ICES Journal of
Marine Science

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

ICES Journal of Marine Science (2020), 77(1), 230–240. doi:10.1093/icesjms/fsz152

Original Article

Age-specific shifts in Greenland halibut (*Reinhardtius hippoglossoides*) distribution in response to changing ocean climate

Laura J. Wheeland * and M. Joanne Morgan

Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, PO Box 5667, St John's, NL, Canada A1C 5X1

**Corresponding author: tel: +1 709-772-7069; e-mail: laura.wheeland@dfo-mpo.gc.ca.*

Wheeland, L. J. and Morgan, M. J. Age-specific shifts in Greenland halibut (*Reinhardtius hippoglossoides*) distribution in response to changing ocean climate. – ICES Journal of Marine Science, 77: 230–240.

Received 14 January 2019; revised 9 July 2019; accepted 13 July 2019; advance access publication 13 September 2019.

Fish distribution is strongly influenced by temperature, with populations predicted to respond to ongoing changes in ocean climate by adapting distribution to maintain preferred thermal habitats. Over the last several decades, the Northwest Atlantic off Newfoundland, Canada has experienced wide variation in temperature and significant changes in the structure of the marine community. A period of particularly cold ocean conditions from the mid-1980s to mid-1990s saw Greenland halibut occupying deeper waters, and moving farther offshore and southward. Distributional shifts across periods of varying thermal conditions were most pronounced in the youngest ages. While no specific nursery areas were evident, these young fish typically occurred in shallower waters where temperatures were more variable, moving deeper with age. Sensitivity to changing ocean climate may vary with age. This adaptation to shifting temperatures suggests that this species is likely to alter its distribution in the face of continued changes in ocean climate. Age-specific differences in response to changing temperature have potential implications for ecosystem interactions and fisheries management.

Keywords: climate, depth, distribution, generalized additive models, *Reinhardtius hippoglossoides*, temperature.

Introduction

The distribution of fish is strongly influenced by temperature because of its major impact on metabolic processes (Brett, 1979; Claireaux *et al.*, 1995). Interactions between temperature and food availability determine decisions about energy allocation and each species has a temperature range that it inhabits and an optimum temperature (Brett, 1979; Bjornsson and Steinarsson, 2002; Morgan *et al.*, 2010). The importance of temperature is reflected in the ability to detect small differences in temperature and avoid unfavourable thermal conditions (Claireaux *et al.*, 1995; Goddard *et al.*, 1997). As a result, fish are predicted to respond to climate change by altering their distribution to maintain preferred temperatures (Frank *et al.*, 1996; Brander *et al.*, 2003). With recent warming, many fish species have shown changes in distribution, moving to more northern, and/or deeper waters (Perry *et al.*, 2005; Dulvy *et al.*, 2008; Nye *et al.*, 2009; Bell *et al.*, 2015).

Populations often show some segregation by age and/or size, with different components of the population occupying different habitats (Able *et al.*, 2005; Bell *et al.*, 2015). This is the result of differing habitat requirements or optima for different sizes or life stages (Methratta and Link, 2007). Optimum temperature can vary with fish size and life stage, with larger fish generally having a lower temperature optimum (Baudron *et al.*, 2014; Sande *et al.*, 2019), and adults and larval fish having a narrower thermal window than juveniles (Pörtner and Farrell, 2008). Flatfish species often have clearly defined nursery areas (Able *et al.*, 2005) in shallower waters with the fish moving deeper as they grow (McCracken, 1963; Lockwood, 1974; Dorel *et al.*, 1991;

Zimmermann and Goddard, 1996; Bailey *et al.*, 2005). Given the differing habitat requirements of different aged fish, it might be expected that not all components of a population would show the same change in distribution in response to changing temperature. How different portions of a fish population will respond to changes in ocean temperatures may have important implications for both the ecology of the species (e.g. distribution, habitat limitations, trophic interactions) and for management of exploited species (e.g. stock mixing, bycatch).

The Northwest Atlantic off Newfoundland Canada has experienced wide variation in temperature over the last several decades. This area was characterized by a notable cold period from the mid-1980s to mid-1990s, during which, normalized temperature anomalies reached >2°C below climatological averages (Figure 1; González-Pola *et al.*, 2018). This was followed by an increase in temperatures, with four of the warmest years on record occurring since 2000 (Colbourne *et al.*, 1997; Colbourne *et al.*, 2018). The area is one of the most rapidly warming large marine ecosystems in the world (Belkin, 2009). Such large changes in temperature pose a challenge for fish and might be expected to result in changes in distribution in an attempt to maintain more homogeneous conditions.

Greenland halibut (*Reinhardtius hippoglossoides*) is a flatfish species with a circumpolar distribution through the north Atlantic and Pacific oceans. Off Newfoundland and Labrador, Greenland halibut have shown changes in distribution across these decades of changing temperature (Morgan *et al.*, 2013), with a move to deeper, warmer water associated with the cold period of the mid-1980s to mid-1990s. This shift in depth during a cold period was reported for the population as a whole, and has not been examined at various ages within the population. Greenland halibut are known to move deeper with age (Bowering and Chumakov, 1989; Gundersen *et al.*, 2013). In addition, specific nursery areas have been identified in some areas (Riget and Boje, 1988; Bowering and Nedreaas, 2000; Youcef *et al.*, 2013; Albert and Vollen, 2015). It therefore might be expected that there could be some variation in the response of different ages to changing temperature. Here, we examine age-disaggregated abundance of Greenland halibut to determine how distribution across ages has varied in relation to available ocean climate conditions.

Material and methods

Thermal conditions off Newfoundland and Labrador since the late 1970s (Colbourne *et al.*, 2018), have been characterized by two periods of contrasting temperatures with transition periods between the extremes. From 1986 to 1994 the region experienced the coldest temperatures over the last several decades, while during 2001–2016 ocean conditions were the warmest over that time period. Based on these clear periods of differing temperatures we divided 1981–2016 into periods of: Declining (1981–1985), Cold (1986–1994), Increasing (1995–2000), and Warmer (2001–2016) thermal conditions (Table 1). Analyses focus on variation between these four time periods, with available bottom temperatures as a proxy for a larger suite of environmental variability that cannot be captured in available data (prey distribution and availability, ecosystem productivity, etc.).

Survey data

Numbers of Greenland halibut at age throughout NAFO Divisions (Divs.) 2J3KL were obtained from depth-stratified random bottom trawl surveys (Doubleday, 1981; Smith and Somerton, 1981) completed by Fisheries and Oceans Canada in autumn (primarily October–December) from 1981 to 2016. Age-length keys were derived annually from otoliths collected across NAFO Divs. 2J3KL and applied to set-by-set length frequencies to obtain number at age in each set. Fishing sets were equipped with a trawl-mounted CTD which provided depth fished and bottom temperature for each set, and position (latitude and longitude) of each survey tow was recorded. Due to inconsistencies in survey

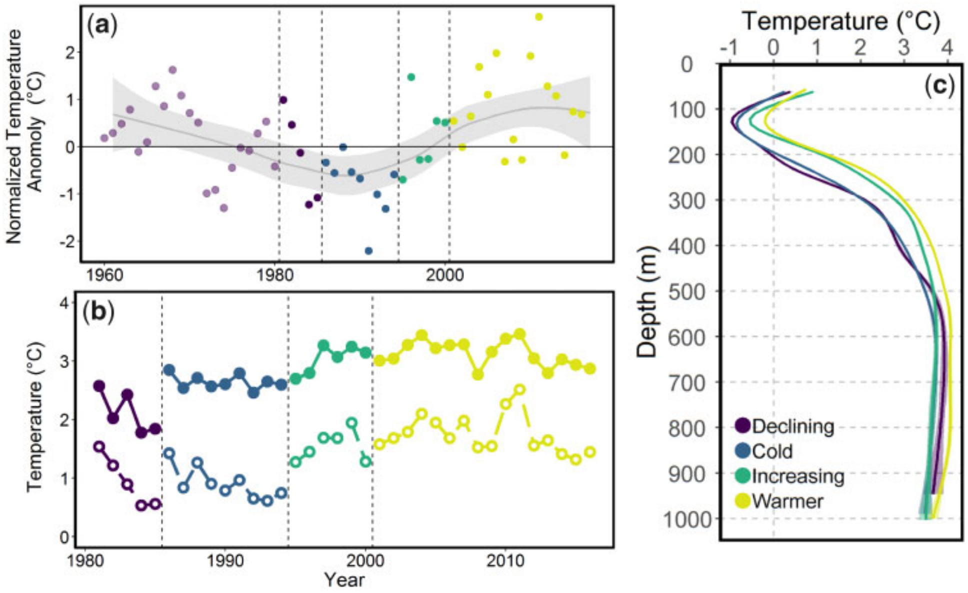


Figure 1. Thermal conditions in NAFO Divs. 2J3KL. (a) Normalized temperature anomalies since 1960 at a long-term monitoring station in Div. 3L [data from ICES Report on Ocean Climate, Station 27, NewfoundlandShelf Temperature (González-Pola *et al.*, 2018)]; (b) mean available (open symbols) and occupied (solid symbols) temperatures by Greenland halibut from trawl surveys in NAFO Divs. 2J3KL; (c) temperature at depth from bottom trawl-mounted CTDs, with a loess smoother applied to all records from within each period.

Table 1. Average temperature available to, and occupied by, Greenland halibut in the surveyed area during fall research trawl surveys.

		Temperature (°C)					
		Available		Occupied		Occupied–available	
Period	**Years**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Declining	1981–1985	0.95	0.39	2.13	0.32	1.18	0.24
Cold	1986–1994	0.91	0.26	2.64	0.12	1.73	0.19
Increasing	1995–2000	1.55	0.24	3.04	0.22	1.48	0.19
Warmer	2001–2016	1.75	0.32	3.12	0.21	1.37	0.19

coverage over time (Rideout *et al.*, 2017), inshore strata were excluded from analysis and depths were limited to <1000 m in Divs. 2J and 3K, and <730 m in Div. 3L.

From 1981 to 1982 survey tows were completed using an Engel 145 Otter trawl in Divs. 2J and 3K, and a Yankee 41.5 Otter trawl in Div. 3L. From 1983 to 1994, the entire survey was completed using the Engel trawl. This gear was switched in 1995 to a Campelen 1800 shrimp trawl, which has been subsequently used through the rest of the time series. Full details on the trawl gears used can be found in McCallum and Walsh (1996). Conversion factors for catches between trawls are not available for Greenland halibut across the whole of Divs. 2J3KL, therefore unconverted data were used to maintain continuity in gear type across the region surveyed within each time period. The Campelen trawl has been identified as having increased catch efficiency, particularly for smaller fish in some species (Warren *et al.*, 1997; Power and Orr, 2001). However, given that trawls used within each thermal period are considered comparable, any catchability differences between gears are not anticipated to have an influence on observed trends in distribution within a period. Although there will be an impact on the number of fish captured over time in the different age classes, there is no indication that this is depth or temperature dependent and so temporal changes in distribution should not be the result of gear changes.

Distribution

Abundance-weighted mean latitude (WML) was calculated at age, and for all ages combined, for each year in the time series to look for evidence of northward or southerly shifts in the population:

$$\mathrm{WML}_y = \frac{\sum_{j=1}^{t} A_j \times L_j/A_j}{n_y},$$

where t is the number of tows in year y, A_j is the abundance of Greenland halibut caught in tow j, L is latitude of set j, and n is the number of tows in year y.

Area-weighted average temperature available and occupied (Swain, 1997) were calculated for Divs. 2J3KL combined. The area-weighted average temperature surveyed (average temperature available) in the surveyed area to the fish in year y, was calculated as:

$$\mathrm{TA}_y = \sum_{i=1}^{S}\sum_{j=1}^{n_i}\frac{\mathrm{PA}_i}{n_i}X_{ij},$$

where S is the number of strata, PA_i is the proportion of the survey area in stratum i, n_i is the number of tows in stratum i, X_{ij} is the bottom temperature or depth in tow j in stratum i. The average temperature occupied (TO_y), by Greenland halibut in year y, was calculated as:

$$\mathrm{TO}_y = \sum_{i=1}^{s}\sum_{j=1}^{n_i}\frac{\mathrm{PA}_i}{n_i}\frac{Y_{ij}}{\overline{Y}}X_{ij},$$

where Y_{ij} is the weight of fish caught in tow j in stratum i, $\overline{Y}$ is the stratified mean weight per tow over the whole survey area, and the other variables are as defined above.

Generalized additive models (GAMs) were applied to age-disaggregated abundance (A) data to examine the factors that describe the distribution of Greenland halibut. Model variables included environmental conditions (depth d, temperature t) and geographical position (latitude and longitude), with error ε.

$$A \sim \mathrm{age} + \mathrm{year} + s(d, \mathrm{age}) + s(t, \mathrm{age}) + te(\mathrm{lat}, \mathrm{long}, \mathrm{age}) + \varepsilon,$$

where s indicates a spline smoother, and te a tensor product. Here, age class (*age*) is considered as a category, with ages 0–2 and 9+ grouped, respectively, due to limited catchability within the survey series. GAMs were fit with a negative binomial distribution using the *gam()* function within *mgcv* package v.1.8-23 in R version 3.3.3 (R Core Team, 2017). Smoothing parameters were estimated using restricted maximum likelihood with fREML computation, with maximum knots for temperature and depth smoothers set to 10. Trials were completed during model development across a variety of knot ranges, with 10 determined to be an appropriate number based on overall model fit, large number of observations, number and range of depth and temperature values, effective degrees of freedom relative to the number of knots, and robustness of trends to knot specifications. Separate GAMs were run for each of the four defined time periods, with smoothers from each of the four time periods compared to describe observed differences in distribution and habitat (temperature, depth) at age, both within the time period and across time periods characterized by shifts in ocean climate conditions.

Pairwise comparisons of fitted smoothers for each of temperature, depth, and position were conducted among ages following the methods described by Rose *et al.* (2012), where significant differences between smooths are considered as approximate 95% confidence intervals on the pairwise difference that do not overlap with 0.

Results

Thermal conditions

Average temperature available within the surveyed area varied throughout the time series, decreasing from 1.54°C in 1981 to a time series low of 0.54°C in 1984 (Figure 1)—continuing an earlier decrease from at least 1978 (Morgan *et al.*, 2013). Temperatures remained low to 1994 with a subsequent increase to 1.94°C in 1999, varying around this relatively warm level to 2016. A time series high was observed in 2011 at 2.51°C, coinciding with near record high ocean temperatures and climate indices observed in Divs. 2J3KL in that year (Colbourne *et al.*, 2018).

Greenland halibut consistently occupied waters warmer than the average available within the survey (Table 1), with mean temperature occupied increasing from the beginning of the Cold period through to the recent Warmer period (Figure 1). The difference in occupied temperature relative to available temperature was greatest in the Cold period, where Greenland halibut were, on average, found in waters 1.73°C warmer than that available. These temperatures were warmer than those occupied during the Declining period despite the increased prevalence of colder water overall.

Temperature at depth varied among these four periods (Figure 1), with the cold intermediate layer (CIL) 0.5–1°C colder at similar depths in the Cold and Declining period relative to the recent Warmer period. The coldest waters of the CIL were located just below 100 m throughout the time series, reaching as low as −1°C during the Declining period. The extent of this layer was greatest during the Declining and Cold periods, with sub-zero temperatures extending across depths of 75–200 m, compared to 100–175 m in the Increasing and Warmer periods. Water temperatures were also slower to increase with depth in the Cold and Declining periods, exceeding 3°C near 400 m deep, while in the Increasing and Warmer periods 3°C water was found near 300 m. Temperature in the deepest water (500–1000 m) has been ∼0.5°C higher in the Warmer period relative to the Declining and Cold periods.

Distribution

Population-level trends in distribution are apparent in WML across the time series (Figure 2), with a southward shift of ∼120 km observed through the Declining period, moving from 52.27°N in 1982 to 51.19°N in 1985. The population remained near this lower latitude throughout the Cold period, before moving northward during the Increasing period and into the recent Warmer period, achieving an average WML of 52.22°N ($SD = 0.21$). A 159 km difference was observed between the most southerly (51.15°N in 1994) and northerly (52.58°N in 2004) WML across the time series. Latitudinal shifts were most pronounced in ages 0–2, while WML varied without trend across the series at older ages (Ages 5+).

GAMs indicated significant influence of depth, temperature, and location (latitude/longitude), as well as significant year effects in some cases, on age-disaggregated abundance of Greenland halibut within all four defined time periods (Table 2). While factors examined here are subject to inherent spatial autocorrelation, there is no evidence of spatial patterns within model residuals (Supplementary Figure S1). Deviance explained by the models ranged from 66.4 to 84.3%. While models here consider temperature, depth, and space as separate parameters, it is important in interpreting results to consider smoothers for one parameter in the context of the others, given the inherent relationships typical of these measurements.

Large confidence intervals in pairwise comparisons (Supplementary Figures S2–S9), particularly in deep water (>800 m) in the declining period and warm temperatures (>4°C) in the cold period, are likely driven by limited sampling at these values due to a limited depth extent of the survey and lack of available warm water, respectively. Pairwise comparisons highlight the gradient of difference between ages, with nearer ages typically being more similar across all explanatory variables. Comparisons of temperature smoothers by age indicate that with few exceptions, smoothers were not significantly different between adjacent ages except at the highest and lowest temperatures.

Smoothers demonstrate a consistent relationship with depth at age, with fish moving to deeper waters as they get older. Notably, this shift to deeper waters occurred at an earlier age in the Cold period (Figure 3), where maximum smoother values for depth were centred around age 5 at 800 m, compared to ages 6–8 in the Declining period. Smoothers indicated a pronounced negative effect of shallow (<300 m) waters on abundance of Greenland halibut across all ages, with this negative effect most evident in the oldest fish (Ages 9+) after the Cold period. During the Declining period there was also a distinct negative effect of depths >700 m on ages 0–2, which lessened significantly in the Cold period and has remained more moderate since.

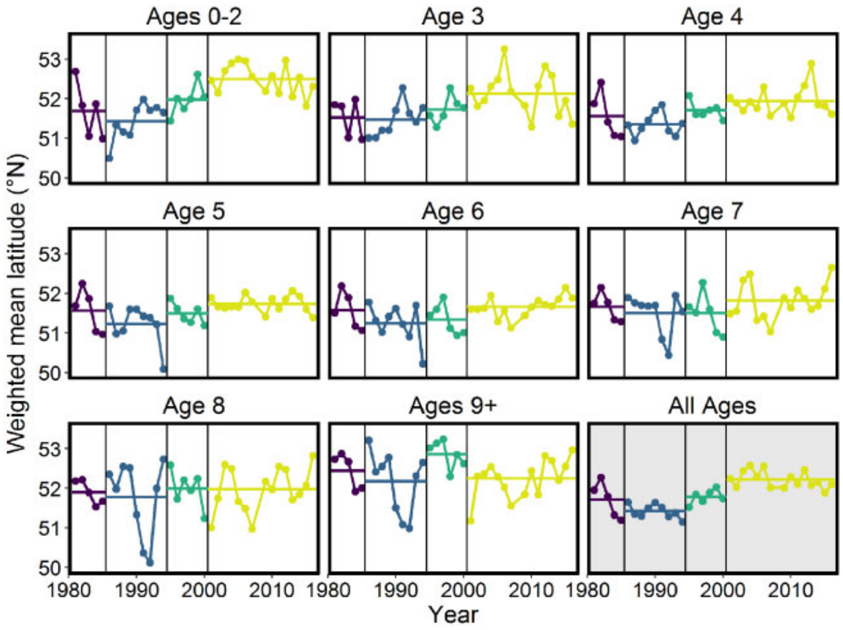
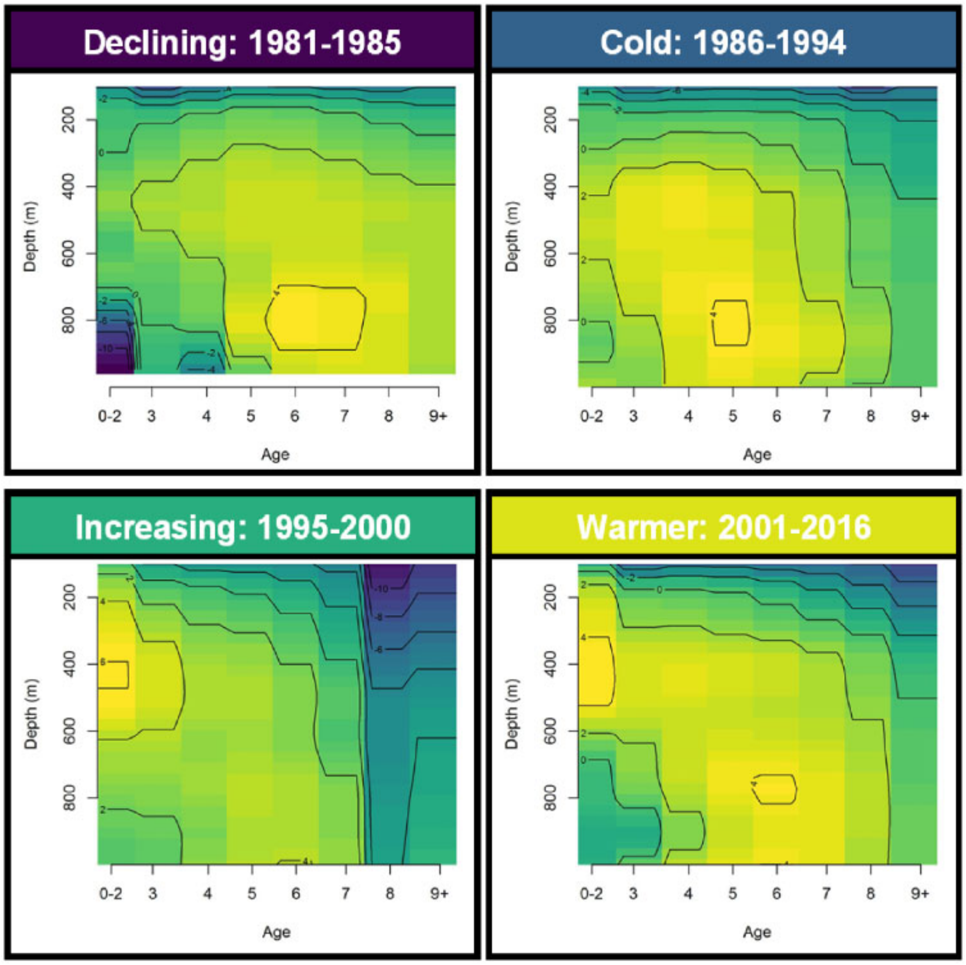


Figure 2. Abundance-WML, by age and for all ages combined (bottom right panel) for Greenland halibut across the four time periods considered. Horizontal lines indicate mean values for each period.

Table 2. GAM results for abundance of Greenland halibut in each of the four time periods.

Formula:	**abundance ~ age + year + *s*(temp, by = age) + *s*(depth, by = age) + *te*(long, lat, by = age)**							
	Declining		**Cold**		**Increasing**		**Warmer**	
Years	**1981–1985**		**1986–1994**		**1995–2000**		**2001–2016**	
Deviance explained	**66.4%**		**67.4%**		**84.3%**		**74.7%**	
N	**16 592**		**31 560**		**17 744**		**44 064**	
Parametric coefficients	**Est.**	**$p(>\|t\|)$**	**Est.**	**$p(>\|t\|)$**	**Est.**	**$p(>\|t\|)$**	**Est.**	**$p(>\|t\|)$**
Intercept	−0.410	<0.001	0.346	<0.001	1.306	<0.001	1.570	<0.001
Age 3	−0.278	0.049	−0.253	0.002	−1.121	<0.001	−1.678	<0.001
Age 4	−0.010	0.944	0.227	0.003	−1.159	<0.001	−1.392	<0.001
Age 5	0.583	<0.001	0.192	0.021	−1.287	<0.001	−1.378	<0.001
Age 6	0.616	<0.001	−0.192	0.044	−2.300	<0.001	−1.964	<0.001
Age 7	0.364	0.020	−0.930	<0.001	−4.125	<0.001	−2.545	<0.001
Age 8	−0.128	0.483	−2.948	<0.001	−14.396	0.014	−3.826	<0.001
Age 9+	−0.063	0.679	−2.350	<0.001	−8.447	<0.001	−5.827	<0.001
Year	1982 0.135	<0.001	1987 −0.197	<0.001	1996 0.569	<0.001	2002 −0.468	<0.001
	1983 −0.028	0.509	1988 −0.297	<0.001	1997 0.852	<0.001	2003 −0.215	<0.001
	1984 −0.160	<0.001	1989 −0.411	<0.001	1998 0.923	<0.001	2004 −0.143	0.001
	1985 −0.188	<0.001	1990 −0.347	<0.001	1999 0.952	<0.001	2005 −0.073	0.119
			1991 −1.125	<0.001	2000 0.689	<0.001	2006 0.051	0.238
			1992 −1.033	<0.001			2007 0.131	0.004
			1993 −0.715	<0.001			2009 −0.015	0.746
			1994 −0.977	<0.001			2010 −0.043	0.350
							2011 0.500	<0.001
							2012 0.335	<0.001
							2013 0.520	<0.001
							2014 0.404	<0.001
							2015 −0.124	0.006
							2016 −0.069	0.131
Approximate significance of smooth terms	**edf**	***p*-Value**	**edf**	***p*-Value**	**edf**	***p*-Value**	**edf**	***p*-Value**
s(temp): ages0–2	6.34	<0.001	6.28	<0.001	8.09	<0.001	8.63	<0.001
s(temp): age3	5.89	<0.001	7.40	<0.001	6.88	<0.001	8.26	<0.001
s(temp): age4	4.71	<0.001	5.05	<0.001	6.51	<0.001	8.42	<0.001
s(temp): age5	4.72	<0.001	4.45	<0.001	4.88	<0.001	8.02	<0.001
s(temp): age6	4.71	<0.001	5.83	<0.001	2.42	<0.001	8.40	<0.001
s(temp): age7	4.85	<0.001	6.34	<0.001	3.33	<0.001	7.03	<0.001
s(temp): age8	6.70	<0.001	6.24	<0.001	3.33	0.009	6.22	<0.001
s(temp): ages9+	4.25	<0.001	6.38	<0.001	1.49	0.788	4.18	0.010
s(depth.mean): ages0–2	7.49	<0.001	8.43	<0.001	7.98	<0.001	8.29	<0.001
s(depth.mean): age3	7.96	<0.001	8.59	<0.001	7.57	<0.001	8.71	<0.001
s(depth.mean): age4	7.79	<0.001	8.42	<0.001	8.50	<0.001	8.73	<0.001
s(depth.mean): age5	8.39	<0.001	8.38	<0.001	8.26	<0.001	8.78	<0.001
s(depth.mean): age6	8.50	<0.001	8.50	<0.001	7.77	<0.001	8.71	<0.001
s(depth.mean): age7	8.42	<0.001	8.52	<0.001	7.01	<0.001	8.42	<0.001
s(depth.mean): age8	8.23	<0.001	8.53	<0.001	4.92	<0.001	6.96	<0.001
s(depth.mean): ages9+	6.94	<0.001	7.90	<0.001	3.39	<0.001	5.68	<0.001
te(long, lat): ages0–2	18.31	<0.001	21.55	<0.001	18.68	<0.001	21.63	<0.001
te(long, lat): age3	20.48	<0.001	19.01	<0.001	15.77	<0.001	20.57	<0.001
te(long, lat): age4	18.82	<0.001	16.84	<0.001	16.40	<0.001	19.90	<0.001
te(long, lat): age5	17.47	<0.001	16.15	<0.001	16.02	<0.001	19.08	<0.001
te(long, lat): age6	16.18	<0.001	18.43	<0.001	15.88	<0.001	17.68	<0.001
te(long, lat): age7	16.21	<0.001	18.30	<0.001	14.33	<0.001	18.04	<0.001
te(long, lat): age8	16.06	<0.001	16.99	<0.001	3.57	0.013	16.38	<0.001
te(long, lat): ages9+	14.36	<0.001	15.27	<0.001	5.31	<0.001	13.98	<0.001

The effect of temperature on abundance was significant in most cases and was especially evident for younger fish where smoother gradients were steepest. The association of particular ages with temperature changed over time (Figure 4). The peak in temperature smoother for ages 0–2 occurred around 1.5°C in the Declining period, increasing to 2.5°C in Cold period as they shifted deeper, and has since increased to near 3°C. This increase in peak temperature smoother from the Declining period to the


Declining: 1981-1985

Cold: 1986-1994

Increasing: 1995-2000

Warmer: 2001-2016

Figure 3. GAM smoothers for abundance of Greenland halibut at age by depth in the four time periods, with light colours indicating more positive associations, and dark negatives.

Cold was observed across age groups, and in many cases has continued to the Warmer period. In the Increasing period, temperature was not significant for ages 8 and 9+.

Smoother surfaces for latitude and longitude by age (Figure 5) demonstrate spatial associations of Greenland halibut once the effects of depth and temperature have been removed. Smoothers indicate an overall shift with increasing ages from waters on the shelf to areas characterized by deeper holes and channels, and along the shelf edge. This was consistent among the four time periods examined, however the negative effect near the outer shelf edge for ages 0–2 was most pronounced prior to the Cold period. In the Declining period, smoothers for ages 0–2 were most positive in the inshore areas off the Northeast coast of Newfoundland, and off the coast of Labrador in Div. 2J. This area of positive effect shifted farther offshore on the continental shelf throughout Divs. 2J3KL in the Cold period, and remained in this area through to the Warmer period. Ages 9+ were least associated with inshore areas off the Northeast Newfoundland Coast, with the exception of during the Declining period. Smoothers across ages and periods were typically positive over the southeastern section of the surveyed area, composed of a portion of the Grand Bank in NAFO Div. 3L, suggesting a higher abundance of Greenland halibut than would be expected given the shallow depth and cold conditions that characterize this area.

Discussion

Greenland halibut off Newfoundland and Labrador shifted to deeper waters during the Cold period of 1986–1994 (Morgan *et al.*, 2013). Here we confirmed this occurred across all age classes examined (0–2 to 9+), with a shift to deeper waters from a period of declining temperature to the Cold period. As waters warmed in recent years, results suggest that abundance has moved back into relatively shallower waters than that of the Cold period, but has not fully returned to the depth distribution observed in the Declining period.

Greenland halibut in this population occupy deeper waters with age. However, in the Cold period, this move to greater depth occurred at earlier ages, with the youngest age classes shifting to deeper waters where warmer temperatures were available. All ages were shown to avoid waters <200 m in depth, with the greatest negative association with these depths observed during the Cold period. During this time, the extent of the CIL was largest, with sub-zero temperatures extending across a greater range of depths than during the Increasing and Warmer periods, and waters reaching nearly a degree colder that those observed in the Warm and Increasing periods. The magnitude of the negative association with shallower waters was observed to intensify with age; older individuals showed an affinity for the deepest available

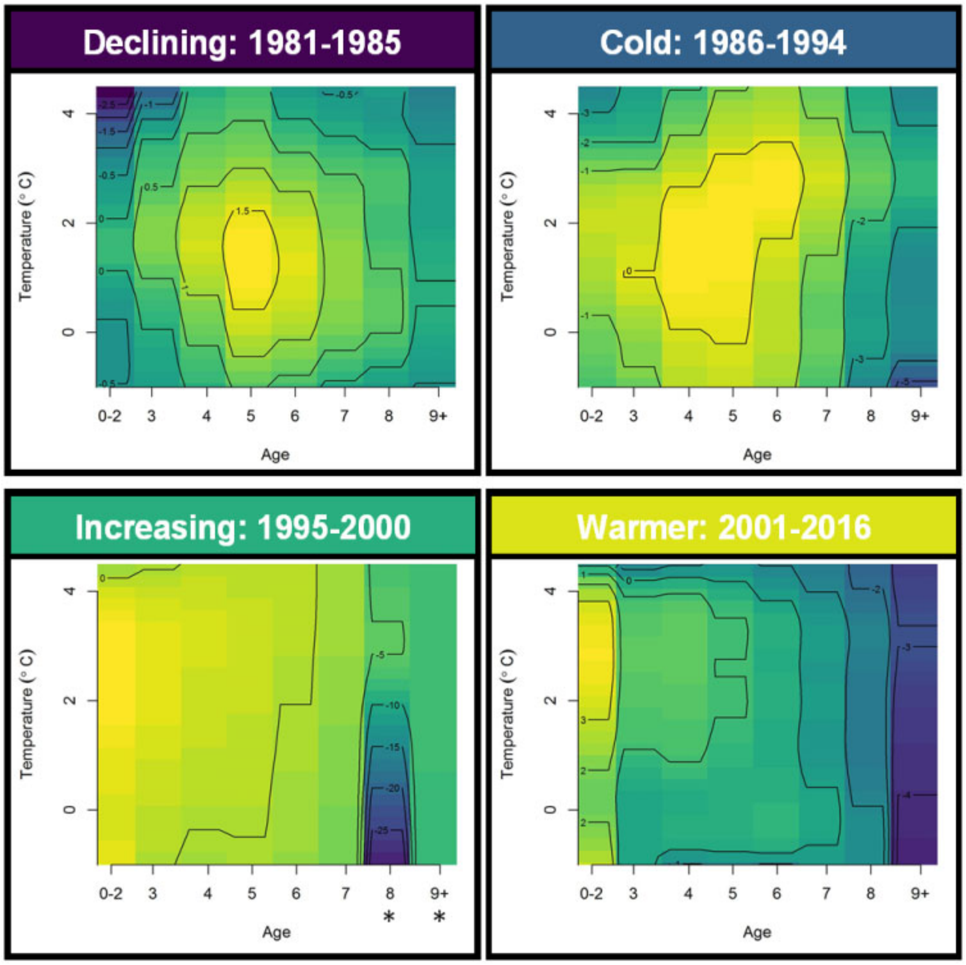


Figure 4. GAM smoothers for abundance of Greenland halibut at age by bottom temperature in the four time periods, with light colours indicating more positive associations, and dark negatives. Asterisks (*) indicate non-significant smoothers.

waters within the survey, with this most pronounced in the Ages 9+, while ages 0–2 avoided these deepest waters in most periods. Cannibalism may be a factor in this segregation between youngest juveniles, and older, larger individuals, as younger fish are subject to predation by larger conspecifics (Dwyer *et al.*, 2010).

Frank *et al.* (2018) observed that changes in depth distribution of Atlantic cod on the eastern Scotian Shelf could be partially attributed to size-selective commercial exploitation. The fishery for Greenland halibut in NAFO Divs. 2J3KL occurs primarily in deep waters along the shelf edge of NAFO Divs. 2J3KL, harvesting at depths typically >400 m and extending to 1400 m (Brodie *et al.*, 2011; Fomin and Pochtar, 2018; González-Costas *et al.*, 2018; Vargas *et al.*, 2018). Commercial catch is primarily composed of individuals from ages 5 to 9 (Regular *et al.*, 2017), with an average of 92% of catch numbers being taken from these age groups since 1981. Given that changes in depth distribution were observed across ages and across depths shallower than those targeted by the fishery, deepening in this population is not considered to be the result of fishery removals, but rather reflective of changes in thermal habitat conditions.

While temperature was a significant factor in age-disaggregated abundance of Greenland halibut, this was most notable in young fish which occupy shallower waters where annual and interannual temperature variability is higher, and a higher magnitude of change in thermal conditions was observed across the time series. Older fish in the population consistently occupied deeper waters where temperatures were more constant. Changes observed in both temperature and depth associations were therefore less pronounced with age. Bottom temperatures across the time series were most stable in waters >500 m, showing relatively small differences in mean temperature. Given the apparent moderating effect these depths have on temperature, deep areas may to some degree provide a refuge from changes in ocean climate for those fish able to survive in such depths. However, continuing shifts of fishes into deep water would be expected to result in increased competition for limited resources, and may result in the competitive exclusion of some species and/or size classes of various marine organisms.

Here, we considered distribution in terms of geographic location (latitude and longitude) as well as occupied depths and water temperatures. We acknowledge the intertwined relationship between the included variables: temperature changes variably with depth (e.g. CIL, thermoclines), certain depths are associated with specific locations (e.g. shelf breaks, banks), and temperature shifts with location relative to latitude and ocean currents. Depth is also a proxy for pressure which limits species distribution

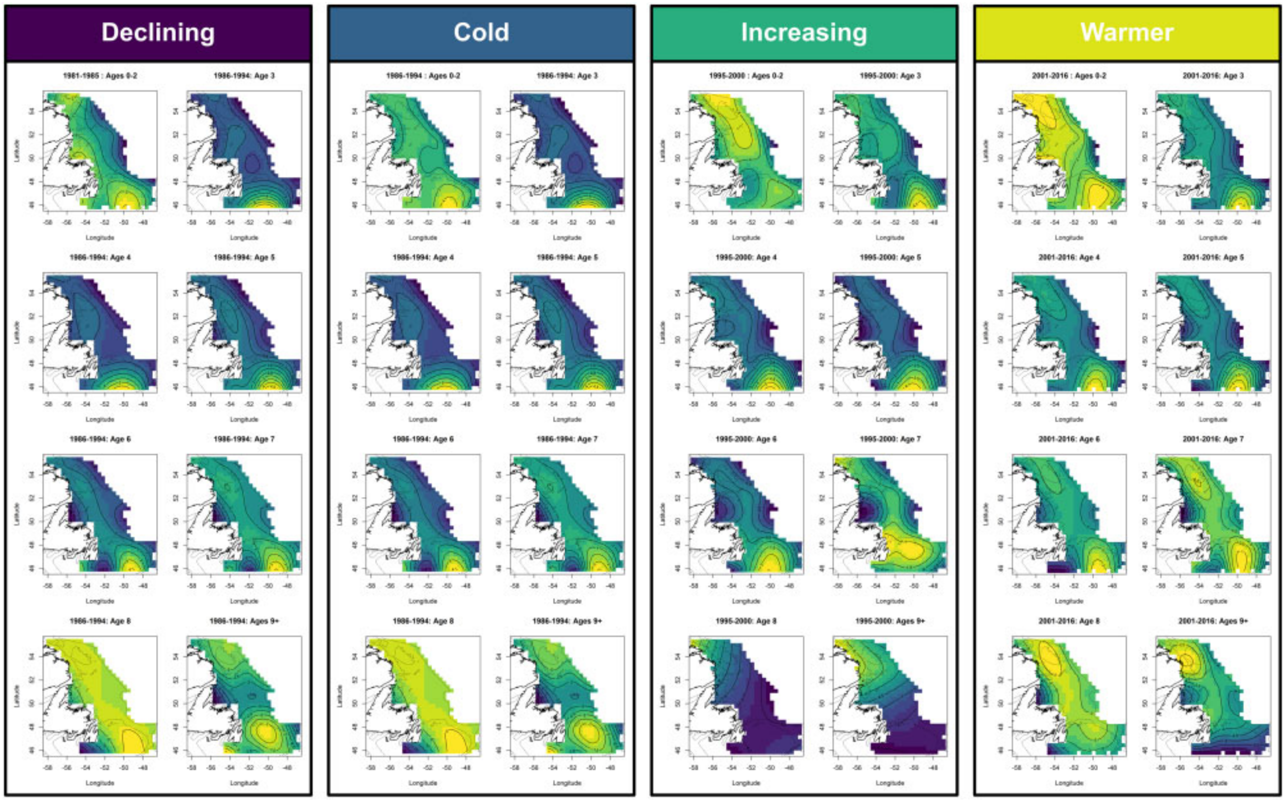


Figure 5. GAM smoother results for latitude and longitude surfaces by age group for the four time periods. Light colours represent more positive smoother values, dark more negative. Dashed lines indicate the 200m and 1000m depth contours.

through hydrostatic pressure, physiological and biochemical mechanisms, and resource availability (Carney, 2005). It should be acknowledged that other factors not examined here—substrate, salinity, dissolved oxygen, competition, etc.—are likely to also be involved in determining distribution. These may be related to depth and/or temperature and/or location, but are not directly accounted for in the variables included in the model either due to the unavailability of data or complex nature of interactions. In addition, Greenland halibut spend a portion of their time in the pelagic environment (Jørgensen, 1997) and therefore experience a wider range of temperatures than captured in available depth and bottom temperature data.

Many species are undergoing—or are expected to experience—distributional shifts with as global temperatures rise (Hickling *et al.*, 2006; VanDerWal *et al.*, 2013; Fei *et al.*, 2017). For marine fishes, these shifts are largely attributed to increasing seawater temperatures, with fish moving with changes in the distribution of ideal thermal habitat (Perry *et al.*, 2005; Morley *et al.*, 2018). In recent years there have been reports of more southerly species being recorded in Newfoundland waters for the first time (Devine and Fisher, 2014) or increasing in abundance at this northerly extent of their range (Nye *et al.*, 2011; Rideout and Ings, 2018), as available thermal habitat increases (Rogers *et al.*, 2016). Here, we observed a southerly shift in the population of Greenland halibut in response to cooling temperatures from the mid-1980s to the mid-1990s, followed by a northward redistribution with subsequent warming. This adaptation to shifting temperatures suggests that this species is likely to alter its distribution in the face of continued changes in ocean climate.

Age-specific shifts such as those observed here could impact ecosystem interactions and the management of fisheries. Directed harvesting may target specific sizes based on market conditions, and management measures can limit allowable catches of small fish. Differing responses to changing ocean climate across age classes can result in increasing overlap between size and age-classes with potential implications for the avoidance of pre-recruit bycatch and for intraspecific competition between different life stages. The consideration of ongoing distributional shifts of commercially harvested species may be particularly relevant with anticipated increases in fisheries in Northern regions (Cheung *et al.*, 2010; Christiansen *et al.*, 2014; Becker Jacobsen *et al.*, 2018).

Areas identified by the GAMs to be positively associated with abundance of Age 0–2 Greenland halibut covered a broad portion of the Northeast Newfoundland Shelf and Southern Hamilton Bank, in all four time periods. Analyses did not indicate strong evidence to suggest particular nursery hotspots within NAFO Divs. 2J3KL, but rather a widespread distribution across areas of the continental shelf, with distributions shifting further offshore in response to changing thermal availability. For other populations of Greenland halibut nursery areas have been found within the coastal areas and fjords of Greenland (Riget and Boje, 1988; Gundersen *et al.*, 2013), around the Svalbard archipelago in the Barents sea (Albert and Vollen, 2015), and in the estuary of the Gulf of St. Lawrence (Youcef *et al.*, 2013). In all of these areas where a wide range of depths were sampled, juveniles were shown to spread from nursery areas to deeper waters with age. Although we did not find nursery areas *per se* in this study, younger fish were found in more shallow waters than older individuals. In addition, data presented here indicate an apparent shift in juveniles to deeper waters with cooling conditions, shifting farther offshore towards the shelf edge. There is little evidence to suggest a return to a significant negative association with these slope areas since the shift occurred, suggesting distribution may have not returned to that typical of times prior to the temperature-induced shift.

Greenland halibut move deeper with age (Bowering and Chumakov, 1989; Gundersen *et al.*, 2013) and the shallower depths occupied by the younger fish in the Newfoundland area are more subject to temperature variation. Although large fish generally benefit from colder waters (Baudron *et al.*, 2014; Sande *et al.*, 2019) the wider thermal window of small fish (Pörtner and Farrell, 2008) may allow them to occupy these areas of more variable temperature, taking advantage of some other environmental factor (such as prey type and/or availability) and or avoiding predation by larger conspecifics (Dwyer *et al.*, 2010). However, the shift in distribution with changing ocean climate here was greatest for younger ages with fish moving to warmer waters when temperatures cooled, with some return to their previous distribution as conditions warmed again, indicates that temperatures became too cold even for the thermal window of the younger fish. Adults are known to be highly mobile, with tagging studies indicating movements of individuals across a wide distances, including among Newfoundland, Baffin Bay, and Greenland (Bowering, 1984; Boje, 2001), and genetic evidence indicating mixing throughout the North Atlantic (Vis *et al.*, 1997; Roy *et al.*, 2014). These data suggest individuals are likely able to undertake large scale movements to maintain preferred habitat conditions. This difference in mobility between small and large fish may further affect the response of different ages to changing ocean climate.

Juvenile Greenland halibut have been observed off Greenland to experience faster growth in warmer conditions (Sünksen *et al.*, 2010), though this increase in temperature was associated with higher mortality rates. In the Gulf of St. Lawrence, growth of juveniles was found to be more impacted by oxygen levels than changes to temperature (Youcef *et al.*, 2013), however this was across a small temperature range near the extreme high temperature (5°C) observed within the data used here from the northeast Newfoundland shelf. Fishes may not be able to adequately adapt to ocean warming, exceeding physiological tolerances with increases in water temperatures (Sandblom *et al.*, 2016). Further research is required on the impact of temperature and pressure (depth) on the growth, survival, and reproduction of Greenland halibut to better understand likely consequences of continued changes in ocean climate, and resulting shifts in distribution for this species across its range.

Supplementary data

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

Acknowledgements

We thank all those involved in the collection and processing of data used here, in particular DFO Science and Canadian Coast Guard vessel crews, without who the RV surveys could not be completed.

Funding

This work was part of a Natural Sciences and Engineering Research Council of Canada strategic grant entitled “Outils de gestion intégrés pour une exploitation durable du flétan du Groenland dans tout l’est du Canada.”

References

Able, K. W., Neuman, M. J., and Wennhage, H. 2005. Ecology of juvenile and adult stages of flatfishes: distribution and dynamics of habitat associations. *In* Flatfishes Biology and Exploitation, pp. 164–184. Ed. by R. N. Gibson. Blackwell Science Ltd., Oxford, UK. 391 pp.

Albert, O. T., and Vollen, T. 2015. A major nursery area around the Svalbard archipelago provides recruits for the stocks in both Greenland halibut management areas in the Northeast Atlantic. ICES Journal of Marine Science, 72: 872–879.

Bailey, K. M., Nakata, H., and Van der Veer, H. W. 2005. The planktonic stages of flatfishes: physical and biological interactions in transport processes. *In* Flatfishes Biology and Exploitation, pp. 94–119. Ed. by R. N. Gibson. Blackwell Science Ltd., Oxford, UK. 391 pp.

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 Bioenergy, 20: 1023–1031.

Becker Jacobsen, R., Hedeholm, R., Robert, D., and Wheeland, L. J. 2018. Sustainable fisheries. *In* Adaptation Actions for a Changing Arctic: Perspectives From the Baffin Bay/Davis Strait Region, pp. 163–176. Ed. by M. Lemay and K. Falk. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway. 374 pp.

Belkin, I. M. 2009. Rapid warming of large marine ecosystems. Progress in Oceanography, 81: 207–213.

Bell, R. J., Richardson, D. E., Hare, J. A., Lynch, P. D., and Fratantoni, P. S. 2015. Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the Northeast US shelf. ICES Journal of Marine Science, 72: 1311–1322.

Bjornsson, B., and Steinarsson, A. 2002. The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 59: 494–502.

Boje, J. 2001. Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies. Fishery Bulletin, 100: 414–422.

Bowering, W. R. 1984. Migrations of Greenland halibut, *Reinhardtius hippoglossoides*, in the Northwest Atlantic from Tagging in the Labrador-Newfoundland Region. Journal of Northwest Atlantic Fisheries Science, 5: 85–91.

Bowering, W. R., and Chumakov, A. K. 1989. Distribution and relative abundance of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)) in the Canadian northwest Atlantic from Davis Strait to the northern Grand Bank. Fisheries Research, 7: 301–327.

Bowering, W. R., and Nedreaas, K. H. 2000. A comparison of Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) fisheries and distribution in the Northwest and Northeast Atlantic. Sarsia, 85: 61–76.

Brander, K., Blom, G., Borges, M. F., Erzini, K., Henderson, G., MacKenzie, B. R., Mendes, H. *et al.* 2003. Changes in fish distribution in the Eastern North Atlantic: are we seeing a coherent response to changing temperature? ICES Marine Science Symposia, 219: 261–270.

Brett, J. R. 1979. Environmental factors and growth. *In* Fish Physiology, 8, pp. 599–675. Ed. by W. S. Hoar, D. J. Randall, and J. R. Brett. Academic Press, New York. 785 pp.

Brodie, W., Power, D., and Healey, B. 2011. The Canadian Fishery for Greenland halibut in SA 2+ Div. 3KLMNO, with emphasis on 2010. NAFO Scientific Council Research Document 11/44.

Carney, R. S. 2005. Zonation of deep biota on continental margins. Oceanography and Marine Biology: An Annual Review, 43: 211–278.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R. E. G., Zeller, D., and Pauly, D. 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. Global Change Biology, 16: 24–35.

Christiansen, J. S., Mecklenburg, C. W., and Karamushko, O. V. 2014. Arctic marine fishes and their fisheries in light of global change. Global Change Biology, 20: 352–359.

Claireaux, G., Webber, D. M., Kerr, S. R., and Boutilier, R. G. 1995. Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating temperature conditions. Journal of Experimental Biology, 198: 49–60.

Colbourne, E. B., de Young, B., Narayanan, S., and Helbig, J. 1997. Comparison of hydrography and circulation on the Newfoundland shelf during 1990–1993 with the long-term mean. Canadian Journal of Fisheries and Aquatic Sciences, 54: 68–80.

Colbourne, E., Holden, J., Snook, S., Lewis, S., Cyr, F., Senciall, D., Bailey, W. *et al.* 2018. Physical oceanographic environment on the Newfoundland and Labrador Shelf in NAFO Subareas 2 and 3 during 2017. NAFO Scientific Council Research Document 18/009.

Devine, B., and Fisher, J. A. D. 2014. First records of the blue runner *Caranx crysos* (Perciformed: Carangidae) in Newfoundland waters. Journal of Fish Biology, 85: 540–545.

Dorel, D., Koutsikopoulos, C., Desaunay, Y., and Marchand, J. 1991. Seasonal distribution of young sole (*Solea solea* (L.)) in the nursery ground of the Bay of Vilaine (northern Bay of Biscay). Netherlands Journal of Sea Research, 27: 297–306.

Doubleday, W. G. 1981. Manual on groundfish surveys in the Northwest Atlantic. NAFO Scientific Council Studies, 2: 55.

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmller, V., Dye, S. R., and Skjoldal, H. R. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology, 45: 1029–1039.

Dwyer, K., Buren, A., and Koen-Alonso, M. 2010. Greenland halibut diet in the Northwest Atlantic from 1978 to 2003 as an indicator of ecosystem change. Journal of Sea Research, 64: 436–445.

Fei, S., Desprez, J. M., Potter, K. M., Jo, I., Knott, J. A., and Oswalt, C. M. 2017. Divergence of species responses to climate change. Science Advances, 3: e1603055.

Fomin, K., and Pochtar, M. 2018. Russian research report for 2017. NAFO Scientific Council Summary Document 18/13.

Frank, K. T., Carscadden, J. E., and Simon, J. E. 1996. Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Canadian Journal of Fisheries and Aquatic Sciences, 53: 1473–1486.

Frank, K. T., Petrie, B., Leggett, W. C., and Boyce, D. G. 2018. Exploitation drives an ontogenetic-like deepening in marine fish. Proceedings of the National Academy of Sciences, 115: 6422–6427

Goddard, S. V., Morgan, M. J., and Fletcher, G. L. 1997. Influence of plasma antifreeze glycoproteins on temperature selection by Atlantic cod (*Gadus morhua*) in a temperature gradient. Canadian Journal of Fisheries and Aquatic Sciences, 54: 88–93.

González-Costas, F., Ramilo, G., Román, E., Lorenzo, J., Gago, A., González-Troncoso, D., and Sacau, M. 2018. Spanish research report for 2017. NAFO Scientific Council Summary Document 18/07.

González-Pola, C., Larsen, K. M. H., Fratantoni, P., and Beszczynska-Möller, A. (Ed.) 2018. ICES Report on Ocean Climate 2017. ICES Cooperative Research Report, 345. 119 pp.

Gundersen, A. C., Kennedy, J., Woll, A., Fossen, I., and Boje, J. 2013. Identifying potential Greenland halibut spawning areas and nursery grounds off East and South-western Greenland and its management implications. Journal of Sea Research, 75: 110–117.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R., and Thomas, C. D. 2006. The distribution of a wide range of taxonomic groups are expanding polewards. Global Change Biology, 12: 450–455.

Jørgensen, O. A. 1997. Pelagic occurrence of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in West Greenland waters. Journal of Northwest Atlantic Fishery Science, 21: 39–50.

Lockwood, S. J. 1974. The settlement, distribution and movements of 0-group plaice *Pleuronectes platessa* (L.) in Filey Bay, Yorkshire. Journal of Fish Biology, 6: 465–477.

McCallum, B. R., and Walsh, S. J. 1996. Groundfish survey trawls used at the Northwest Atlantic Fisheries Centre, 1971 to present. NAFO Scientific Council Research Document 96/50.

McCracken, F. D. 1963. Seasonal movements of the winter flounder, *Pseudopleuronectes americanus* (Walbaum), on the Atlantic coast. Journal of the Fisheries Research Board of Canada, 20: 551–586.

Methratta, E. T., and Link, J. S. 2007. Ontogenetic variation in habitat associations for four flatfish species in the Gulf of Maine-Georges Bank region. Journal of Fish Biology, 70: 1669–1688.

Morgan, M. J., Garabana, D., Rideout, R. M., Romàn, E., Pérez-Rodriguez, A., and Saborido-Rey, F. 2013. Changes in distribution of Greenland halibut in a varying environment. ICES Journal of Marine Science, 70: 352–361.

Morgan, M. J., Rideout, R. M., and Colbourne, E. B. 2010. Atlantic cod (*Gadus morhua*) energy allocation to growth, condition and reproduction. In a varying environment. Marine Ecology Progress Series, 404: 185–195.

Morley, J. W., Selden, R. L., Latour, R. J., Frölicher, T. L., Seagraves, R. J., and Pinsky, M. L. 2018. Projecting shifts in thermal habitat for 686 species on the North American continental shelf. PLoS One, 13: e0196127.

Nye, J. A., Joyce, T. M., Kwon, Y., and Link, J. S. 2011. Silver hake tracks changes in Northwest Atlantic circulation. Nature Communications, 2: 412.

Nye, J. A., Link, J. S., Hare, J. A., and Overholtz, W. J. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series, 393: 111–129.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. Science, 308: 1912–1915.

Pörtner, H. O., and Farrell, A. P. 2008. Physiology and climate change. Science, 322: 690–692.

Power, D., and Orr, D. 2001. Canadian Research Survey Data and Conversions for Redfish in SA2 + Div. 3K Based on Comparative Fishing Trials Between Engel 145 Otter Trawl and a Campelen 1800 Shrimp Trawl. Canadian Science Advisory Secretariat Research Document 2001/103: 1480–4883.

R Core Team. 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Regular, P. M., Cadigan, N. G., Morgan, M. J., and Healey, B. P. 2017. A simple SAM-style state-space stock assessment model for Greenland halibut in NAFO Subarea 2 and Divisions 3KLMNO. NAFO Scientific Council Research Document 17/010.

Rideout, R. M., and Ings, D. W. 2018. Research vessel bottom trawl survey report (NL Region): a stock-by-stock summary of survey information up to and including the 2017 spring and autumn surveys. Canadian Technical Reports of Fisheries and Aquatic Sciences, Fs97-6/3267E-PDF: vii + 59 pp.

Rideout, R. M., Power, D., Ings, D. W., Wheeland, L. J., and Healey, B. P. 2017. Canadian Multi-species Bottom Trawl Surveys in NAFO Subarea 2 + Divisions 3KLNOPs: Vessel Performance, Catch Distribution and Survey Biomass Trends of Key Finfish Resources With Emphasis on 2016. NAFO Scientific Council Research Document 17/044(REV).

Riget, F., and Boje, J. 1988. Distribution and abundance of young Greenland halibut (*Reinhardtius hippoglossoides*) in West Greenland waters. NAFO Scientific Council Studies, 12: 7–12.

Rogers, R., Rowe, S., and Morgan, M. J. 2016. Depth and temperature associations of haddock *Melanogrammus aeglefinus* off southern Newfoundland. Journal of Fish Biology, 89: 2306–2325.

Rose, N. L., Yang, H., Turner, S. D., and Simpson, G. L. 2012. An assessment of the mechanisms for the transfer of lead and mercury from atmospherically contaminated organic soils to lake sediments with particular reference to Scotland, UK. Geochimica et Cosmochimica Acta, 82: 113–135.

Roy, D., Hardie, D. C., Treble, M. A., Reist, J. D., and Ruzzante, D. E. 2014. Evidence supporting panmixia in Greenland halibut (*Reinhardtius hippoglossoides*) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 71: 763–774.

Sandblom, E., Clark, T. D., Gräns, A., Ekström, A., Brijs, J., Fredrik Sundström, L., Odelström, A. *et al.* 2016. Physiological constraints to climate warming in fish follow principles of plastic floors and concrete ceilings. Nature Communications, 7: 11447.

Sande, H. A., Persson, A., Mehl, A., Devine, J. A., dos Santos Schmidt, T. C., Karlsen, Ø., Godiksen, J. A. *et al.* 2019. Temperature and age effects on latitudinal growth dynamics of the commercially valuable gadoid Northeast Arctic saithe (*Pollachius virens*). Fisheries Research, 213: 94–104.

Smith, S. J., and Somerton, G. D. 1981. STRAP: a user-oriented computer analysis system for groundfish research trawl survey data. Canadian Technical Report of Fisheries and Aquatic Sciences, 1030: iv + 66.

Sünksen, K., Stenberg, C., and Grønkjær, P. 2010. Temperature effects on growth of juvenile Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) in West Greenland waters. Journal of Sea Research, 64: 125–132.

Swain, D. P. 1997. Sex-specific temperature distribution of American plaice (*Hippoglossoides platessoides*) and its relation to age and abundance. Canadian Journal of Fisheries and Aquatic Sciences, 54: 1077–1087.

VanDerWal, J., Murphy, H. T., Kutt, A. S., Perkins, G. C., Bateman, B. L., Perry, J. J., and Reside, A. E. 2013. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. Nature Climate Change, 3: 239–243.

Vargas, J., Alpoim, R., Santos, E., and Ávila de Melo, A. M. 2018. Portuguese research report for 2017. NAFO Scientific Council Summary Document 18/08.

Vis, M. L., Carr, S. M., Bowering, W. R., and Davidson, W. S. 1997. Greenland halibut (*Reinhardtius hippoglossoides*) in the North Atlantic are genetically homogeneous. Canadian Journal of Fisheries and Aquatic Sciences, 54: 1813–1821.

Warren, W., Brodie, W., Stansbury, D., Walsh, S., Morgan, M. J., and Orr, D. 1997. Analysis of the 1996 comparative fishing trial between the *Alfred Needler* with the Engel 145 Trawl and the *Wilfred Templeman* with the Campelen 1800 Trawl. NAFO Scientific Council Research Document 97/68.

Wood, S. 2017. Generalized Additive Models: An Introduction With R, 2nd edn. CRC Press, Boca Raton, FL.

Youcef, W. A., Lambert, Y., and Audet, C. 2013. Spatial distribution of Greenland halibut *Reinhardtius hippoglossoides* in relation to abundance and hypoxia in the estuary and Gulf of St. Lawrence. Fisheries Oceanography, 22: 41–60.

Zimmermann, M., and Goddard, P. 1996. Biology and distribution of arrowtooth, *Atheresthes stomias*, and Kamchatka, *A. evermanni*, flounders in Alaskan waters. Fishery Bulletin, 94: 358–370.

Handling editor: Manuel Hidalgo