Predicting fish recruitment from juvenile abundance and environmental indices

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

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

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

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

INTRODUCTION

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

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

For any given pre-recruit life stage, it would also seem reasonable that the inclusion of environmental variables, such as water temperature and indices of predator or competitor abundance, should increase the ability to predict the survival of that life stage to recruitment. Understanding the effects of climate on fisheries has been a central research topic since the foundation of the International Council for the Exploration of the Sea (ICES) in 1902 (e.g. Cushing 1982, Beamish 1993, Alheit & Hagen 1997, Borja et al. 1998, Rothschild 2000, Drinkwater et al. 2005, Hollowed et al. 2011). In recent years, there has been an effort to develop models incorporating climate and other environmental indices for the prediction of recruitment (e.g. Chen & Ware 1999, Borja et al. 2008, MacKenzie et al. 2008, Andonegi et al. 2011, Mueter et al. 2011). For example, Zabel et al. (2011), working with bocaccio *Sebastes paucispinis* in the California Current system, found that a recruitment model, which included juvenile abundance and climate and the interaction of these factors, explained 68% of the recruitment variation, whereas a model with population density alone explained only 1.4% of the recruitment variance. Using cross validation (i.e.

separating the data set into 'training' and 'testing' data sets and using the training data set to predict the response in the testing data set), Zabel et al. (2011) found that the interaction model was also better at predicting 'new' observations not used when estimating the parameters in the model. In the Barents Sea, a number of recruitment models have been developed for cod *Gadus morhua* that have included environmental variables, such as the yearly average temperature along the Kola line (0 to 200 m) and predator and prey biomasses (e.g. Hjermann et al. 2007, Dingsør et al. 2010). To assess accurately the stock size and advise corresponding catch limits for the management of this stock, analogous recruitment models are used to predict the recruitment of 3 yr olds to the fishery in the coming 3 yr (ICES 2010). In the management of most other stocks, environmental information is not routinely used (De Oliveira & Butterworth 2005), which can be partly explained by the difficulty in identifying recruitment–environment correlations that remain robust over time (Myers 1998).

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

MATERIALS AND METHODS

Data on fish abundance

Barents Sea cod, haddock, and capelin

To examine the relationships between indices at different life stages and recruitment of 3 fish stocks in the Barents Sea, we obtained data from several sources (Table 1). For northeast Arctic (NEA) cod *Gadus morhua* and NEA haddock *Melanogrammus aeglefinus*, we considered the following indices:

spawning stock biomass (SSB_t), egg abundance in April to May (E_t), larval abundance in April to July (L_t), Age 0 abundance in August to September ($N0_t$), Age 1 and Age 2 abundances in January to March ($N1_t$ and $N2_t$), and recruitment at Age 3 year (R_t). For the Barents Sea (BS) capelin *Mallotus villosus*, we considered spawning stock biomass (SSB_t), larval abundance in April to July (L_t), Age 0 abundance in August and September ($N0_t$), and recruitment in September to October at Age 1 year (R_t). Sources and manipulation of abundance data for the Barents Sea stocks are described in Appendix 1.

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

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

Gulf of Alaska and eastern Bering Sea walleye pollock

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

Environmental correlates

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

Barents Sea cod, haddock, and capelin

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

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

(3) $TEMP_t$: For a climate index for all 3 stocks, we used the integrated water column temperature at 0 to 200 m depth at the Kola section (70.5 to 72.5° N, 33.5° E) in the south-central Barents Sea. Annual mean winter temperatures for 1921 to 2006 were computed from monthly averages of December

(year t) through March (year $t + 1$) temperatures. Kola temperature correlates positively to recruitment of all 3 species (e.g. Stige et al. 2010).

Gulf of Alaska walleye pollock

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

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

Eastern Bering Sea walleye pollock

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

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

(3) ICE_t: sea ice cover index.

Modeling and statistical analyses

Correlation analysis

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

To explore if and how the correlation between recruitment and early life-stage abundance or environmental indices varied over time, we computed correlations between interannual variability in recruitment and the different indices in 15 yr moving windows and displayed the results graphically. That is, we sliced the time-range into overlapping time-

slots of 15 yr (years 1,...,15; years 2,...,16; ... ; years $(n-14),..., n$), computed the correlation for each time-slot, and plotted the resulting series of correlation coefficients against the mid-year of the time-slots.

Baseline and environmental recruitment models

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

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

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

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

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

In the 'environmental' model, the covariates were selected using an information theoretic approach: we started with a model with all terms included (Eq. 1),

then removed (or added back) terms one by one until we found the model formulation that provided the lowest value of Akaike's information criterion corrected for small sample size (AIC_C; Hurvich & Tsai 1989).

Measuring hindcast strength

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

Measuring forecast strength

To assess the forecast strengths of the baseline and environmental models, we computed 1 yr prior predictions using a sequential approach. We compared 2 approaches to forecast recruitment, one based on juvenile indices ($N0_t$ or $N1_t$) alone and one that considers environmental information. For each year from the 11th year onward for each stock, 2 regression models were constructed based on the data from the years collected up until that point. The first was the 'baseline' model (Eq. 2). The second was the 'envi-

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

Only linear and additive effects of the environmental variables were considered in the statistical models used to forecast or hindcast recruitment. Quantification of nonlinear and nonadditive effects demands long time series and was not feasible with the forecasting approach used here, starting with only 10 yr

of data on which to base the first prediction (see above). Moreover, we wanted to assess to what degree simple, linear approaches might still be helpful, even if the true effects of the environmental factors are likely to be considerably more complex than modeled. The programming environment R was used for all statistical analyses (R Development Core Team 2010). The R code and data used for the analyses are available in an electronic supplement that accompanies the online version of the paper (see Supplement at www.int-res.com/articles/suppl/m480p245_supp/).

RESULTS

Use of egg and larvae surveys vs. juvenile surveys

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

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

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

[a]Missing larval data for years 1980 and 1984 and missing Age 1 and Age 2 data for years 1982, 1987, and 1999. Only the correlations in the second row for GOA walleye pollock are calculated for exactly the same years
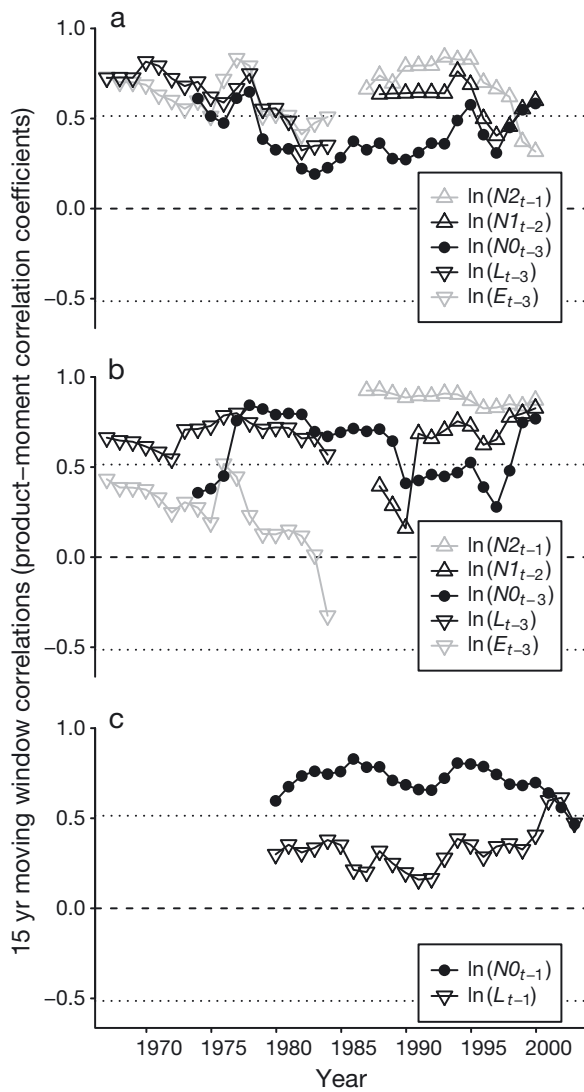
Fig. 1. Temporal change in the correlations between recruitment and early life-stage abundance indices for (a) NEA cod, (b) NEA haddock, and (c) BS capelin. Correlation coefficients (r) were calculated for 15 yr moving windows centered at the *x*-axis values. The symbols indicate with which early life-stage abundance index recruitment $(\ln(R_t))$ was correlated (*E*: eggs, *L*: larvae, *N0*: Age 0, *N1*: Age 1, *N2*: Age 2; see 'Materials and methods' for details). Broken lines: r = 0. Stippled lines: r = ±0.51. The 15 yr correlations larger than ±0.51 are statistically significant (p < 0.05, ignoring autocorrelation)
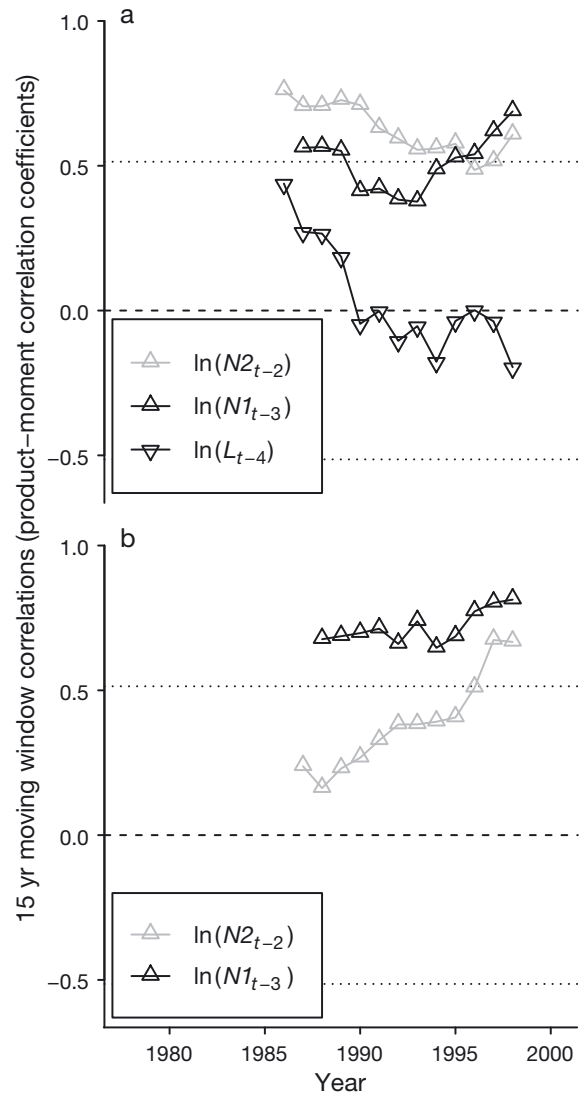

Fig. 2. Temporal change in correlations between walleye pollock recruitment and early life-stage abundance indices in the (a) Gulf of Alaska and (b) eastern Bering Sea. Correlation details as in Fig. 1

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

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

Temporal stability of correlations between pre-recruit indices and recruitment

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

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

Inclusion of environmental correlates in hindcasts and forecasts

The results of applying linear regression models to explain recruitment variation using juvenile indices, with and without the addition of environmental cor-

relates, are presented in Table 3. In all cases, both the R^2 and the AIC_C of the model were substantially improved with the addition of the environmental correlates. With these encouraging results, we then examined forecasts using a sequential approach to compute predictions for 'new' observations not used when fitting the model.

Barents Sea cod, haddock, and capelin

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

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

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

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

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

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

Gulf of Alaska and eastern Bering Sea walleye pollock

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

In the GOA, the addition of environmental variables (specifically, ATF) improved the hindcasts of walleye pollock recruitment (Table 3), although not when tested on the more restricted year range, when no environmental variables were selected (Table 4). Forecasts of GOA walleye pollock recruitment with

and without the inclusion of environmental correlates show that, by accounting for environmental information, our predictions of pollock recruitment were generally closer to the observed values for the last years of the present study. For the earlier years, the forecasts were identical because no environmental covariates were selected in the 'environmental' model (Fig. 6). This finding is supported by the (non-significantly) 12% lower RMSE and the 11% lower MAPE in the model with environmental predictors (Table 4).

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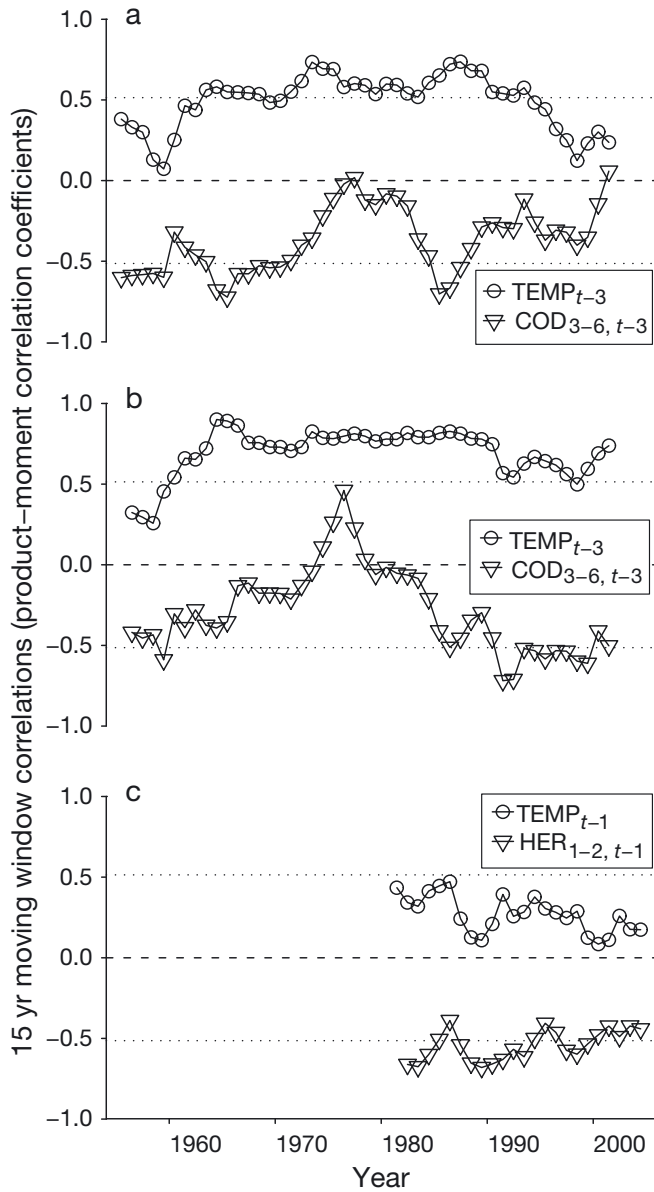
Fig. 3. Temporal change in correlations between recruitment and environmental indices for (a) NEA cod, (b) NEA haddock, and (c) BS capelin. Correlation details as in Fig. 1. TEMP: integrated water column temperature, COD_{3-6}: Age 3 to 6 cod abundance

DISCUSSION

Our results suggest that large and variable measurement errors and nonstationary dynamics are the rule rather than the exception in investigations of fish recruitment. Determining the predictive value of alternative pre-recruit abundance and environmental indices then remains an empirical question, which we have assessed using a comparative approach for 5 fish stocks.
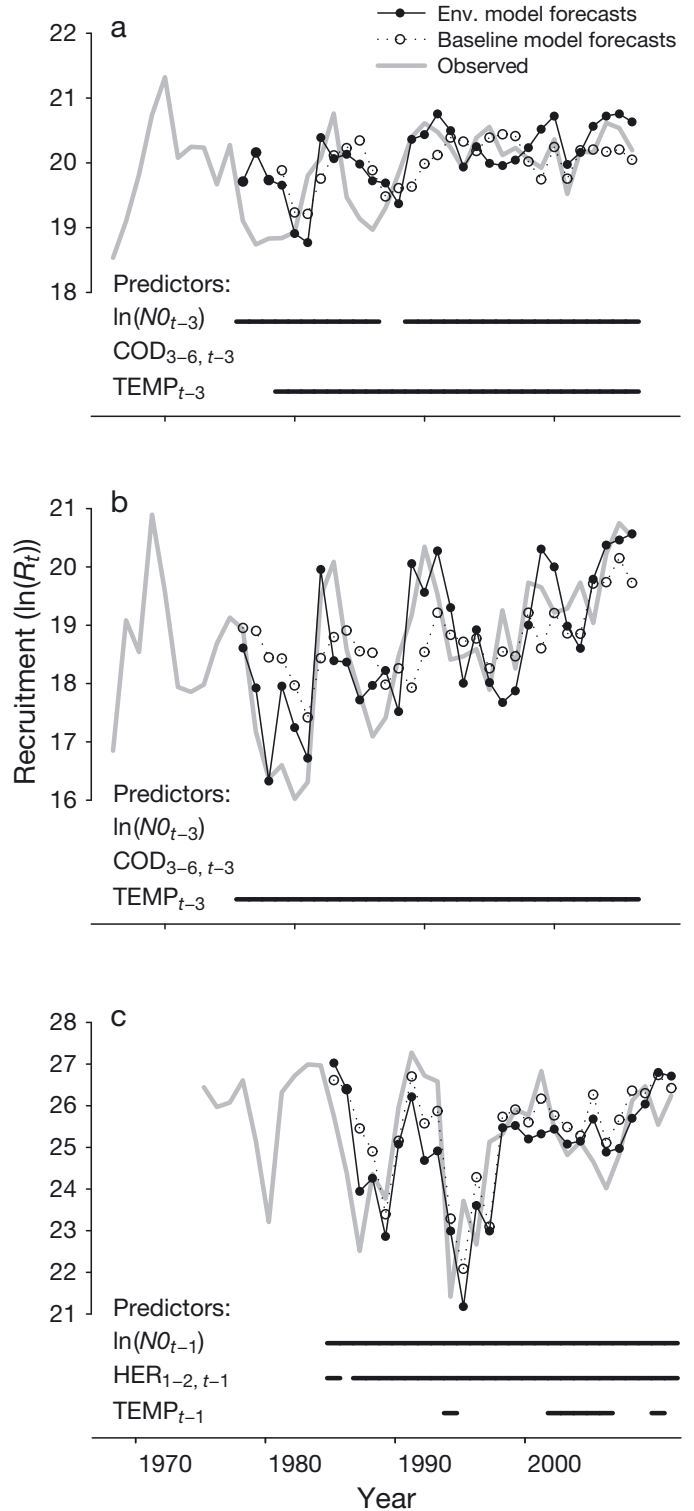
Fig. 4. Observed recruitment time series and recruitment forecast from early life-stage abundance and environmental indices for (a) NEA cod, (b) NEA haddock, and (c) BS capelin. Models and variables as detailed in Tables 3 & 4. The horizontal lines near the lower end of each panel indicate when each variable (Age 0 and environmental) entered the environmental models
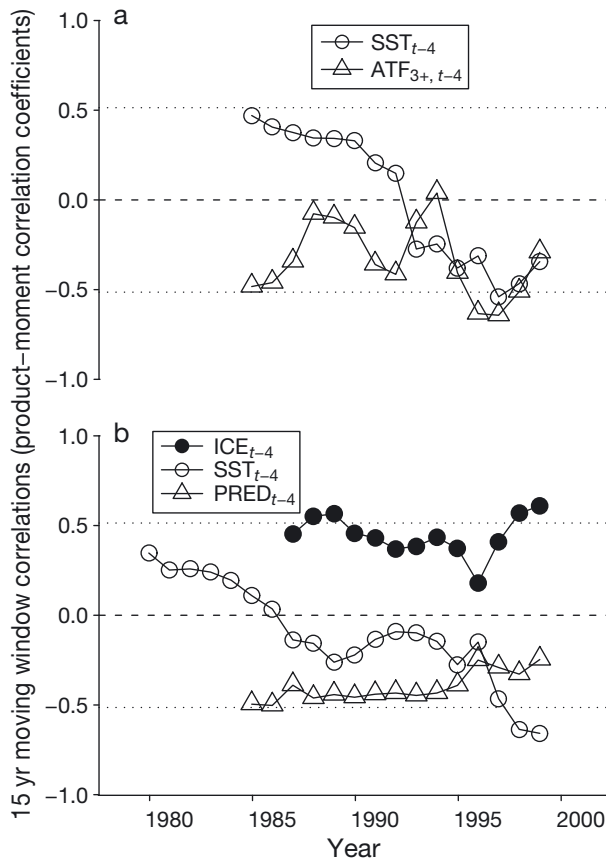
Fig. 5. Temporal change in correlations between walleye pollock recruitment and environmental indices in the (a) Gulf of Alaska and (b) eastern Bering Sea. SST: sea surface temperature, ICE: ice cover index, ATF: Age 3+ arrowtooth flounder abundance, PRED: aggregated predator index. Further details as in Fig. 1

Predictive value of larval compared to juvenile abundance indices

Our findings show that different life-history stages predict recruitment better in different populations. Indices of the abundance of older life-history stages in some cases (BS capelin, GOA walleye pollock), but not all (NEA cod, NEA haddock, and EBS walleye pollock), provided better bases for predicting recruitment than earlier life-history stages such as indices of egg or larval abundance. Low correlation between the recruitment and the larval index for the BS capelin is consistent in particular with variable predation by immature herring on capelin larvae (e.g. Hjermann et al. 2004). This low correlation is probably not only due to noise. In a regression analysis using the same larval index, it was found that 64% of its variability could be explained by capelin stock size and indices of prey (zooplankton) and predators (cod, feeding on the spawners, and herring, feeding
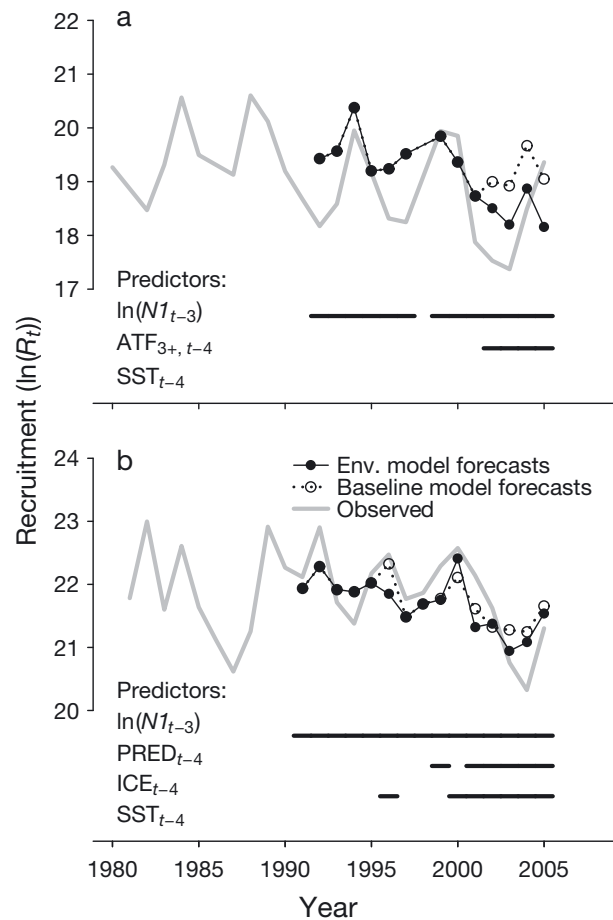

Fig. 6. Observed recruitment time series and recruitment forecast from pollock early life-stage abundance (Age 1) and environmental indices in the (a) Gulf of Alaska and (b) eastern Bering Sea. Models and variables as detailed in Tables 3 & 4. The horizontal lines near the lower end of each panel indicate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

on the larvae) (Stige et al. 2010), suggesting that the index indeed contains a biological signal. Likewise, low correlation between the recruitment and the larval index for the GOA walleye pollock is consistent with high and variable juvenile mortality in this system (Bailey 2000). This finding is in agreement with the results of Bailey et al. (2005), who showed that, over the range of population abundances available at the time, there was no correlation between estimated natality (egg abundance) and recruitment and that the relationship between recruitment and estimates of stage-specific abundances from life tables (some values were interpolated) became stronger for the older predictor variables. The authors found a weakly positive correlation of recruitment with estimated late-stage larval abundance, and the strength of the

relationship increased for Age 0 abundance and Age 1 abundance. These results matched our *a priori* expectations, as the forecast should improve with both more accuracy and precision as the forecast target gets closer in time to the predictor variable (Bradford 1992).

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

Consistency of correlations between juvenile indices and recruitment

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

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

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

The changing correlations should be interpreted with considerable caution because they are likely to reflect both biological and sampling issues, as catchability is likely to have varied over time. For example, the increasing correlation between the recruitment and the Age 2 index for the EBS walleye pollock seems unlikely to have a demographic basis, as the

correlation between the recruitment and the Age 1 index was consistently strong in the same period. For the NEA cod and haddock, the correlations with egg and larval indices showed similar trends as the correlations with the Age 0 indices, supporting the hypothesis of a biological basis—a basis that should be considered for further research.

The value of using environmental correlates to predict recruitment

A fisheries management perspective

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

Fisheries managers may use forecasts of recruitment a few years ahead to set catch limits that buffer some of the effects of the interannual variability in productivity. For fishermen, abrupt changes in catches are clearly undesirable. In the harvest control rule for the NEA cod, for example, the total allowable catch (TAC) is set based on the stock forecasts, taking into account the predicted recruitment of 3 yr olds 3 yr ahead, with the constraint that the TAC should change by no more than 10% from the previous year (ICES 2010). The NEA haddock is managed using a 1 yr forecast with the constraint that the TAC should change by no more than 25% from the previous year (ICES 2010). Under such a scheme, im-

provements in forecast strength by use of environmental information, as shown here for the NEA haddock, can potentially improve the quality of the advice and reduce the uncertainty in setting the TAC. Note that such short-term predictions do not necessarily require predictions of environmental conditions, as the predictions can be based on current environmental conditions within the 3 yr forecast window.

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

Unstable recruitment–environment correlations

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

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

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

Nonlinear and nonadditive environmental effects

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

Simple models of complex dynamics

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

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

NEA cod and NEA haddock

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

BS capelin

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