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Environmental influences on Norwegian spring-spawning herring (*Clupea harengus* L.) larvae reveal recent constraints in recruitment success

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The lack of any abundant recruiting year class of Norwegian spring-spawning (NSS) herring between 2005 and 2015 contributed to an approximate reduction of 40% in the spawning-stock biomass since 2009, i.e. from 7 to 4 million tonnes. Warming of the North Atlantic is suggested to contribute to this reduction in recruitment. In the past, a warm phase induced by a positive Atlantic Multidecadal Oscillation (AMO) in the North Atlantic was positively correlated to the NSS herring stock size. Recent unprecedented ocean warming in the Norwegian Sea ecosystem, besides elevated temperatures due to a positive AMO, seems to be outside optimal environmental conditions for early life history stages of NSS herring. We analysed 28 years of survey data using generalized additive models to reconstruct environmental conditions for drifting yolksac and preflexion stage larvae. Our results indicate that strong recruitment years were more likely when the larvae occurred simultaneously with a negative AMO during positive temperature anomalies. The transition from yolksac stages towards preflexion stages occurred while there was a slow increase in water temperature during the larval drift. Weak recruitment years generally occurred when larvae experienced elevated temperatures during the life stage transition under a positive AMO. These results augment evidence that the historical positive relationship between AMO and stock dynamics is reversed between 1988 and 2015. Albeit not implying any specific mechanistic biological interactions, we can assume that the unprecedented warming has modified the ecosystem drivers that negatively affect drifting larvae. Since 2016, the North Atlantic is shifting into a negative AMO phase, possibly resulting in the 10-year recruitment suppression of NSS herring ending soon.

Keywords: Atlantic Multidecadal Oscillation, climate change, early life history stages, North Atlantic Oscillation, Norwegian Sea ecosystem, recruitment suppression, small pelagics, spawning-stock biomass

Introduction

The survival of early life history stages was suggested by Hjort (1914) to be the main determiner of the year-class strength in fish populations. A slight shift in survival rates of these stages has considerable effects on recruitment success (Houde, 1987). Every life stage has specific requirements on the environment, and changes will modify the chances of survival. In marine environments, fish species exhibit a dome-shaped relationship to many

factors that control survival rates (e.g. Cury and Roy, 1989; MacKenzie *et al.*, 1994; Takasuka *et al.*, 2007). In theory, early life stages will survive best at the peak of the dome-shaped relationship representing optimal environmental conditions. In the course of ongoing climate changes, ocean warming will modify the state of ecosystems (Bopp *et al.*, 2013; Boyd *et al.*, 2016). This can lead to either positive, no, or negative impacts on the productivity of fishes (Free *et al.*, 2019). By shifting the temperature regime in the ocean, early life stages may encounter conditions that are outside their optimal ranges for survival (Rijnsdorp *et al.*, 2009). In addition to other parts of the world oceans, the North Atlantic has faced unprecedented ocean warming (Robson *et al.*, 2018; Hand *et al.*, 2019). Comprehending climate change effects on fish populations is difficult, since climate impacts a variety of ocean processes that in turn influence a cascade of processes at several biological organization levels (Lehodey *et al.*, 2006). In this study, we shed light on the historic and current climate effects affecting Norwegian spring-spawning (NSS) herring (*Clupea harengus*) population dynamics, by investigating environmental regimes during the very early larval stages between 1988 and 2015.

The long period without strong recruitment success and ongoing fishing resulted in reductions in estimated NSS herring stock size from 7 million tonnes in 2009 to 4 million tonnes in 2018 (ICES, 2018). This is attributed to a warming climate and a reduction in the zooplankton production in the Norwegian Sea ecosystem (Toresen *et al.*, 2019). Similar observations were reported for the North Sea herring stock since 2000 where a shift of the zooplankton community is assumed to be a main driver of recruitment suppression (Payne *et al.*, 2008). In the Gulf of the St. Lawrence, a decrease in the recruitment in spring-spawning herring was concomitant with a long-term decline in cold-water copepod abundances (Brosset *et al.*, 2019). Historic observations have shown that, when a stock size declines and fishing practices are ongoing, stock collapses are possible (Dragesund *et al.*, 1980). The NSS herring stock collapse in the 1960s and 1970s coincided with weak catch regulations during a period of poor recruitment (Dragesund *et al.*, 1980). Unfavourable environmental conditions were suggested to suppress recruitment during a cold phase in the Atlantic (Toresen and Østvedt, 2000). Recovery of the stock was attributed to an exceptionally strong year class in 1983 along with a fishing moratorium (Nakken, 2008; Gullstad *et al.*, 2018). At present, the stock is overseen by an operational harvest control rule implying a management strategy with a relatively low fishing pressure and with mechanisms to further reduce fishing effort when the stock is declining to avoid future stock collapses (ICES, 2018). Until 1998, NSS herring stock dynamics positively correlated with temperature regimes in North Atlantic waters (Toresen and Østvedt, 2000). Thereby, a higher influx of *Calanus finmarchicus* was attributed to higher food availability for NSS herring larvae (Aksnes and Blindheim, 1996). However, since 2002, an exceptional warm phase in the North Atlantic indicates a shift from a positive correlation to a negative correlation between ocean temperature and stock size (Toresen *et al.*, 2019).

Ocean temperature fluctuations are mainly governed by atmospheric forcing and climate cycles. Two main drivers in the North Atlantic are the Atlantic Multidecadal Oscillation (AMO) (Schlesinger and Ramankutty, 1994) and the North Atlantic Oscillation (NAO), both outlined below. These periodic oscillations have shown to be positively correlated with size of the North Sea herring stock (Gröger *et al.*, 2010). Since 2000,

however, an increase in ocean temperature seems to have suppressed recruitment of the same stock (Payne *et al.*, 2008; Corten, 2013). Until 2010, the NSS herring stock and other stocks of small pelagic species in the North East Atlantic, for instance round sardinella (*Sardinella aurita*) in the western and eastern Mediterranean and European pilchard (*Sardina pilchardus*) in the English Channel, were also positively correlated with the AMO, whereas the Mediterranean anchovy (*Engraulis encrasicolus*) stock seems to be negatively correlated (Alheit *et al.*, 2014).

Although climate cycles can control stock variations (Skern-Mauritzen, 2016), climate warming-induced changes in recruitment characteristics are becoming more apparent (Rijnsdorp *et al.*, 2009). Shifting of spawning grounds, lengthened migrations, habitat displacements, and changes in plankton communities are only a few examples that can be related to human-induced changes in the ocean climate (Sundby and Nakken, 2008; Barton *et al.*, 2016; Boyd *et al.*, 2016; Morley *et al.*, 2018). Thus, ignoring anthropogenically driven ocean warming would suggest that environmentally driven population dynamics will be controlled by naturally occurring climate fluctuations. However, a rapid increase in ocean temperature may counteract and may even have the potential to reverse a long-time correlation (Toresen *et al.*, 2019). As one of the main bottlenecks for successful recruitment is based on the survival of early life history stages of fishes, our aim was to model environmental conditions during the drift of yolksac and preflexion larvae to understanding what environments may lead to variation in recruitment success between 1988 and 2015. The main research question we address here is whether early larval stages experienced different environmental regimes that resulted in years of strong, moderate, and weak recruitment. We discuss our results with underlying mechanisms that may control NSS herring recruitment from top-down and bottom-up processes that may be caused by this marked temperature shift since 2002 in the Norwegian Sea ecosystem (Robson *et al.*, 2018).

Material and methods
Larval NSS herring drift along the Norwegian Coast
To the west of the Norwegian coastline is a narrow, 40–200 km, continental shelf (Figure 1). The main spawning grounds of NSS herring (<250 m bottom depth) are on the continental shelf where the substratum consists of sandy, gravelly, stony, and rocky bottoms (Runnström, 1941). Spawning occurs mainly off Møre, at Haltenbanken, and at Røstbanken in February and March (Sætre *et al.*, 2002a); however, other suitable spawning grounds are also utilized to a variable degree, e.g. off Lofoten (Dragesund *et al.*, 1980). The benthic eggs develop in bottom temperatures 7.5°C (winter temperature at Møre; Sætre, 2007), hatching after 15–20 d (Russell, 1976). Yolksac larvae ascend to the surface and both yolksac and subsequently preflexion larvae are primarily carried by the Norwegian Coastal Current northwards in March and April (Vikebø *et al.*, 2010; Stenevik *et al.*, 2012; Skagseth *et al.*, 2015). Farther offshore off the Norwegian coast flow branches of the Atlantic Current carrying additional larvae. Both currents enter the Barents Sea releasing larvae into their main nursery areas.

Sea surface temperature anomalies, AMO and NAO between 1988 and 2015
We report on changes in the Norwegian Sea climate and the link to NSS herring larvae using different indices for the period
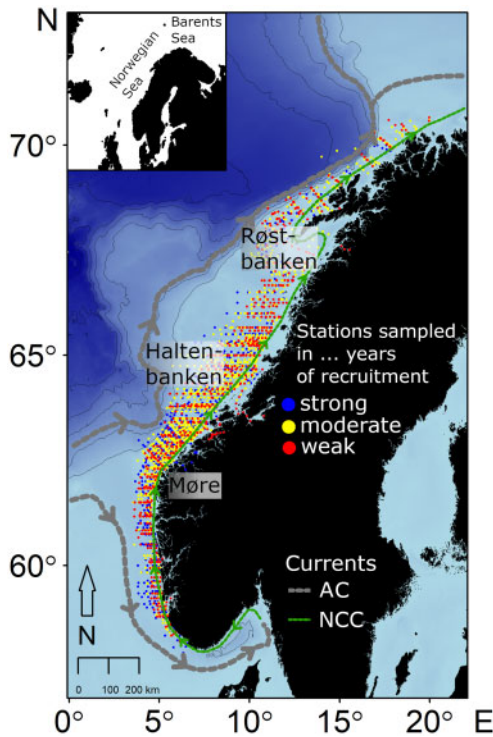
Figure 1. Map of sampling stations during the drift phase of yolksac and preflexion larvae of Norwegian spring-spawning herring during the period 1988–2015. Sampling station colour codes are based on recruitment years (Figure 2a, blue = strong, yellow = moderate, and red = weak). The representation of the Atlantic Current (AC) and Norwegian Coastal Current (NCC) is sketched only.

1988–2015. Sea surface temperature (SST) and anomalies (SSTa) were extracted from the fifth version of the extended reconstructed SST data set ERSSTv5 (Huang *et al.*, 2017). In the ERSSTv5 data set, monthly SSTa values are converted from monthly SST observations by subtracting *in situ* monthly SST climatology between 1971 and 2000. Monthly SST and SSTa data were compiled for the central Norwegian Sea at 69°N 2°E using the SeaDAS software version 7.5.1. (https://seadas.gsfc.nasa.gov/), where the purpose is to feature general trends related to the recruitment success of NSS herring. Unsmoothed and detrended monthly indices of the AMO were extracted from a time series based on Kaplan's SST dataset (Kaplan *et al.*, 1998; Enfield *et al.*, 2001). The AMO is a term for a periodic occurring variation in the ocean current based on SSTs in the North Atlantic. A periodic duration between 50 and 70 years comprises a positive phase and a negative phase driven by changes in the circulation velocities of the global thermohaline circulation. A positive phase of the AMO is characterized by an accelerated warm water mass transport from the tropics into high latitudes, while a negative phase is characterized by a decelerated transport (Delworth and Mann, 2000). Monthly indices of the NAO were extracted from https://crudata.uea.ac.uk/cru/data/nao/, Jones *et al.*, 1997). The NAO is a climate cycle fluctuating in atmospheric pressures at sea level between the Azores High and the Icelandic Low. A positive NAO is characterized by a strong contrast between the high and the low. It facilitates westerly winds over the North Atlantic transporting warm and stormy weather. A negative phase is characterized by a relatively small contrast between the two air pressure centres

leading to calm wind conditions and low temperatures in the North Atlantic.

The larval NSS herring survey

To model the environmental window of yolksac and preflexion larvae, we used annual larval NSS herring survey data from 1988 to 2015 (Figure 1). In these surveys, larvae were sampled in spring (March–April) during their drift in the Norwegian Coastal Current and Atlantic Current. Perpendicular transects to the coastline were set up, 15–20 nautical miles apart, with sampling stations established approximately five nautical miles apart. The direction of the surveys was either from the north southward or vice versa (Stenevik *et al.*, 2012). Sampling along each transect was undertaken until reaching the first station offshore with zero observation of NSS herring larvae. Before 1992, a vertical towed T-80 ring net (80 cm diameter with 375 μm net, retrieval speed 0.5 m s^{-1}) or a double oblique towed Gulf III (nose-cone diameter 20 cm, mesh size 375 μm, towed at 2.6 m s^{-1}) (Gehringer, 1952) collected larvae (Stenevik *et al.*, 2012). Since 1992, the T-80 was only deployed during the night while the Gulf III during the day to reduce larval net avoidance, which was detected by comparing sampling performance during daytime of both gears (Gulf III was tenfold more efficient, pilot study). However, night-time sampling resulted in similar larval numbers and size-classes so that T-80 night-time sampling was continued as this gear collects larvae in better condition. Larval staging (yolksac approximately at age 3–13 and preflexion at 14–65 d) is based on Doyle (1977) with the addition of a stage (1 d) representing larvae with no yolk remains and absent dorsal fin anlagen (Øiestad, 1983). Data on physical parameters [*in situ* temperature (°C) and salinity], location (see below), and bottom depth were collected during the larval surveys.

Defining strong, moderate, and weak recruitment years between 1988 and 2015 by recruitment strength

Recent stock assessment estimates from the International Council for the Exploration of the Sea were used to relate numbers at age 2 years (R_{age2}) to spawning-stock biomass (SSB) (in tonnes). More specifically, SSB was lagged back 2 years to compute recruitment success (R_{st-2}) for the period 1988–2015 (ICES, 2018) (Figure 2a); $R_{st-2} = R_{age2}/SSB_{t-2}$. This period covers the larval survey data available. Within this period, 32% ($n = 9$ years) of the years (with the highest R_{age2}/SSB_{t-2} relationship) were assigned as years of "strong" recruitment. Another 32% ($n = 9$ year) (with the lowest R_{age2}/SSB_{t-2} relationship) were assigned as years of "weak" recruitment. The remaining years ($n = 10$ years) were used to model environmental conditions of "moderate" recruitment years.

Modelling environmental windows of drifting NSS herring larvae

Environmental windows for yolksac and preflexion larvae for strong, moderate, and weak recruitment years were reconstructed using generalized additive models (GAMs). GAMs were computed using the mgcv package (Wood, 2006) in R version 3.5.1 (R Development Core Team, 2016). Before splitting the time series data set, a GAM was performed on all 28 years using a factor variable according to "years" of recruitment using the same set of co-variables described in the following. The factor variable
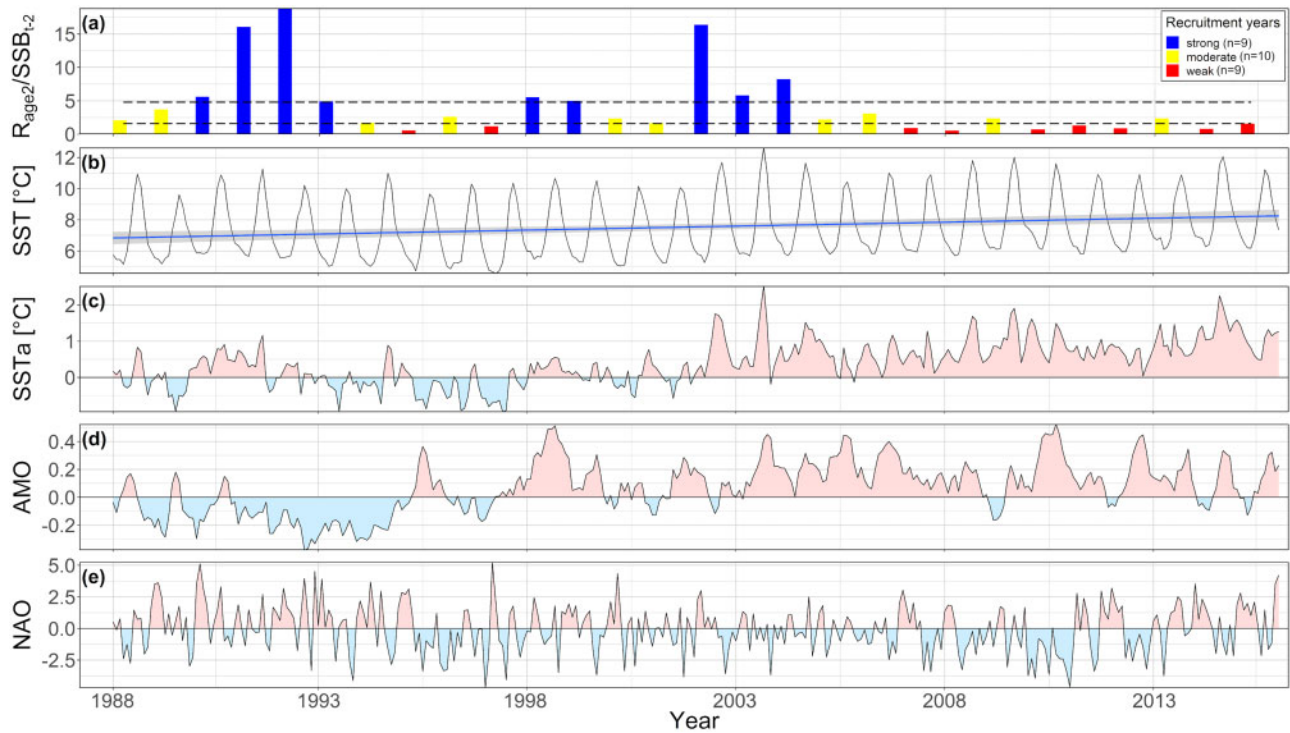
Figure 2. Climate indices of the period 1988–2015 and (a) recruitment considered as numbers at age 2 years (R_{age2})/SSB at t-2 (SSB_{t-2}) relationship with colour-coded years indicating strong in blue, moderate in yellow, and weak years of recruitment in red; (b) SST with linear trend and 95% confidence interval and (c) anomalies = SSTa of the central Norwegian Sea 69°N 2°E; (d) detrended AMO and (e) NAO.

"years" represents the split into strong, moderate, and weak recruitment to verify if the split is reasonable. A significant effect of the factor variable allowed a further split of the year-specific larval data sets to address single effects of the tested co-variables on recruitment success related to the two life history stages.

GAMs were fitted with observations from 4544 sampling stations in the full model, 1230 sampling stations in the strong years, 1975 in moderate years, and 1339 in the weak years of recruitment model (Figure 1). Based on niche theory (Holt, 2009), thin-plate regression splines (bs = "tp") were used to produce ideally dome-shaped regressions for the following explanatory variables: bottom depth, temperature at 20 m depth, and salinity at 20 m depth. The latter two represent ambient larval conditions as they are mainly distributed above the thermocline, although larvae can occur 30–40 m deeper during daytime and 10–20 m shallower during night-time (Ferreira *et al.*, 2012). Bottom depth is used because spawning occurs on the continental shelf limited at bottom depths of approximately <250 m, see above. To produce optimal environmental windows for the three parameters, smooth terms were constrained using maximum possible degrees of freedom of $k = 3$ in the model construction. This allowed the computation of either dome-shaped or linear relationships between larval count data (i), yolksac (stage I) and (ii) preflexion larvae (stage II) avoiding overfitting of single effects.

Another type of thin-plate regression splines (bs = "ts") was used for the co-variable location expressed as a two-dimensional term s(latitude × longitude) in the GAM. The co-variable location was used to correct for spatial autocorrelation that naturally appears in survey data (Wood, 2003). Pseudo replication due to sampling the same cohort was possible, but according to the coarse sampling grid, we assume less impact on spatial patchiness.

Temporal autocorrelation was addressed using monthly detrended AMO and NAO indices at time of the surveys. The AMO index accounts for temporal autocorrelation on a multidecadal basis and the NAO on an interdecadal basis. Both co-variables signify a cycle (used as a cyclic smooth term here) and address autocorrelation in the residuals (Wood, 2006). Both parameters were used in the GAM construction as the main climate cycles in the North Atlantic. Smooth terms for climate cycle indices in the GAMs were constrained using maximum possible degrees of freedom of $k = 4$ in the model construction (see above). This enables an S-curved, dome-shaped, or linear relationship between dependent and independent variables avoiding overfitting.

Log-transformed filtered water volume from larval sampling was treated as offset in the GAMs. The offset functions as a fixed vector added to the linear predictor (Wood, 2006). This enables the usage of models based on count data. Due to a high degree of zero counts, we used a negative binomial approach with a log-link between the dependent variable (larval count data = number of larvae at each station) and the co-variables. All four GAMs produced dispersal parameters close to 1.0 (Table 1). A dispersal parameter of 1.0 means that the statistical model can predict data with the same variability as the empirical data. Multicollinearity was tested by the variance inflation factor (VIF). All independent variables used in the GAM construction produced VIF values <2 indicating that multicollinearity was not an issue of major concern (Supplementary SI1). Smoothness selection was based on the Generalized Cross Validation method. Full models with all co-variables included resulted in best GAMs using the Akaike information criterion as model selection method. Diagnostic plots of the residuals (Supplementary SI2–4) were produced for model

Table 1. Test statistics of generalized additive models including full models Yolksac$_{all}$ and Preflexion$_{all}$, in particular testing the factor variable "Year" (strong, moderate, and weak recruitment year) with other explanatory variables.

Responds variable	Explanatory variables	EDF	p-Value	Obs. (n)	ZI (%)	Disp.	Total ED (%)
Yolksac$_{all}$	Year^f	na	<0.001	4,544	64.9	1.26	27.4
	Long × lat	27.39	<0.001	–	–	–	–
	$T_{20\,m}$	1.98	<0.001	–	–	–	–
	$S_{20\,m}$	1.95	<0.001	–	–	–	–
	Bottom$_{depth}$	1.00	<0.001	–	–	–	–
	AMO$_{month}$	2.81	<0.001	–	–	–	–
	NAO$_{month}$	2.94	<0.001	–	–	–	–
Preflexion$_{all}$	Year^f	na	<0.001	4,544	33.0	1.00	32.6
	Long × lat	25.09	<0.001	–	–	–	–
	$T_{20\,m}$	1.87	<0.001	–	–	–	–
	$S_{20\,m}$	1.96	<0.001	–	–	–	–
	Bottom$_{depth}$	1.07	<0.001	–	–	–	–
	AMO$_{month}$	2.92	<0.001	–	–	–	–
	NAO$_{month}$	2.99	<0.001	–	–	–	–
Yolksac$_{strong}$	Long × lat	21.74	<0.001	1,230	61.3	1.14	54.8
	$T_{20\,m}$	1.00	>0.05	–	–	–	–
	$S_{20\,m}$	1.87	<0.05	–	–	–	–
	Bottom$_{depth}$	1.17	<0.001	–	–	–	–
	AMO$_{month}$	2.77	<0.001	–	–	–	–
	NAO$_{month}$	2.92	<0.001	–	–	–	–
Yolksac$_{moderate}$	Long × lat	25.77	<0.001	1,975	97.3	1.21	29.8
	$T_{20\,m}$	1.93	<0.01	–	–	–	–
	$S_{20\,m}$	1.91	<0.01	–	–	–	–
	Bottom$_{depth}$	1.00	<0.001	–	–	–	–
	AMO$_{month}$	2.27	<0.05	–	–	–	–
	NAO$_{month}$	2.84	<0.001	–	–	–	–
Yolksac$_{weak}$	Long × lat	25.31	<0.001	1,339	66.6	1.00	39.3
	$T_{20\,m}$	1.98	<0.001	–	–	–	–
	$S_{20\,m}$	2.00	<0.001	–	–	–	–
	Bottom$_{depth}$	1.00	<0.001	–	–	–	–
	AMO$_{month}$	2.74	<0.001	–	–	–	–
	NAO$_{month}$	2.88	<0.001	–	–	–	–
Preflexion$_{strong}$	Long × lat	21.81	<0.001	1,230	28.0	1.03	45.8
	$T_{20\,m}$	1.87	<0.05	–	–	–	–
	$S_{20\,m}$	1.79	<0.001	–	–	–	–
	Bottom$_{depth}$	1.00	<0.01	–	–	–	–
	AMO$_{month}$	2.02	<0.001	–	–	–	–
	NAO$_{month}$	2.96	<0.001	–	–	–	–
Preflexion$_{moderate}$	Long × lat	21.12	<0.001	1,975	40.2	0.98	46.6
	$T_{20\,m}$	1.00	<0.001	–	–	–	–
	$S_{20\,m}$	1.88	<0.001	–	–	–	–
	Bottom$_{depth}$	1.00	<0.001	–	–	–	–
	AMO$_{month}$	2.98	<0.001	–	–	–	–
	NAO$_{month}$	2.99	<0.001	–	–	–	–
Preflexion$_{weak}$	Long × lat	22.84	<0.001	1,339	27.0	1.03	46.6
	$T_{20\,m}$	1.91	<0.001	–	–	–	–
	$S_{20\,m}$	1.88	<0.001	–	–	–	–
	Bottom$_{depth}$	1.01	<0.001	–	–	–	–
	AMO$_{month}$	2.95	<0.001	–	–	–	–
	NAO$_{month}$	2.96	<0.001	–	–	–	–

Long × lat, longitude × latitude; $T_{20\,m}$, temperature at 20 m water depth; $S_{20\,m}$, salinity at 20 m water depth; Bottom$_{depth}$, bottom depth, AMO$_{month}$, detrended AMO index; NAO$_{month}$, detrended NAO index, as well as models without the factor variable "Year^f" (Yolksac$_{strong}$, Yolksac$_{weak}$, Yolksac$_{moderate}$, Preflexion$_{strong}$, Preflexion$_{weak}$, Preflexion$_{moderate}$); EDF, estimated degrees of freedom; Obs., observations; ZI, zero-inflation; Disp., dispersion parameter (over-/underdispersion); ED, explained deviance; na, not available.

inspection testing homogeneity of variance and autocorrelation (residual plots), normality (Q–Q plots), and outliers (Cook distance). With the use of the cyclic smooth terms, we could improve residual plots substantially, but a rest of the temporal autocorrelation was left in the final models (Supplementary SI2).

Results

Norwegian Sea climate between 1988 and 2015

The central Norwegian Sea has experienced an overall increase in SST of 1.2°C between 1988 and 2015 (Figure 2b). This increase is reflected in the SSTa time series with alternating negative and

positive anomalies before 2002 and almost constant positive anomalies since 2002 (Figure 2c). The period after 2002 is characterized by anomalies frequently exceeding 1°C. The monthly detrended AMO time series shows a shift from a predominately negative phase in 1988–1998 to a predominately positive phase in 1999–2015 (Figure 2d). The monthly NAO time series indicates alternating negative and positive phases over the whole period (Figure 2e).

Strong, moderate, and weak recruitment years

Based on the R_{age2}/SSB$_{t-2}$ relationship, all the strongest recruitment years between 1988 and 2015 happened before 2005, i.e. in 1990–1993, 1998, 1999, and 2002–2004 (Figure 2a). The biggest ratio of 18.9 was observed in 1992, compared to an average relationship of 9.6 ± 5.8. In stark contrast to this pattern, weak recruitment years with an average relationship of 1.0 ± 0.3 were primarily observed after 2005, i.e. in 2007, 2008, 2010–2012, 2014, and 2015, with the lowest relationship of 0.5 observed in 2008. Two years of weak recruitment occurred before 2005, which were 1995 and 1997. Moderate years with an average relationship of 2.4 ± 0.6 occurred throughout the whole period, i.e. in the years 1988, 1989, 1994, 1996, 2000, 2001, 2005, 2006, 2009, and 2013. In 2004 and earlier, strong years of recruitment matched with positive SSTa either in negative or positive AMO phases. After 2005, the combination of positive SSTa and a positive AMO phase yielded only moderate or weak recruitment.

Environmental windows of drifting NSS herring larvae in strong, moderate, and weak years of recruitment between 1988 and 2015

Using all 28 years of the time series, the GAM outputs evidenced yolksac and preflexion larval distribution patterns being affected by all environmental variables tested (Table 1). A significant effect of the factor variable "Year" representing the different recruitment years indicates the feasibility of a split of the time series into strong, moderate, and weak recruitment years. The combination of temperature, salinity, AMO, and NAO windows differs between drifting yolksac and preflexion stages amongst years of different recruitment success (Figures 3–7). Regarding temperature variation in strong recruitment years, the insignificant and almost flat regression for yolksac larvae suggests a widespread occurrence (Figure 3a), whereas the transition to preflexion larvae indicates increased occurrence at temperatures between 5.7 and 7.7°C (Figure 3b). The overall temperature effect implies stable temperature conditions and homogenously spread larvae for both life stages indicated by low effect sizes. Similar temperature conditions are experienced by yolksac larvae in years of moderate recruitment (Figure 3c). However, a stronger shift of the temperature regime from yolksac to preflexion larvae reveals greater differences compared to strong years. This difference is also observed in weak years with much higher effect sizes indicating a very strong shift of the temperature regime from yolksac to preflexion stages (Figure 3e–f).

Water masses during the larval drift from strong years of recruitment are influenced by freshwater input (Figure 4a and b). For both early life history stages, lower salinity conditions (<34) characterized the environment and no shift towards elevated salinities are observed in years of strong recruitment. Larvae drifting in moderate years of recruitment show a relation to water masses with a lower salinity, but the yolksac stages indicate both drift in
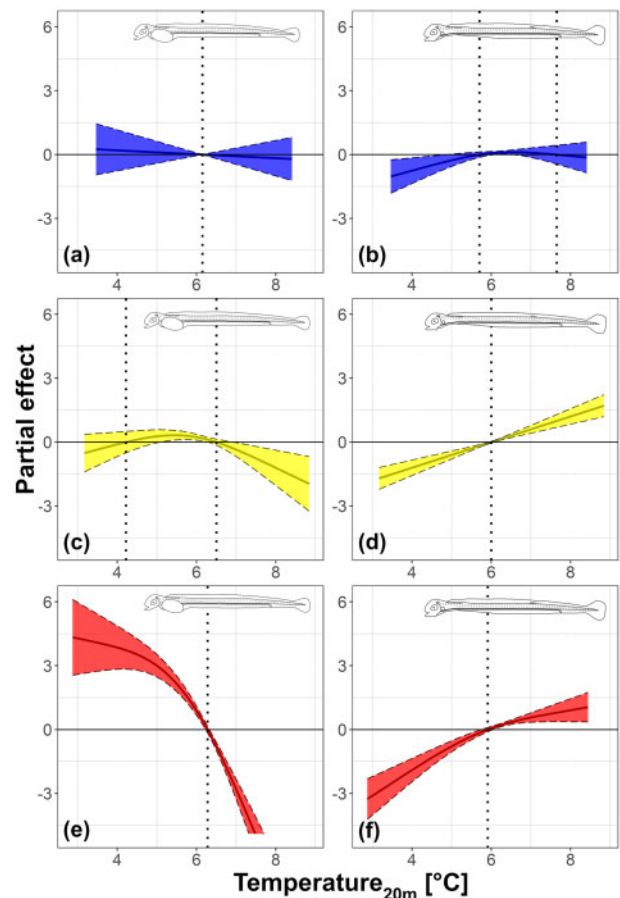

Figure 3. Generalized additive model output of the relationship between temperature at 20 m depth (Temperature$_{20\,m}$) and densities of yolksac (left) and preflexion larvae (right); (a, b) strong, (c, d) moderate, and (e, f) weak years of recruitment. Vertical dashed lines denote intercept of positive and negative temperature effects on larval densities.

higher and lower salinity water masses (Figure 4c and d). This pattern changes in weak recruitment years when yolksac staged larvae first occur under strongly marine conditions (>34.1) switching to lower salinity conditions during the preflexion stage drift period (Figure 4e and f).

A negative phase of the AMO characterizes the climate cycle of drifting yolksac stages that resulted in strong years of recruitment (Figure 5a). This type of negative-phase influence was markedly less noticeable at the preflexion stage (Figure 5b). In moderate years, the regression of the AMO follows a similar pattern to the strong years of recruitment, but the size of the effect is very small (Figure 5c). There is a tendency in moderate years that preflexion larvae experience a positive AMO phase (Figure 5d). The opposite situation for yolksac staged larvae occurred during weak years of recruitment where most larvae were observed during a positive AMO phase (Figure 5e and f). This is also indicated during the preflexion stage drift but is less pronounced as the regression also indicates a year where most of the preflexion larvae occurred during a negative AMO phase.

A positive correlation of yolksac and preflexion larvae and an NAO close to zero is apparent from strong years of recruitment (Figure 6a and b). Another positive correlation with a strong
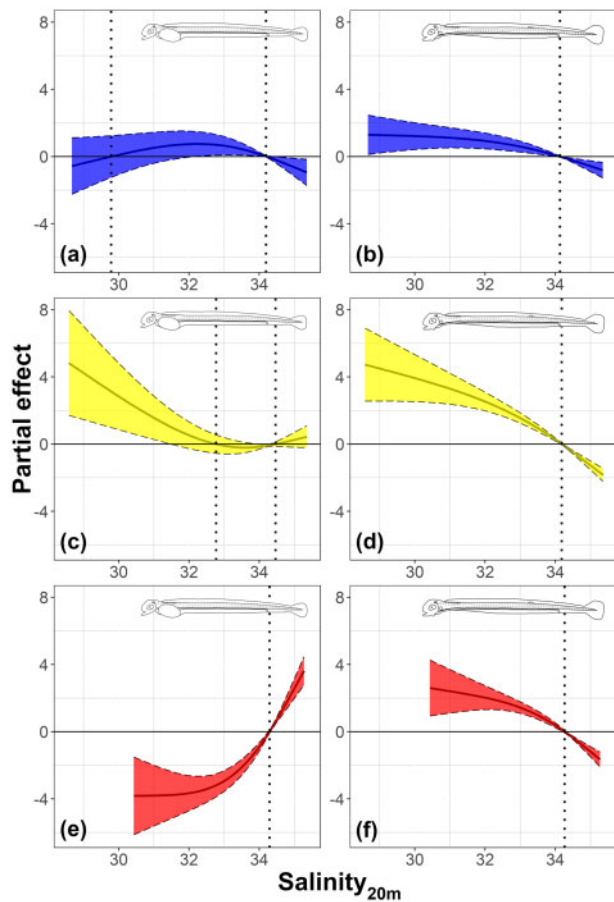
Figure 4. Generalized additive model output of the relationship between salinity at 20 m depth (Salinity$_{20\,m}$) and densities of yolksac (left) and preflexion larvae (right); (a, b) strong, (c, d) moderate, and (e, f) weak years of recruitment. Vertical dashed lines denote intercept of positive and negative salinity effects on larval densities.

Figure 5. Generalized additive model output of the relationship between monthly AMO (AMO$_{month}$) and densities of yolksac (left) and preflexion larvae (right); (a, b) strong, (c, d) moderate, and (e, f) weak years of recruitment. Vertical dashed lines denote intercept of positive and negative AMO effects on larval densities.

NAO is modelled for yolksac larvae. In moderate years, larvae mostly experience a negative NAO (Figure 6c and d). Thereby, yolksac larvae occur almost exclusively during a negative NAO, whereas a slight shift of the NAO towards a slight positive NAO is observed for preflexion stages. A distinct shift from a positive correlation between yolksac larvae towards a negative correlation for preflexion larvae characterizes the NAO effect for weak years (Figure 6e and f). This indicates again a strong environmental change during the transition between these early life history stages.

Larvae in all years indicate peak occurrences in relatively shallow water (<250 m) over the continental shelf (Figure 7). Partial plots of bottom depth indicate a higher degree of yolksac stages being present above the continental shelf, whereas regressions for preflexion larvae, compared to yolksac larvae, flatten with bottom depth indicating some larval dispersal towards oceanic regions. However, larvae are rarely observed at bottom depths >250 m and indicate main drift along the coast. Larvae from strong years of recruitment are observed over slightly shallower bottom depths than larvae in weak and moderate years.

Discussion

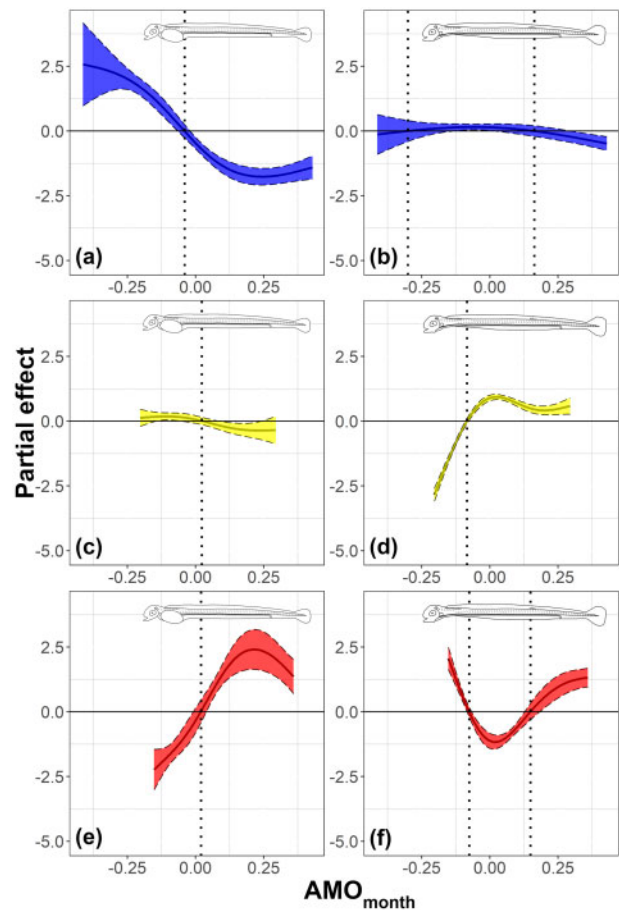The GAM analyses undertaken here on 28 years of larval NSS herring survey data reveal distinct variation between environmental conditions (windows) for yolksac and preflexion stages from strong, moderate, and weak years of recruitment. In years with strong recruitment, larvae experienced a slight temperature difference during a negative AMO when shifting from yolksac to preflexion stages. This augments evidence that, during the early larval drift, a slower increase in water temperature in spring towards summer is coincident with heightened recruitment. This is also in line with larvae experiencing a moderate NAO that induces a slow temperature increase with moderate westerly winds. The relationships between the two larval stages and temperature as well as salinity in strong years of recruitment are flattened and are in stark contrast with the relationships in weak years. The flattened relationships suggest that larvae are more widespread along their drift routes and the slight shift of the regimes between the two stages indicates a much slower change in their environmental regimes than in weak years. This evidences that, in the last almost three decades, a slow changing regime in ocean properties during the transition from yolksac to preflexion stages benefitted recruitment. On the contrary, abrupt changes during the very early transition of NSS herring larvae suggest negative effects on recruitment.

The state of both climate cycles (negative AMO and NAO close to zero) generally fosters slower warming of water masses, which
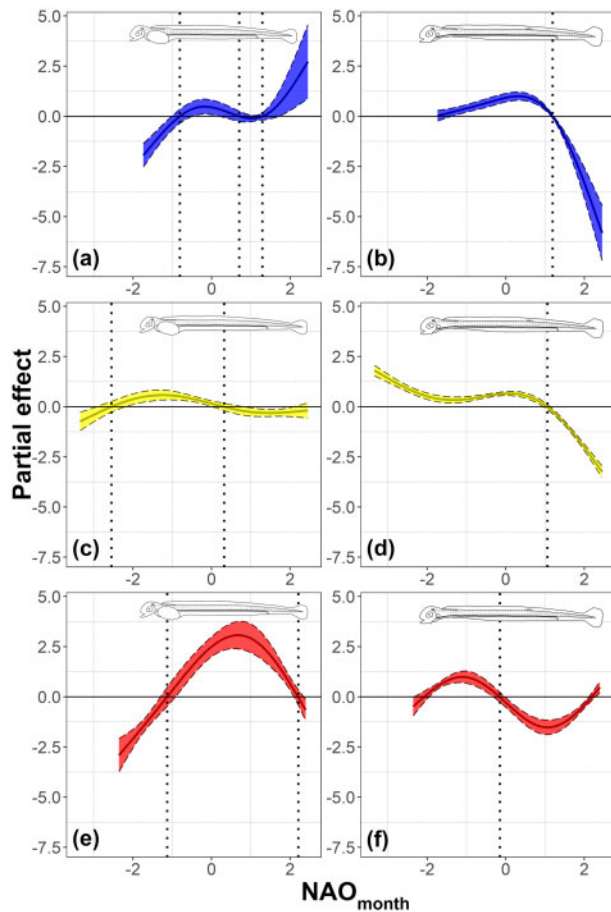
Figure 6. Generalized additive model output of the relationship between monthly NAO (NAO_{month}) and densities of yolksac (left) and preflexion larvae (right); (a, b) strong, (c, d) moderate, and (e, f) weak years of recruitment. Vertical dashed lines denote intercept of positive and negative NAO effects on larval densities.

Figure 7. Generalized additive model output of the relationship between bottom depth and densities of yolksac (left) and preflexion larvae (right); (a, b) strong, (c, d) moderate, and (e, f) weak years of recruitment. Vertical dashed lines denote intercept of positive and negative bottom depth effects on larval densities.

can be transported in a northward pulse of the Norwegian Coastal Current. Such characteristic pulses can be observed through low-salinity anomalies northwards along the Norwegian coast (Skagseth *et al.*, 2015). Low-salinity anomalies were associated with exceptionally high recruitment years between 1935 and 2009 (Skagseth *et al.*, 2015). An enhanced Norwegian Coastal Current is evidenced by salinities of <35 (Sætre and Ljøen, 1971). The partial plot of the GAM output for strong years of recruitment indicates a positive relationship between yolksac and preflexion stages with water masses of salinities <34. That suggests that an enhanced Norwegian Coastal Current and a reduced influence of Atlantic water (salinities >35) were apparent in years that resulted in strong years of recruitment. Furthermore, a strengthened northward flow would suggest that larvae are rapidly transported towards nursery grounds either in fjords or in their main nurseries in the Barents Sea. This is consistent with a positive correlation between an accelerated larval drift and enhanced recruitment (Dragesund, 1970; Skagseth *et al.*, 2015). A more rapid drift is assumed to decrease the probabilities of a spatiotemporal overlap between predators that increase in number while the year progresses and herring larvae become a potential prey (Husebø *et al.*, 2009). In this context, it is suggested that, when spawning occurs early in the year, this contributes to
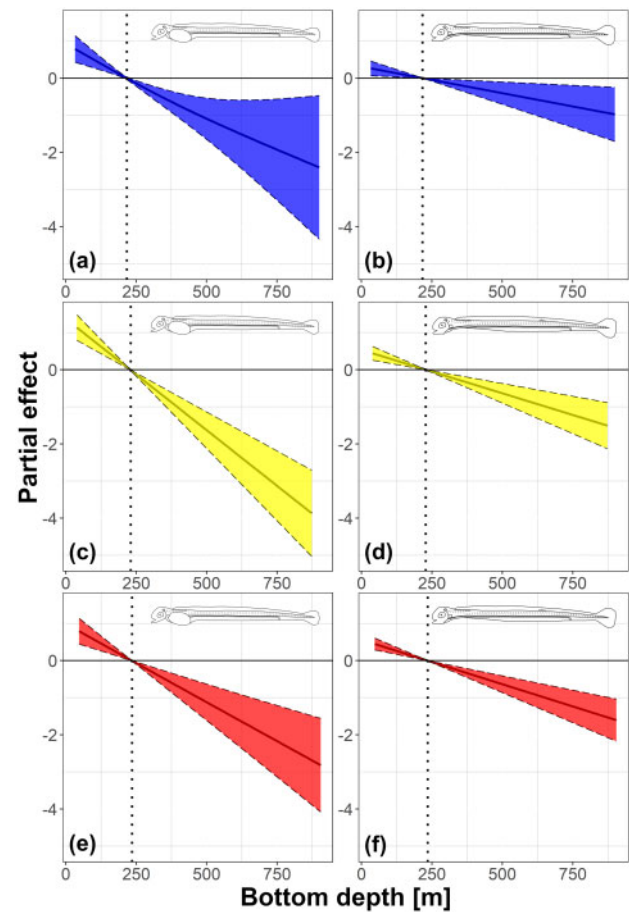
improved larval survival (Vikebø *et al.*, 2010; Slotte *et al.*, 2019). Even though evidence is rich that an accelerated larval transport increases recruitment success, larval retention may happen on the prominent banks along the drift route of herring larvae along the Norwegian coast or in other parts of the North Atlantic (Sætre *et al.*, 2002b; Sinclair and Power, 2015). The debate on whether larval retention or transport is beneficial for larval survival is ongoing (Cowen and Sponaugle, 2009; Deschepper *et al.*, 2020). While in certain ecosystems like upwelling or reef ecosystems larval retention may be beneficial (Bakun, 2006; Woodson *et al.*, 2012), in others transport is key (Pineda *et al.*, 2007). For instance, successful transport of herring larvae in the North Sea has been addressed to be key for heightened recruitment (Corten, 2013). However, in all years covered in this study, the model outputs suggest that larvae are retained or transported mostly above the continental shelf indicated by a positive relationship between the two larval stages and areas shallower than ≈250 m. It seems that larvae disperse above bottom depths where the main spawning grounds are normally observed (Runnström, 1941). Hence, larval offshore transport implies a minor process in determining year-class strength for NSS herring. In other ecosystems, a larval offshore transport can be an important process to replenish local stocks, for instance the European pilchard stock near the Canary

Islands (Rodríguez *et al.*, 1999). In every ecosystem and in those years, in which many contributing factors of increased offspring survival concur, the higher the chance is for a large year class. Exceptionally large year classes in herring populations are, however, seldom compared to years in which recruitment is weak (McQuinn, 1997; Nash and Dickey-Collas, 2005; Skagseth *et al.*, 2015).

Coinciding negative AMO phases with peak recruitment in the years 1988–2015 poses questions. Before 2000, the NSS herring stock size was positively correlated with the AMO, so a beneficial effect of a warmer ocean (Alheit *et al.*, 2014). This was also shown by a reasonably close co-variation between ocean temperature from the Barents Sea (Kola hydrographic transect time series) and stock status represented by SSB (Toresen and Østvedt, 2000). A shift from a negative to a positive AMO phase characterized the North Atlantic climate around the year 1998. This would have suggested that some strong recruitment years between 2005 and 2015 should have emerged if the historical positive relationship between a warmer phase (positive AMO) and stock size persisted. However, the absence of strong year classes was seen and resulted in an estimated SSB decline of about 3 million tonnes (ICES, 2018). So, in contrast to expectations, the strongest recruitment years before the 10-year recruitment suppression occurred during a negative AMO phase. A negative AMO phase is normally accountable for a colder regime in the North Atlantic (Delworth and Mann, 2000). However, during a negative AMO, temperature anomalies can still be positive. Here, we show that in years of strong recruitment, NSS herring larvae experienced a negative AMO phase, but largely within positive SST anomalies. This emphasizes that an earlier "warmer" environment under a negative AMO has benefitted the survival of drifting larvae (Vikebø *et al.*, 2010).

So far, we observe species dynamics driven by climate cycles, e.g. NAO and AMO driving herring populations (Gröger *et al.*, 2010) and other stocks in the Atlantic (Alheit *et al.*, 2014), as well as the Pacific Decadal Oscillation and El Nino-Southern Oscillation driving anchovy and sardine populations (Chavez *et al.*, 2003; Lehodey *et al.*, 2006). The term "warmer" in this context, however, can be misleading. Basing a "warmer" state only on historic climate cycles like the AMO would not properly account for today's ocean warming triggered by anthropogenic sources. For the 10-year recruitment suppression, a question arises what the recently unprecedented temperature increase in the Norwegian Sea ecosystem implies for ocean life. From our results we can infer that only weak and moderate recruitment years emerged from larvae that experienced a positive AMO along with positive SST anomalies. In addition, a strong shift of the NAO for larvae in weak recruitment years and a corresponding distinct shift from colder to warmer temperature regimes during the transition from yolksac to preflexion stages prevailed. When an ecosystem changes quickly in hydrographic traits, e.g. temperature, it has consequences for the whole ecosystem accelerating a change in biological interactions. For example, a change in temperature can modify the occurrence of the phytoplankton bloom in spring (Bissinger *et al.*, 2008). Timing of the bloom and the onset of spawning is essential for larval survival during the critical period when first-feeding larvae are depended on sufficient food supply (Hjort, 1914). Considering the whole spawning area, the onset of the phytoplankton bloom in southern regions like Møre or more northern regions like Røstbanken can differ by up to ≈40 d (Vikebø *et al.*, 2012). Therefore, in years where increased

temperature rises occur, the onset of the bloom may change and may ensure either matching predator–prey situations or vice versa (Cushing, 1969). Between 1998 and 2007, the phytoplankton bloom matched the area of larval occurrence in southern regions, e.g. Møre (Vikebø *et al.*, 2012). In more northern regions, e.g. Røstbanken, the years 1998, 1999, 2006, and 2007 were years of a match of NSS herring larvae and the phytoplankton bloom while a mismatch in the years 2000–2005 (Vikebø *et al.*, 2012). While the years 1998, 1999, 2002–2004 resulted in strong years of recruitment, weak or moderate year classes emerged in 2000, 2001, 2005, and 2006. That implies that match–mismatch conditions between fish larvae and their prey are only one of several possible factors affecting recruitment dynamics in NSS herring. Although the phytoplankton bloom is a plausible indicator for the onset of critical feeding periods of herring larvae, other larval life stage periods (Denis *et al.*, 2016) and considering all possible prey communities (Bils *et al.*, 2017) are essential to identify a match–mismatch between predator and prey.

In changing environments, the total carrying capacity of an ecosystem can vary (Woodworth-Jefcoats *et al.*, 2017). A shift of the *Calanus* spp. communities in the southwestern Norwegian Sea was observed in 2003 (Kristiansen *et al.*, 2016). *Calanus* spp. is the main food source for all life history stages of NSS herring (Dalpadado *et al.*, 2000; Prokopchuk, 2009; Ferreira *et al.*, 2012; Bachiller *et al.*, 2016). In 2003, *C. finmarchicus* decreased in numbers of the overwintering stock and *Calanus hyperboreus* disappeared. These shifts were observed with increasing temperature and salinity regimes (Kristiansen *et al.*, 2016) and provide further indications of a distinct change in the Norwegian Sea ecosystem since 2004. The zooplankton production seems to have changed after 2002 along the drift route of NSS herring larvae and may have contributed to the 10-year suppressed recruitment (Toresen *et al.*, 2019). In the North Sea, warming triggered a plankton community change coincident with two recruitment suppression events of herring in the 1980s and 2000s (Payne *et al.*, 2008). In the Gulf of St. Lawrence, a decline in cold-water copepod abundances was concomitant with a decrease in herring recruitment between 1971 and 2014 (Brosset *et al.*, 2019). In Newfoundland, a shift of the copepod *Pseudocalanus* sp., a main diet of Atlantic herring larvae (standard length >13 mm), has shifted its peak occurrence from spring to autumn probably decreasing feeding success since the mid-2000s (Wilson *et al.*, 2018). Further ocean warming is predicted to increase the temporal mismatch between sandeel (*Ammodytes marinus*) larvae and their prey (Régnier *et al.*, 2019). The present study including the above-mentioned studies relates bottom-up controlled effects on larval fish survival. However, an important next step is to investigate how climate change effects top-down processes on early life history stages, the second major source of recruitment variability (Bailey and Houde, 1989), as discussed in the following paragraph.

During their development, NSS herring eggs and larvae are exposed to different fish predators like haddock (*Melanogrammus aeglefinus*) feeding on the demersal eggs (Toresen, 1991) and pelagic predators like saithe (*Pollachius virens*) (Nedreaas, 1985), adult NSS herring (Holst, 1992), or Atlantic mackerel (*Scomber scombrus*) (Skaret *et al.*, 2015) during the larval stages. When an ecosystem warms, it allows species to migrate into habitats of their preferred temperature ranges (Perry *et al.*, 2005). In spring–summer, Atlantic mackerel expands along the Norwegian coast. In recent years, this species has increased their migration westward and northward constrained by ambient temperatures

between 5 and 15°C, with preferred temperatures 9–12°C (Nikolioudakis *et al.*, 2019; Olafsdottir *et al.*, 2019). Early in the year, environments steadily become warmer, especially in recent years of suppressed recruitment of NSS herring. This is particularly indicated by the noted difference in environments that NSS herring larvae experience during their transition from yolksac to preflexion stages in weak years of recruitment. Early in the year, this temperature acceleration may provide earlier access for Atlantic mackerel along the Norwegian coast and, thus, along the drift route of herring larvae. This may result in a broadened spatiotemporal overlap of adult Atlantic mackerel and NSS herring larvae. If this overlap occurs, potentially high feeding rates upon herring larvae may be expected (Skaret *et al.*, 2015). Any mechanistic interactions were not examined in this study but may provide an additional causal coherence between this long-time recruitment suppression of NSS herring with the marked habitat expansion of Atlantic mackerel. In this context, a quantification of predation on early life history stages of NSS herring is needed. However, field-based estimates of total predation mortality are difficult to assess (Bailey and Houde, 1989). Molecular methods quantifying predation mortality from the field may contribute to our understanding of top-down controlled recruitment processes (King *et al.*, 2008).

Current causes of recruitment suppression in NSS herring are uncertain, but a fast-changing environment seems to have triggered an abrupt alteration in typical ecological patterns in the Norwegian Sea ecosystem. In this study, we investigated recruitment dynamics of NSS herring by analysing environmental conditions encountered by drifting yolksac and preflexion stages over the last three decades (28 years). Survival of these stages is assumed to be a main regulator of recruitment success of this stock (Sætre *et al.*, 2002a). Recruitment success is improved under optimal environmental conditions with low predation and enough food supply. However, if recruitment is suppressed in consecutive years, like in recent years (2005–2015), a reduction in the stock size is expected through ongoing fishing practices and natural mortality, even with a reduction in fishing effort, as in the existing management strategy (ICES, 2018). Here, we could identify general environmental conditions that occurred simultaneously with successful recruitment years. We show that, in the last decades, recruitment success of NSS herring is concomitant with a negative AMO, a moderate NAO, a strong Norwegian Coastal Current, and slow temperature increases during the early larval drift. The potential for better recruitment in a given year is increased since the AMO has turned into a negative phase since 2016 (Frajka-Williams *et al.*, 2017) and may increase the chances of a good year class after this long period of suppression. Currently, the management of stocks still largely focuses on stock productivity and thereby to a lesser degree on climate influences (Skern-Mauritzen *et al.*, 2016). This is particularly true when it comes to underlying processes attributed to anthropogenic climate change (Gaines *et al.*, 2018). Hence, in dynamic altering ecosystems, management practices need to adapt accordingly to maintain long-term sustainable harvest regimes.

Supplementary data

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

References

Aksnes, D. L., and Blindheim, J. 1996. Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. Ophelia, 44: 7–28.

Alheit, J., Licandro, P., Coombs, S., Garcia, A., Giráldez, A., Santamaría, M. T. G., Slotte, A. et al. 2014. Reprint of 'Atlantic Multidecadal Oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic'. Journal of Marine Systems, 133: 88–102.

Bachiller, E., Skaret, G., Nøttestad, L., and Slotte, A. 2016. Feeding ecology of Northeast Atlantic mackerel, Norwegian spring-spawning herring and blue whiting in the Norwegian Sea. PLoS One, 11: e0149238.

Bailey, K., and Houde, E. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Advances in Marine Biology, 25: 1–83.

Bakun, A. 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Scientia Marina, 70: 105–122.

Barton, A. D., Irwin, A. J., Finkel, Z. V., and Stock, C. A. 2016. Anthropogenic climate change drives shift and shuffle in North Atlantic phytoplankton communities. Proceedings of the National Academy of Sciences of the United States of America, 113: 2964–2969.

Bils, F., Moyano, M., Aberle, N., Hufnagl, M., Alvarez-Fernandez, S., and Peck, M. A. 2017. Exploring the microzooplankton-ichthyoplankton link: a combined field and modeling study of Atlantic herring (*Clupea harengus*) in the Irish Sea. Journal of Plankton Research, 39: 147–163.

Bissinger, J. E., Montagnes, D. J. S., Sharples, J., and Atkinson, D. 2008. Predicting marine phytoplankton maximum growth rates from temperature: improving on the Eppley curve using quantile regression. Limnology and Oceanography, 53: 487–493.

Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., Halloran, P. et al. 2013. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. Biogeosciences, 10: 6225–6245.

Boyd, P. W., Cornwall, C. E., Davison, A., Doney, S. C., Fourquez, M., Hurd, C. L., Lima, I. D. et al. 2016. Biological responses to environmental heterogeneity under future ocean conditions. Global Change Biology, 22: 2633–2650.

Brosset, P., Doniol-Valcroze, T., Swain, D. P., Lehoux, C., Van Beveren, E., Mbaye, B. C., Emond, K. et al. 2019. Environmental variability controls recruitment but with different drivers among spawning components in Gulf of St. Lawrence herring stocks. Fisheries Oceanography, 28: 1–17.

Chavez, F. P., Ryan, J., Lluch-Cota, S. E., and Niquen, M. C. 2003. From anchovies to sardines and back: multidecal change in the Pacific Ocean. Science, 299: 217–221.

Corten, A. 2013. Recruitment depressions in North Sea herring. ICES Journal of Marine Science, 70: 1–15.

Cowen, R. K., and Sponaugle, S. 2009. Larval dispersal and marine population connectivity. Annual Review of Marine Science, 1: 443–466.

Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Canadian Journal of Fisheries and Aquatic Sciences, 46: 670–680.

Cushing, D. H. 1969. The regularity of the spawning season of some fishes. Conseil Permanent International pour l'Exploration de la Mer, 33: 81–92.

Dalpadado, P., Ellertsen, B., Melle, W., and Dommasnes, A. 2000. Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. ICES Journal of Marine Science, 57: 843–857.

Delworth, T. L., and Mann, M. E. 2000. Observed and simulated multidecadal variability in the Northern Hemisphere. Climate Dynamics, 16: 661–676.

Denis, J., Vallet, C., Courcot, L., Lefebvre, V., Caboche, J., Antajan, E., Marchal, P. et al. 2016. Feeding strategy of Downs herring larvae (*Clupea harengus* L.) in the English Channel and North Sea. Journal of Sea Research, 115: 33–46.

Deschepper, I., Lyons, K., Lyashevska, O., and Brophy, D. 2020. Biophysical models reveal the role of tides, wind, and larval behaviour in early transport and retention of Atlantic herring (*Clupea harengus*) in the Celtic Sea. Canadian Journal of Fisheries and Aquatic Sciences, 77: 90–107.

Doyle, M. J. 1977. A morphological staging system for the larval development of the herring, *Clupea harengus* l. Journal of the Marine Biological Association of the United Kingdom, 57: 859–867.

Dragesund, O. 1970. Factors influencing year-class strength of Norwegian spring spawning herring (*Clupea harengus* Linneé). Fiskeridirektoratet Skrifter Serie Havundersøkelser, 15: 381–450.

Dragesund, O., Hamre, J., and Ulltang, Ø. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. Rapports et procès-verbaux des réunions Conseil International pour l'Exploration de la Mer, 177: 43–71.

Enfield, D. B., Mestas-Nuñez, A. M., and Trimble, P. J. 2001. The Atlantic Multidecadal Oscillation and its relationship to rainfall and river flows in the continental U.S. Geophysical Research Letters, 28: 2077–2080.

Ferreira, A. S. D. A., Stenevik, E. K., Vollset, K. W., Korneliussen, R., and Folkvord, A. 2012. Vertical migration of Norwegian spring-spawning herring larvae in relation to predator and prey distribution. Marine Biology Research, 8: 605–614.

Frajka-Williams, E., Beaulieu, C., and Duchez, A. 2017. Emerging negative Atlantic Multidecadal Oscillation index in spite of warm subtropics. Scientific Reports, 7: 11224.

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., and Jensen, O. P. 2019. Impacts of historical warming on marine fisheries production. Science, 363: 979–983.

Gaines, S. D., Costello, C., Owashi, B., Mangin, T., Bone, J., Molinos, J. G., Burden, M. et al. 2018. Improved fisheries management could offset many negative effects of climate change. Science Advances, 4: eaao1378.

Gehringer, J. W. 1952. High speed plankton samplers. 2. An all-metal plankton sampler (Model Gulf III). United States Fish and Wildlife Service Special Scientific Report - Fisheries, 88: 7–12.

Gröger, J. P., Kruse, G. H., and Rohlf, N. 2010. Slave to the rhythm: how large-scale climate cycles trigger herring (*Clupea harengus*) regeneration in the North Sea. ICES Journal of Marine Science, 67: 454–465.

Gullstad, P., Howell, D., Stenevik, R. K., Sandberg, P., and Bakke, G. 2018. Management and rebuilding of herring and cod in the Northeast Atlantic. In Rebuilding of marine fisheries. Part 2: Case studies, p. 232. Ed. by S. M. Garcia and Y. Ye. FAO Fisheries and Aquaculture Technical Paper No. 630/2, Rome.

Hand, R., Keenlyside, N. S., Omrani, N. E., Bader, J., and Greatbatch, R. J. 2019. The role of local sea surface temperature pattern changes in shaping climate change in the North Atlantic sector. Climate Dynamics, 52: 417–438.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe. Conseil Permanent International pour l'Exploration de la Mer, 20: 1–228.

Holst, J. C. 1992. Cannibalism as a factor regulating year class strength in the Norwegian spring-spawning herring stock. ICES Document C.M.1992/H:14. 15 pp.

Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences of the United States of America, 106: 19659–19665.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium, 2: 17–29.

Huang, B., Thorne, P. W., Banzon, V. F., Boyer, T., Chepurin, G., Lawrimore, J. H., Menne, M. J. et al. 2017. Extended reconstructed sea surface temperature, Version 5 (ERSSTv5): Upgrades, validations, and intercomparisons. Journal of Climate, 30: 8179–8205.

Husebø, Å., Stenevik, E. K., Slotte, A., Fossum, P., Salthaug, A., Vikebø, F., Aanes, S. et al. 2009. Effects of hatching time on year-class strength in Norwegian spring-spawning herring (*Clupea harengus*). ICES Journal of Marine Science, 66: 1710–1717.

ICES. 2018. Herring (*Clupea harengus*) in subareas 1, 2, and 5, and in divisions 4.a and 14.a, Norwegian spring-spawning herring (the Northeast Atlantic and the Arctic Ocean). ICES. 1–8 pp.

Jones, P. D., Jonsson, T., and Wheeler, D. 1997. Extension to the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and South-West Iceland. International Journal of Climatology, 17: 1433–1450.

Kaplan, A., Cane, M. A., Kushnir, Y., Clement, A. C., Blumenthal, B. M., and Rajagopalan, B. 1998. Analyses of global sea surface temperature 1856-1991. Journal of Geophysical Research, 103: 18567–18589.

King, R. A., Read, D. S., Traugott, M., and Symondson, W. O. C. 2008. Molecular analysis of predation: a review of best practice for DNA-based approaches. Molecular Ecology, 17: 947–963.

Kristiansen, I., Gaard, E., Hátún, H., Jónasdóttir, S., and Ferreira, A. S. 2016. Persistent shift of *Calanus* spp. in the southwestern Norwegian Sea since 2003, linked to ocean climate. ICES Journal of Marine Science, 73: 1319–1329.

Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J. M. et al. 2006. Climate variability, fish, and fisheries. Journal of Climate, 19: 5009–5030.

MacKenzie, B. R., Miller, T. J., Cyr, S., and Leggett, W. C. 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. Limnology and Oceanography, 39: 1790–1799.

McQuinn, I. H. 1997. Year-class twinning in sympatric seasonal spawning populations of Atlantic herring, *Clupea harengus*. Fishery Bulletin, 95: 126–136.

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.

Nakken, O. 2008. Norwegian Spring-Spawning Herring & Northeast Arctic Cod. Tapir Academic Press, Trondheim. 177 pp.

Nash, R. D. M., and Dickey-Collas, M. 2005. The influence of life history dynamics and environment on the determination of year

class strength in North Sea herring (*Clupea harengus* L). Fisheries Oceanography, 14: 279–291.

Nedreaas, K. 1985. Food and feeding habits of young saithe (*Pollachius virens* L.) on the coast of western Norway. C.M. 1985/G:22. 1–44 pp.

Nikolioudakis, N., Skaug, H. J., Olafsdottir, A. H., Jansen, T., Jacobsen, J. A., and Enberg, K. 2019. Drivers of the summer-distribution of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic Seas from 2011 to 2017; a Bayesian hierarchical modelling approach. ICES Journal of Marine Science, 76: 530–548.

Øiestad, V. 1983. Growth and survival of herring larvae and fry (*Clupea harengus* L.) exposed to different feeding regimes in experimental ecosystems: Outdoor basin and plastic Bags. University of Bergen, Bergen. 299 pp.

Olafsdottir, A. H., Utne, K. R., Jacobsen, J. A., Jansen, T., Óskarsson, G. J., Nøttestad, L., Elvarsson, B. *et al.* 2019. Geographical expansion of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic Seas from 2007 to 2016 was primarily driven by stock size and constrained by low temperatures. Deep-Sea Research Part II: Topical Studies in Oceanography, 159: 152–168.

Payne, M. R., Hatfield, E. M. C., Dickey-Collas, M., Falkenhaug, T., Gallego, A., Gröger, J., Licandro, P. *et al.* 2008. Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. ICES Journal of Marine Science, 66: 272–277.

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.

Pineda, J., Hare, J., and Sponaugle, S. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography, 20: 22–39.

Prokopchuk, I. 2009. Feeding of the Norwegian spring spawning herring *Clupea harengus* (Linne) at the different stages of its life cycle. Deep-Sea Research Part II: Topical Studies in Oceanography, 56: 2044–2053.

R Development Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Régnier, T., Gibb, F. M., and Wright, P. J. 2019. Understanding temperature effects on recruitment in the context of trophic mismatch. Scientific Reports, 9: 13.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. 2009. Resolving the effect of climate change on fish populations. ICES Journal of Marine Science, 66: 1570–1583.

Robson, J., Sutton, R. T., Archibald, A., Cooper, F., Christensen, M., Gray, L. J., Holliday, N. P. *et al.* 2018. Recent multivariate changes in the North Atlantic climate system, with a focus on 2005–2016. International Journal of Climatology, 38: 5050–5076.

Rodríguez, J. M., Hernández-León, S., and Barton, E. D. 1999. Mesoscale distribution of fish larvae in relation to an upwelling filament off Northwest Africa. Deep Sea Research Part I, 46: 1969–1984.

Runnström, S. 1941. Quantitative investigations on herring spawning and its yearly fluctuations at the west coast of Norway. Report on Norwegian Fishery and Marine Investigation, 6: 1–71.

Russell, F. S. 1976. The Eggs and Planktonic Stages of British Marine Fishes. Academic Press, London. 524 pp.

Sætre, R., and Ljøen, R. 1971. The Norwegian Coastal Current. *In* Proceedings of the First International Conference on Port and Ocean Engineering under Arctic Conditions, Vol. I, pp. 514–535. Ed. by ANON. Technical University of Norway, Trondheim.

Sætre, R., Toresen, R., and Anker-Nilssen, T. 2002a. Factors affecting the recruitment variability of the Norwegian spring-spawning herring (*Clupea harengus* L). ICES Journal of Marine Science, 59: 725–736.

Sætre, R., Toresen, R., Søiland, H., and Fossum, P. 2002b. The Norwegian spring-spawning herring - spawning, larval drift and larval retention. Sarsia, 87: 167–178.

Sætre, R. 2007. The Norwegian Coastal Current: Oceanography and Climate. Tapir Academic Press, Trondheim. 160 pp.

Schlesinger, M. E., and Ramankutty, N. 1994. An oscillation in the global climate system of period 65–70 years. Letter to Nature, 367: 723–726.

Sinclair, M., and Power, M. 2015. The role of 'larval retention' in life-cycle closure of Atlantic herring (*Clupea harengus*) populations. Fisheries Research, 172: 401–414.

Skagseth, Ø., Slotte, A., Stenevik, E. K., and Nash, R. D. M. 2015. Characteristics of the Norwegian Coastal Current during years with high recruitment of Norwegian spring spawning herring (*Clupea harengus* L). PLoS One, 10: e0144117.

Skaret, G., Bachiller, E., Langøy, H., and Stenevik, E. K. 2015. Mackerel predation on herring larvae during summer feeding in the Norwegian Sea. ICES Journal of Marine Science, 72: 2313–2321.

Skern-Mauritzen, M., Ottersen, G., Handegard, N. O., Huse, G., Dingsør, G. E., Stenseth, N. C., and Kjesbu, O. S. 2016. Ecosystem processes are rarely included in tactical fisheries management. Fish and Fisheries, 17: 165–175.

Slotte, A., Husebø, Å., Berg, F., Stenevik, E. K., Folkvord, A., Fossum, P., Mosegaard, H. *et al.* 2019. Earlier hatching and slower growth: a key to survival in the early life history of Norwegian spring spawning herring. Marine Ecology Progress Series, 617-618: 25–39.

Stenevik, E. K., Nash, R. D. M., Vikebø, F., Fossum, P., and Bakkeplass, K. 2012. The effects of survey design and circulation pattern on the perceived abundance of herring larvae: a case study for Norwegian spring spawning herring (*Clupea harengus*). Fisheries Oceanography, 21: 363–373.

Sundby, S., and Nakken, O. 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. ICES Journal of Marine Science, 65: 953–962.

Takasuka, A., Oozeki, Y., and Aoki, I. 2007. Optimal growth temperature hypothesis: why do anchovy flourish and sardine collapse or vice versa under the same ocean regime? Canadian Journal of Fisheries and Aquatic Sciences, 64: 768–776.

Toresen, R. 1991. Predation on the eggs of Norwegian spring-spawning herring (*Clupea harengus* l.) on a spawning ground on the west coast of Norway. ICES Journal of Marine Science, 48: 15–21.

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

Toresen, R., Skjoldal, H. R., Vikebø, F., and Martinussen, M. B. 2019. Sudden change in long-term ocean climate fluctuations corresponds with ecosystem alterations and reduced recruitment in Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae). Fish and Fisheries, 20: 1–11.

Vikebø, F. B., Husebø, Å., Slotte, A., Stenevik, E. K., and Lien, S. V. 2010. Effect of hatching date, vertical distribution, and interannual variation in physical forcing on northward displacement and temperature conditions of Norwegian spring-spawning herring larvae. ICES Journal of Marine Science, 67: 1948–1956.

Vikebø, F. B., Korosov, A., Stenevik, E. K., Husebø, Å., and Slotte, A. 2012. Spatio-temporal overlap of hatching in Norwegian spring-spawning herring and the spring phytoplankton bloom at available spawning substrata. ICES Journal of Marine Science, 69: 1298–1302.

Wilson, C. J., Murphy, H. M., Bourne, C., Pepin, P., and Robert, D. 2018. Feeding ecology of autumn-spawned Atlantic herring (*Clupea harengus*) larvae in Trinity Bay, Newfoundland: is

recruitment linked to main prey availability? Journal of Plankton Research, 40: 255–268.

Wood, S. N. 2003. Thin-plate regression splines. Journal of the Royal Statistical Society, 65: 95–114.

Wood, S. N. 2006. Generalized Additive Models: An Introduction with R. Taylor & Francis Group, Boca Raton. 392 pp.

Woodson, C. B., McManus, M. A., Tyburczy, J. A., Barth, J. A., Washburn, L., Caselle, J. E., Carr, M. H. *et al.* 2012. Coastal fronts set recruitment and connectivity patterns across multiple taxa. Limnology and Oceanography, 57: 582–596.

Woodworth-Jefcoats, P. A., Polovina, J. J., and Drazen, J. C. 2017. Climate change is projected to reduce carrying capacity and redistribute species richness in North Pacific pelagic marine ecosystems. Global Change Biology, 23: 1000–1008.

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