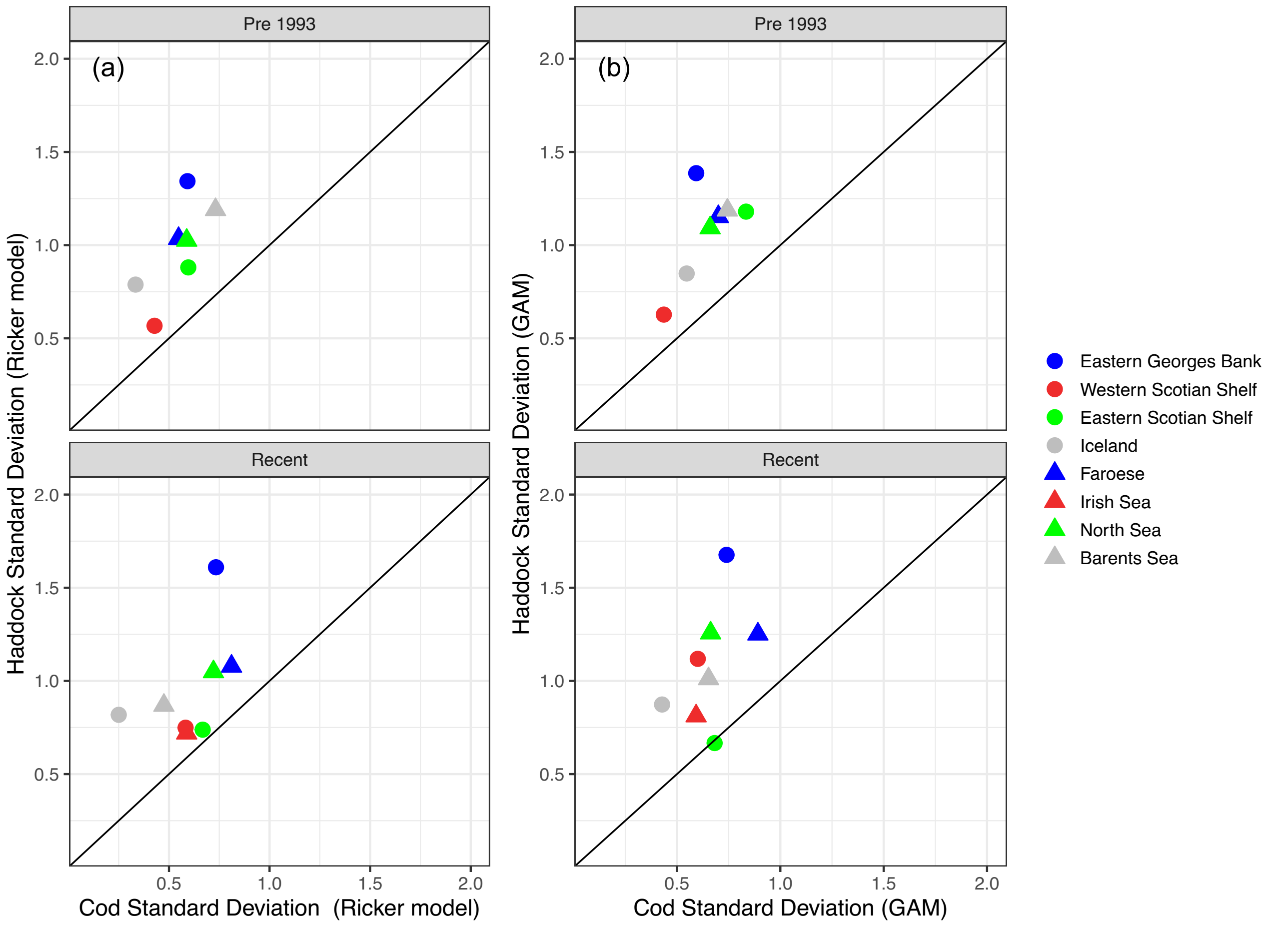

Figure 5. The *SD* of the log residuals from (a) the Ricker S–R Model and (b) the GAMs.

Table 2. Summary of results of the Ricker stock recruitment model for each stock in each period and region. Results include R2, log of the maximum annual reproductive rate (MARR), log(a), and the standard deviation (SD) of log(a).

		Pre-1993				*Recent*			
Region	Species	R^2	MARR	log(a)	*SD*	R^2	MARR	log(a)	*SD*
Barents Sea	C	0.05	1.67	1	0.2	0.67	1.67	0.66	0.17
	H	0.002	0.11	0.1	0.4	0.32	0.85	1.1	0.32
Faroese	C	0.43	0.83	−0.04	0.27	0.19	0.23	−0.57	0.32
	H	0.31	1.43	1.73	0.67	0.26	−0.23	0.13	0.37
Iceland	C	0.62	1.47	0.57	0.11	0.71	1.39	0.49	0.12
	H	0.15	0.3	0.64	0.75	0.07	0.05	−0.57	0.32
Irish Sea	C	0.48	NA	0.51	0.3	0.13	NA	0.59	0.47
	H	NA	NA	NA	NA	0.25	NA	4.57	0.22
North Sea	C	0.26	2.54	2.75	0.28	0.14	1.92	2.26	0.45
	H	0.13	0.15	3.41	0.5	0.34	0.25	3.16	0.47
Eastern Georges Bank	C	0.16	0.53	−0.46	0.78	0.09	−0.57	−1.29	0.41
	H	0.2	0.01	0	0.57	0.08	−0.55	−0.36	0.66
Eastern Scotian Shelf	C	0.29	1.47	0.96	0.36	0.49	−0.38	1.89	0.28
	H	0.37	0.05	0.7	0.35	0.05	−1.03	0.57	0.91
Western Scotian Shelf	C	0.12	−0.31	−0.17	0.91	0.12	−1.26	−0.96	0.23
	H	0.38	0.14	0.63	0.8	0.56	1.78	2.61	0.61

were set to the same age at recruitment (*R*1). Second, we use stock assessment output as input data in our analyses. Brooks and Deroba (2015) make the important point that the output from stock assessment models is estimated with associated uncertainties that need to be taken into account. However, most stock assessment reports do not provide such information, including the time series we examined here.

Covariation in recruitment variability

We found that the correlations between recruitment series for sympatric cod and haddock stocks were mainly nonsignificant but positive, implying that within the same ecosystem, the environmental conditions had similarly weak effects on both species. Covariation in recruitment among species has

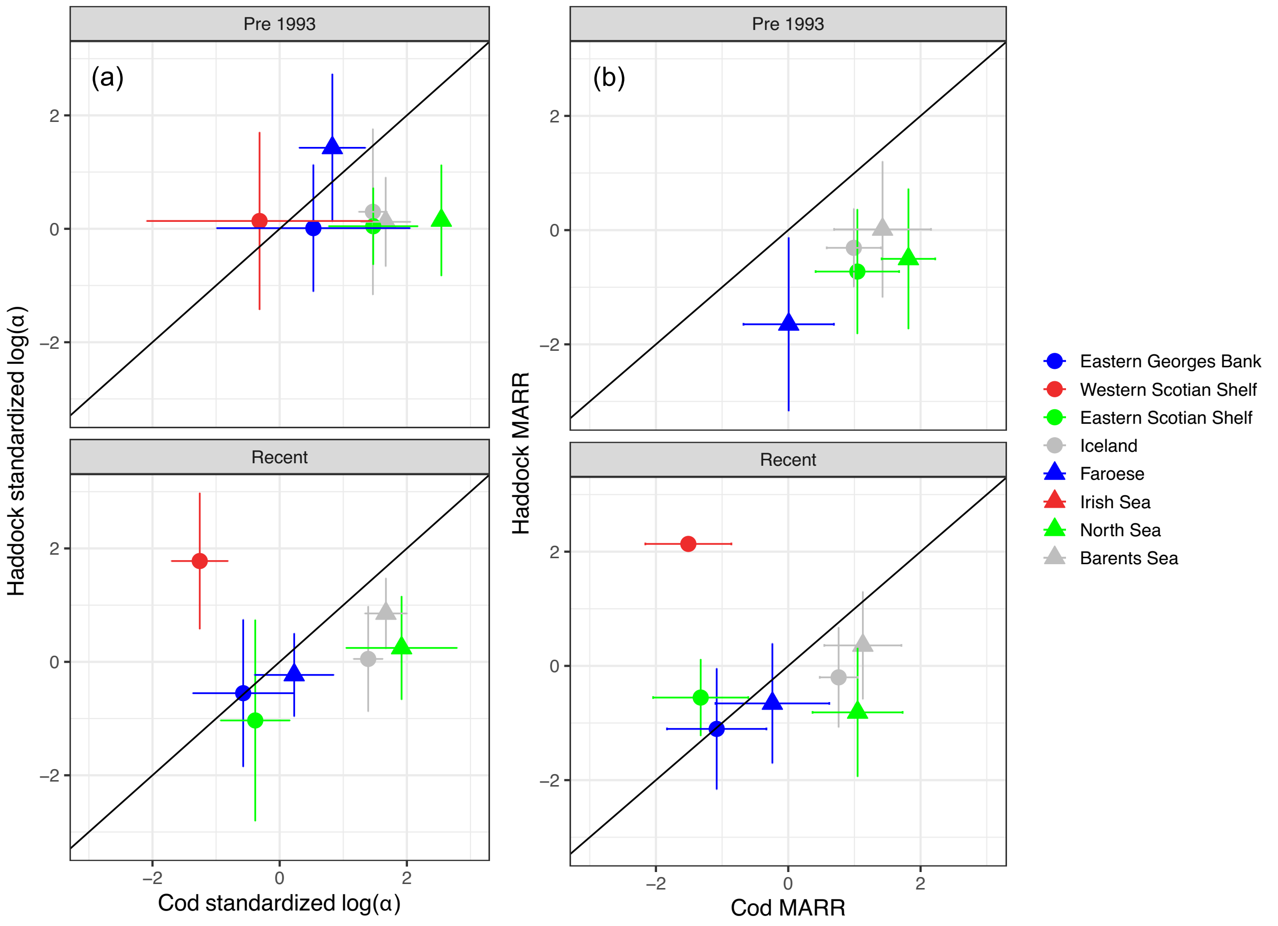

Figure 6. The log of the MARR is estimated using (a) the Ricker stock recruitment model for each stock in the *Pre-1993* and *Recent* period with 95% *CI* (standardized log alpha) and (b) the mean recruitment when SSB = 0.4 of the maximum SSB (MARR). The error bars in (b) represent 1 *SD* from the mean (there was insufficient data in the *Recent* period for western Scotian Shelf haddock to calculate the *SD*).

been reported in the marine environment, but the effect of environmental drivers on recruitment is rarely stationary (Hidalgo *et al.*, 2012; Brosset *et al.*, 2020). For instance, in the Barents Sea, strong year classes of several species appear in warm years (Dingsør *et al.*, 2007; Landa *et al.*, 2014). However, during the recent anomalous warm years, the effect of temperature on cod and haddock recruitment has become less important and the correlation between cod and haddock recruitment has weakened in the Barents Sea (Bogstad *et al.*, 2013).

Reproductive output at low stock size

Fogarty *et al.* (2001) found that reproductive output at low stock size, assessed from the Ricker model was consistently and significantly higher for cod in all but one region (the Browns Bank). While the present study found that the MARR was higher in cod, the differences were typically not significant. The differences also appear to be less pronounced in the *Recent* period, since overall cod recruitment at low stock sizes has declined, whereas the change in haddock remained variable.

The decline in cod maximum reproductive rate since the *Pre-1993* period could be explained by the warming trend in the *Recent* period. Fogarty *et al.* (2008) predicted that cod's maximum reproductive rate and recruitment would decline with warming at the southernmost distribution range. A study comparing the impact of temperature on the maximum reproductive rate across all cod stocks found that temperature reduced reproductive potential when temperatures were >5°C (Mantzouni *et al.*, 2010). Haddock has been found to perform physiologically better than cod in warmer conditions (Norin *et al.*, 2019), but compared to cod, there are fewer studies on the impact of warming on haddock (Klein *et al.*, 2017). The only comparison of the effect of temperature on the MARR of cod and haddock is an unpublished study (Mantzouni and MacKenzie, 2009), which revealed an overall positive temperature effect on haddock and a dome-shaped relationship for cod.

Conclusion

Fogarty *et al.* (2001) evaluated recruitment variability and recruitment at low stock size for co-occurring cod and haddock. We have shown that the two species have demonstrated a persistent difference in recruitment variability during the past several decades despite the noted changes in both environmental conditions: stock size and composition. We have also demonstrated that for most of the stocks, with the notable exception of the Barents Sea cod and haddock, overall recruitment variability has increased in the *Recent* period, compared to the *Pre-1993* period, which was also treated in Fogarty *et*

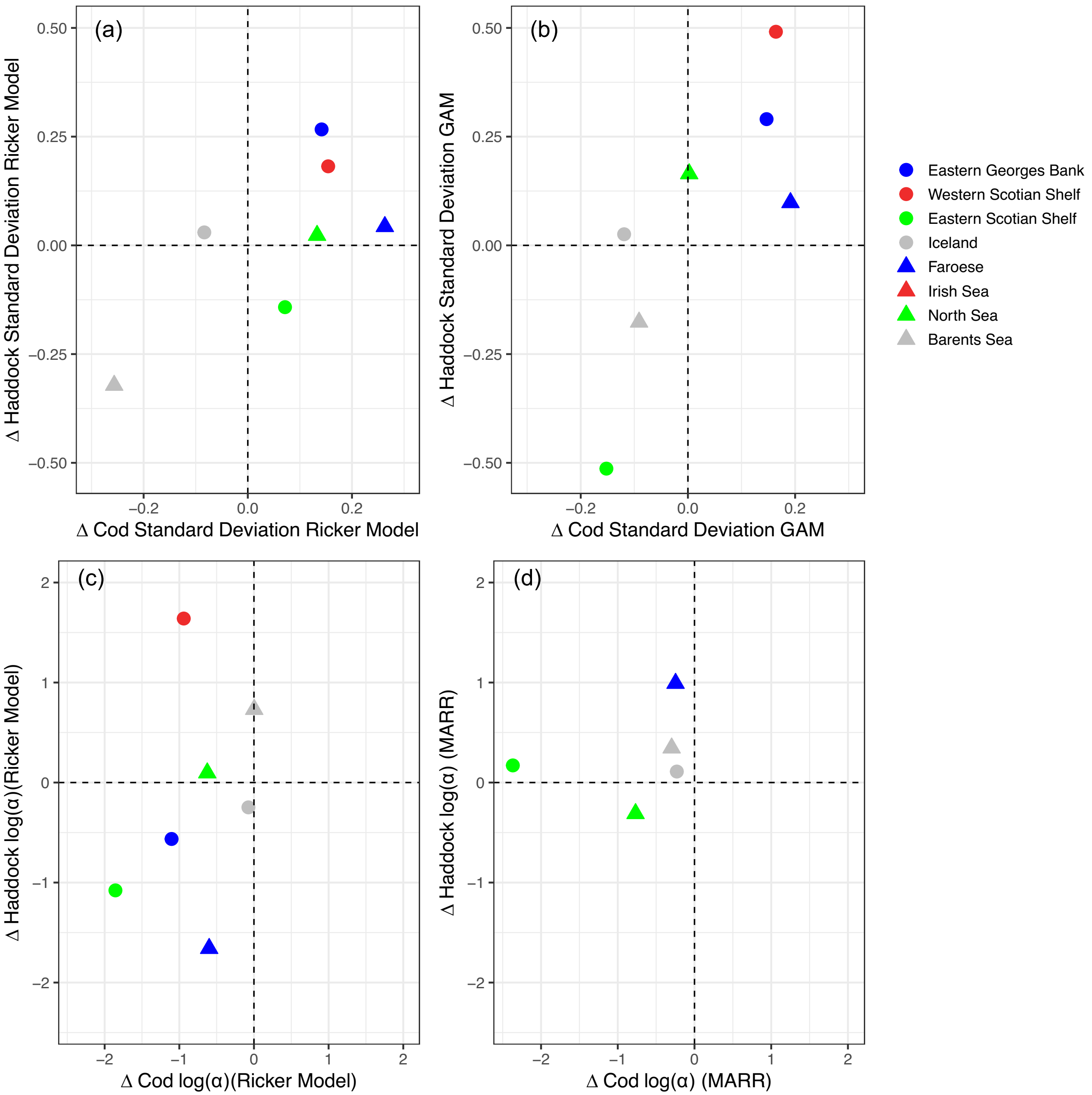

Figure 7. The change in the *SD* of the residuals between the *Recent* and *Pre-1993* periods for the (a) Ricker S–R Model and (b) GAMs. The change in the alpha estimates between the *Recent* and *Pre-1993* periods for the (c) Ricker S–R Model and (d) alpha at 40% of maximum SSB Positive values indicate the estimate in the *Recent* period was larger than *Pre-1993* period.

al. (2001). In the *Recent* period, most cod SSBs were lower (Table 1 of this study), and for many stocks of both species, the age diversity and size of the spawners have declined (Shackell *et al.*, 2010). Hence, some of the buffering capacity against recruitment variability caused by traits related to body size of spawners and age diversity in the spawning stock (longer spawning season, more batches, larger, and more eggs) seems to have been reduced or lost. In the Barents Sea, the recruitment variability as well as the impact of the environment on recruitment have declined as both stocks have increased in size (this study; Bogstad *et al.*, 2013). As the age diversity in the stocks increased due to increased longevity as fishing pressure was reduced (Kjesbu *et al.*, 2014; Ottersen and Holt, 2022), the stocks exhibited a higher buffering capacity against environmental variation. Thus, our results underline and reiterate many previous studies on the danger of overfishing.

Acknowledgements

We thank three anonymous reviewers that greatly improved the manuscript. EJ acknowledges the travel support from IMR Norway and the Norwegian Research Council to visit DFO Canada.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest statement

The authors declare no conflict of interests.

Funding

This work was supported by the Norwegian Research Council (project number 332105), Fisheries and Oceans (DFO) Canada, and the Ministry of Trade, Industry and Fisheries Norway.

Data availability statement

The data underlying this article are available in the article and in its online supplementary material.

Author contributions statement

EJ was the lead author. DK analysed the data. All five authors contributed to discussions, writing, and revisions of the paper.

References

Auditore, P. J., Lough, R. G., and Broughton, E. A. 1994. A review of the comparative development of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) based on an illustrated series of larvae and juveniles from Georges Bank. NAFO Scientific Council Studies, 20: 7–18.

Baudron, A. R., Needle, C. L., and Marshall, C. T. 2011. Implications of a warming North Sea for the growth of haddock *Melanogrammus aeglefinus*. Journal of Fish Biology, 78: 1874–1889.

Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., and Marshall, C. T. 2014. Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. Global Change Biology, 20: 1023–1031.

Bergstad, O. A., Jørgensen, T., and Dragesund, O. 1987. Life history and ecology of the gadoid resources of the Barents Sea. Fisheries Research, 5: 119–181.

Bindoff, N. L., Cheung, W. W. L., Kairo, J. G., Arístegui, J., Guinder, V. A., Hallberg, R., Hilmi, N. *et al*.. 2019. Changing ocean, marine ecosystems, and dependent communities. *In* IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. pp. 447–587. Ed. by Po¨rtner H. O., Roberts D.C., Masson-Delmotte V., Zhai P., Tignor M., Poloczanska E., and Mintenbeck K., *et al*. Cambridge University Press, New York, NY.

Bogstad, B., Dingsør, G. E., Ingvaldsen, R. B., and Gjøsæter, H. 2013. Changes in the relationship between sea temperature and recruitment of cod, haddock and herring in the Barents Sea. Marine Biology Research, 9: 895–907.

Brooks, E. N., and Deroba, J. J. 2015. When "data" are not data: the pitfalls of post hoc analyses that use stock assessment model output. Canadian Journal of Fisheries and Aquatic Sciences, 72: 634–641.

Brosset, P., Smith, A. D., Plourde, S., Castonguay, M., Lehoux, C., and Van Beveren, E. 2020. A fine-scale multi-step approach to understand fish recruitment variability. Scientific Reports, 10: 16064.

DFO. 2019. Stock assessment of Atlantic cod (*Gadus morhua*) in NAFO divisions 4X5Y. 2019/015. 19pp.

Dingsør, G. E., Ciannelli, L., Chan, K. S., Ottersen, G., and Stenseth, N. C. 2007. Density dependence and density independence during the early life stages of four marine fish stocks. Ecology, 88: 625–634.

Fogarty, M., Incze, L., Hayhoe, K., Mountain, D., and Manning, J. 2008. Potential climate change impacts on Atlantic cod (*Gadus morhua*) off the northeastern USA. Mitigation and Adaptation Strategies for Global Change, 13: 453–466.

Fogarty, M. J., Myers, R. A., and Bowen, K. G. 2001. Recruitment of cod and haddock in the North Atlantic: a comparative analysis. ICES Journal of Marine Science, 58: 952–961.

Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic cascades in a fromely cod-dominated ecosystem. Science, 308: 1621–1623.

Garcia-Soto, C., Cheng, L., Caesar, L., Schmidtko, S., Jewett, E., Cheripka, A., Rigor, I. *et al*.. 2021. An overview of ocean climate change indicators: sea surface temperature, ocean heat content, ocean pH, dissolved oxygen concentration, Arctic Sea ice extent, thickness and volume, sea level and strength of the AMOC (Atlantic Meridional Overturning Circulation). Frontiers in Marine Science, 8: 642372.

Gonçalves Neto, A., Langan, J. A., and Palter, J. B. 2021. Changes in the Gulf Stream preceded rapid warming of the Northwest Atlantic Shelf. Communications Earth & Environment, 2: 74. https://doi.org/10.1038/s43247-021-00143-5 (Last accessed 4 October 2022).

Hidalgo, M., Gusdal, Y., Dingsør, G. E., Hjermann, D., Ottersen, G., Stige, L. C., Melsom, A. *et al*.. 2012. A combination of hydrodynamical and statistical modelling reveals non-stationary climate effects on fish larvae distributions. Proceedings of the Royal Society B: Biological Sciences, 279: 275–283.

Hislop, J. R. G. 1984. A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the North Sea. *In* Fish Reproduction: Strategies and Tactics, pp. 311–329. Ed. by Potts G. W.and and Wootton R. J.. Academic Press, London.

Houde, E. D. 2016. Recruitment variability. *In* Fish Reproductive Biology: Implications for Assessment and Management, pp. 98–186. Ed. by Jakobsen T., Fogarty M. J., Megrey B. A., and Moksness E.. John Wiley & Sons Ltd, West Sussex.

ICES. 2013. Report of the Working Group for Celtic Seas Ecoregion (WGCSE). ICES Scientific Reports, 1986.

ICES. 2020. North Western Working Group (NWWG). ICES Scientific Reports, 2: 670.

ICES. 2021a. Arctic Fisheries Working Group (AFWG). ICES Scientific Reports, 3: 817.

ICES. 2021b. Northwestern Working Group (NWWG). ICES Scientific Reports, 3: 556.

ICES. 2021c. Working Group for the Celtic Seas Ecoregion (WGCSE). ICES Scientific Reports, 3: 1082.

ICES. 2021d. Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). ICES Scientific Reports, 3: 988.

Johannesen, E., Yoccoz, N. G., Tveraa, T., Shackell, N. L., Ellingsen, K. E., Dolgov, A. V., and Frank, K. T. 2020. Resource-driven colonization by cod in a high Arctic food web. Ecology and Evolution, 10: 14272–14281.

Kjesbu, O. S., Bogstad, B., Devine, J. A., Gjosaeter, H., Howell, D., Ingvaldsen, R. B., Nash, R. D. M. *et al*.. 2014. Synergies between climate and management for Atlantic cod fisheries at high latitudes. Proceedings of the National Academy of Sciences of the United States of America, 111: 3478–3483.

Klein, E. S., Smith, S. L., and Kritzer, J. P. 2017. Effects of climate change on four new England groundfish species. Reviews in Fish Biology and Fisheries, 27: 317–338.

Landa, C. S., Ottersen, G., Sundby, S., Dingsor, G. E., and Stiansen, J. E. 2014. Recruitment, distribution boundary and habitat temperature of an arcto-boreal gadoid in a climatically changing environment: a case study on northeast Arctic haddock (*Melanogrammus aeglefinus*). Fisheries Oceanography, 23: 506–520.

Link, J. S., Bogstad, B., Sparholt, H., and Lilly, G. R. 2009. Trophic role of Atlantic cod in the ecosystem. Fish and Fisheries, 10: 58–87.

Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish populations. Fisheries Research, 56: 125–131.

Lowerre-Barbieri, S., DeCelles, G., Pepin, P., Catalán, I. A., Muhling, B., Erisman, B., Cadrin, S. X. *et al*.. 2017. Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. Fish and Fisheries, 18: 285–312.

Malmstrøm, M., Matschiner, M., Tørresen, O. K., Star, B., Snipen, L. G., Hansen, T. F., Baalsrud, H. T. *et al*.. 2016. Evolution of the immune system influences speciation rates in teleost fishes. Nature Genetics, 48: 1204–1210.

Mantzouni, I., and MacKenzie, B. R. 2009. Why is Haddock Overtaking Cod? Comparing the Effects of Temperature and Habitat Size on both Species Recruitment Dynamics Across the North Atlantic. ICES Document CM 2009/C:04. 1–18.

Mantzouni, I., Sørensen, H., O'Hara, R. B., and MacKenzie, B. R. 2010. Hierarchical modelling of temperature and habitat size effects on population dynamics of North Atlantic cod. ICES Journal of Marine Science, 67: 833–855.

Marshall, T. C. 2016. Implementing information on stock reproductive potential in fisheries management: the motivation, challenges, and opportunities. *In* Fish Reproductive Biology and its Implications for Assessment and Management, pp. 395–420. Ed. by Jacobsen T., Fogarty M. J., Megrey B. A.and and Moksness E.. Blackwell Scientific, Oxford.

Marty, L., Rochet, M. J., and Ernande, B. 2014. Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout. Marine Ecology Progress Series, 497: 179–197.

Megrey, B. A., Hare, J. A., Stockhausen, W. T., Dommasnes, A., Gjosaeter, H., Overholtz, W., Gaichas, S. *et al.*. 2009. A cross-ecosystem comparison of spatial and temporal patterns of co-variation in the recruitment of functionally analogous fish stocks. Progress in Oceanography, 81: 63–92.

Mohn, R. K., and Simon, J. E. 2002. Biological information relevant to the management of the 4TVW haddock. Canadian Science Advisory Secretariat, 2002/102. 47pp.

Murua, H., and Saborido-Rey, F. 2003. Female reproductive strategies of marine fish species of the North Atlantic. Journal of Northwest Atlantic Fishery Science, 33: 23–31.

Myers, R. A., Bowen, K. G., and Barrowman, N. J. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences, 56: 2404–2419.

Norin, T., Canada, P., Bailey, J. A., and Gamperl, A. K. 2019. Thermal biology and swimming performance of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). PeerJ, 7: e7784.

Ottersen, G., and Holt, R. E. 2022. Long-term variability in spawning stock age structure influences climate-recruitment link for Barents Sea cod. Fisheries Oceanography, 1–15. https://doi.org/10.1111/fog.12605 (last accessed 15 August 2022).

Pardoe, H., and Marteinsdóttir, G. 2009. Contrasting trends in two condition indices: bathymetric and spatial variation in autumn condition of Icelandic cod *Gadus morhua*. Journal of Fish Biology, 75: 282–289.

Petrik, C. M., Kristiansen, T., Lough, R. G., and Davis, C. S. 2009. Prey selection by larval haddock and cod on copepods with species-specific behavior: an individual-based model analysis. Marine Ecology Progress Series, 396: 123–143.

Roa-Varón, A., Dikow, R. B., Carnevale, G., Tornabene, L., Baldwin, C. C., Li, C., and Hilton, E. J. 2021. Confronting sources of systematic error to resolve historically contentious relationships: a case study using gadiform fishes (Teleostei, Paracanthopterygii, Gadiformes). Systematic Biology, 70: 739–755.

Scott, B. E., Marteinsdottir, G., Begg, G. A., Wright, P. J., and Kjesbu, O. S. 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). Ecological Modelling, 191: 383–415.

Shackell, N. L., and Frank, K. T. 2007. Compensation in exploited marine fish communities on the Scotian Shelf, Marine Ecology Progress Series, 336: 235–247.

Shackell, N. L., Frank, K. T., Fisher, J. A. D., Petrie, B., and Leggett, W. C. 2010. Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. Proceedings of the Royal Society B: Biological Sciences, 277: 1353–1360.

Sinclair, A. F., and Murawski, S. A. 1997. Why have groundfish stocks declined?. *In* Northwest Atlantic Groundfish: Perspectives on a Fishery Collapse, pp. 71–93. Ed. by Boreman J., Nakashima B. S., Wilson J. A., and Kendall R. I.. American Fisheries Society, Bethesda, MD.

Stone, H. H., Brooks, E. N., Busawon, D., and Wang, Y. 2015. Assessment of Haddock on Eastern Georges Bank for 2015. 2015/02. 1–84pp.

Swain, D. P., and Benoit, H. P. 2015. Extreme increases in natural mortality prevent recovery of collapsed fish populations in a northwest Atlantic ecosystem. Marine Ecology Progress Series, 519: 165–182.

Swain, D. P., and Mohn, R. K. 2012. Forage fish and the factors governing recovery of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences, 69: 997–1001.

Sørhus, E., Edvardsen, R. B., Karlsen, Ø., Nordtug, T., van der Meeren, T., Thorsen, A., Harman, C. *et al.*. 2015. Unexpected interaction with dispersed crude oil droplets drives severe toxicity in Atlantic haddock embryos. PLoS One, 10: e0124376.

Tam, J. C., Link, J. S., Large, S. I., Bogstad, B., Bundy, A., Cook, A. M., Dingsor, G. E. *et al.*. 2016. A trans-Atlantic examination of haddock *Melanogrammus aeglefinus* food habits. Journal of Fish Biology, 88: 2203–2218.

Thorson, J. T., Jensen, O. P., and Zipkin, E. F. 2014. How variable is recruitment for exploited marine fishes? A hierarchical model for testing life history theory. Canadian Journal of Fisheries and Aquatic Sciences, 71: 973–983.

Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. BioScience, 45: 759–771.

Walsh, S. J., Simpson, M., and Morgan, M. J. 2004. Continental shelf nurseries and recruitment variability in American plaice and yellowtail flounder on the Grand Bank: insights into stock resiliency. Journal of Sea Research, 51: 271–286.

Wang, Y., O'Brien, L. O., Andrushchenko, I., and Clark, K. J. 2015. Assessment of eastern Georges Bank Atlantic cod for 2015. 2015/03. 91pp.

Wang, Y., Stone, H. H., and Finley, M. 2017. Haddock 2016 framework assessment: modelling and reference points. 2017/026. 69pp.

Wiff, R., Flores, A., Neira, S., and Caneco, B. 2018. Estimating steepness of the stock-recruitment relationship in Chilean fish stocks using meta-analysis. Fisheries Research, 200: 61–67.

Winemiller, K. O., and Rose, K. A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences, 49: 2196–2218.

Handling Editors: Manuel Hidalgo and Szymon Smolinski