

Climate-forcing effects on trophically linked groundfish populations: implications for fisheries management

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Abstract: Commercially important groundfish populations in the Bering Sea are connected through the food web as predators and prey. In addition to having different trophic roles, the recruitment of these species varies on interdecadal time scales and may be related to climate forcing. We simulate the effects of fishing mortality on eight trophically linked species under two scenarios of climate regimes using the multispecies virtual population analysis (MSVPA) model and the multispecies forecasting model (MSFOR). Species respond differently to climate change assumptions and fishing mortality depending on their position in the food web. Results suggest that the assumptions regarding climate regime shifts on mean recruitment may produce effects comparable to the ones produced by fishing and predation interactions. Therefore, accurate models for fisheries management would require considering these factors and their potential interactions. Because responses are complex and difficult to predict, it is necessary to take a risk-averse approach in managing the species with the largest potential variation. The incorporation of climate regime shifts in fisheries management will require a better understanding of recruitment during a particular regime and a reliable way to identify regime shifts based on biological and (or) physical indices.

Résumé : Les populations de poissons de fond d'importance commerciale de la mer de Béring sont reliées entre elles dans le réseau alimentaire en tant que prédateurs ou proies. En plus de ces rôles trophiques différents, le recrutement de ces espèces varie sur une échelle de décennies, ce qui peut être dû à un forçage climatique. Nous avons simulé les effets de la mortalité due à la pêche chez huit espèces reliées par le réseau trophique sous deux scénarios de régimes climatiques à l'aide du modèle d'analyse de populations virtuelles multisécifiques (MSVPA) et du modèle de prédiction multisécifique (MSFOR). Les espèces réagissent différemment aux présuppositions de changement climatique et à la mortalité due à la pêche d'après leur position dans le réseau alimentaire. Nos résultats indiquent que nos présuppositions concernant les changements de régime climatique sur le recrutement peuvent avoir des effets comparables à ceux produits par l'interaction de la pêche et de la prédation. En conséquence, des modèles précis de gestion de la pêche nécessitent l'inclusion de ces facteurs et de leurs interactions potentielles. Parce que les réactions sont complexes et difficiles à prédire, il faut adopter une approche qui minimise les risques dans la gestion des espèces qui ont la variation potentielle la plus élevée. L'incorporation des changements de régime climatique dans la gestion des pêches requerra une meilleure compréhension du recrutement au cours d'un régime particulier et une méthode fiable pour identifier les changements de régime d'après des indices biologiques et/ou physiques.

[Traduit par la Rédaction]

Introduction

The Bering Sea is rich in biological resources. Currently, about 25 fish species are commercially exploited (NRC 1996). The total recent average yield of groundfish from the eastern Bering Sea and the Aleutian Islands was 1 775 600 metric tons (t), representing almost 25% of the total U.S. fish harvest (NMFS 1999).

There is concern about the changes observed in the structure of the Bering Sea ecosystem in the last few decades, including population declines for marine mammals, seabirds,

Pacific herring (*Clupea pallasii*), red king crab (*Paralithodes camtschaticus*), and forage fishes. In contrast, populations of walleye pollock (*Theragra chalcogramma*) and some flatfish species have increased (NRC 1996; Livingston et al. 1999). These shifts have likely been caused by a combination of natural environmental fluctuations and human activities (NRC 1996).

Large-scale exploitation of whales occurred during the 1950s to 1970s. During that period, foreign fisheries also reduced the populations of shelf flatfishes and slope rockfishes. The decline of top predator populations probably increased prey availability

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and may have allowed walleye pollock to become the dominant species (NRC 1996).

Climate variability in the North Pacific is important and can affect the organization of the ecosystem by influencing recruitment, migration, and distribution and the survival of young individuals (NRC 1996). The Bering Sea is under the influence of two known sources of climate variability: ENSO (El Niño – Southern Oscillation) and PDO (Pacific Decadal Oscillation). ENSO is a disruption of the ocean–atmosphere system in the Pacific that produces interannual changes in tropical sea level pressure between the eastern and western hemispheres. El Niño conditions, which occur at intervals of 2–7 years, are characterized by low sea level pressure and warm sea surface temperatures (SST) in the southeastern tropical Pacific. These El Niño events in the tropics have been linked to warming effects in the North Pacific and in the Bering Sea in particular (Niebauer 1985). PDO is described as a blend of two independent modes with distinct spatial and temporal characteristics of North Pacific SST variability (S. Hare, International Pacific Halibut Commission, Seattle, Wash., personal communication). PDO is also described as a long-lived ENSO-like pattern of Pacific climate variability (Mantua et al. 1997) that is associated with interdecadal climate variability in the North Pacific. In contrast to ENSO, PDO has shown remarkable persistence and has local influence. It has been suggested that in the last century just two full PDO cycles have occurred. Cool PDO regimes dominated from 1890 to 1924 and again from 1947 to 1976. Warm PDO occurred from 1925 to 1946 and from 1977 through at least the mid-1990s (Mantua and Hare 2002). Sign changes corresponding to 1925, 1947, and 1977 have been labeled regime shifts.

Some authors suggested the possibility of a new regime shift in 1989 (Overland et al. 1999; Hare and Mantua 2000). However, other authors suggest that the conditions of the 1977 regime shift persisted until 1997 (Mantua et al. 1997; Ingraham et al. 1998).

Because of the observed fluctuations in the populations of some species and their potential consequences for their management, it is important to assess the influence of predation, climate regime shifts, fishing, and their interactions, on species dynamics. The International Pacific Halibut Commission developed a single-species model incorporating regime shifts in the recruitment process (Clark et al. 1999). However, this analysis ignores species' interactions. Other authors have suggested adopting a broader view that would include the incorporation of predation interactions in fish population dynamics models (Livingston and Methot 1998; Livingston et al. 1999). Livingston and Jurado-Molina (2000) parameterized a multispecies virtual population analysis (MSVPA) model for the eastern Bering Sea during the period 1975–1996. Their results suggested that cannibalism is the main source of predation mortality $M2$ for age-0 walleye pollock and that arrowtooth flounder (*Atheresthes stomias*) is an important predator of age-1 walleye pollock. The MSVPA model was updated to 1998 data and used a deterministic multispecies forecasting model (MSFOR) to assess the potential changes in the dynamics of an eight-species system resulting from a more even fishing regime proposed for the Bering Sea (Jurado-Molina and Livingston 2002). However, this analysis assumed constant recruitment and did not consider the possible effects of climate variability on recruit-

ment. The current single-species assessment models for Bering Sea ground fisheries assumed that a regime shift occurred in 1977 and thus use recruitment from 1977 to present in the forecast of recruitment. Given the hypothesized new regime shift in 1989, it is important to examine our recruitment assumptions in both a single-species and multispecies context. Gislason (1991) examined the effects of different levels of mean recruitment on North Sea stocks in a multispecies context. We now extend that work and place it in a north Pacific context by examining mean recruitment levels associated with different regime shift periods and comparing single-species and multispecies forecasts based on those recruitment levels.

In the present analysis, we applied single-species and multispecies simulation models to explore the consequences of four levels of fishing mortality and two assumptions about climate regime on the population dynamics of the assemblage of species selected from the Bering Sea. The effects of climate regime shifts were incorporated into the model by assuming that climate regimes influence the mean and the standard deviation of recruitment. The spawning stock biomass (SSB) of six groundfish species was used as indicator of performance. Monte Carlo simulations were used to estimate the frequency distribution of the SSB of the species in the medium term and to track the temporal trend of the median of SSB.

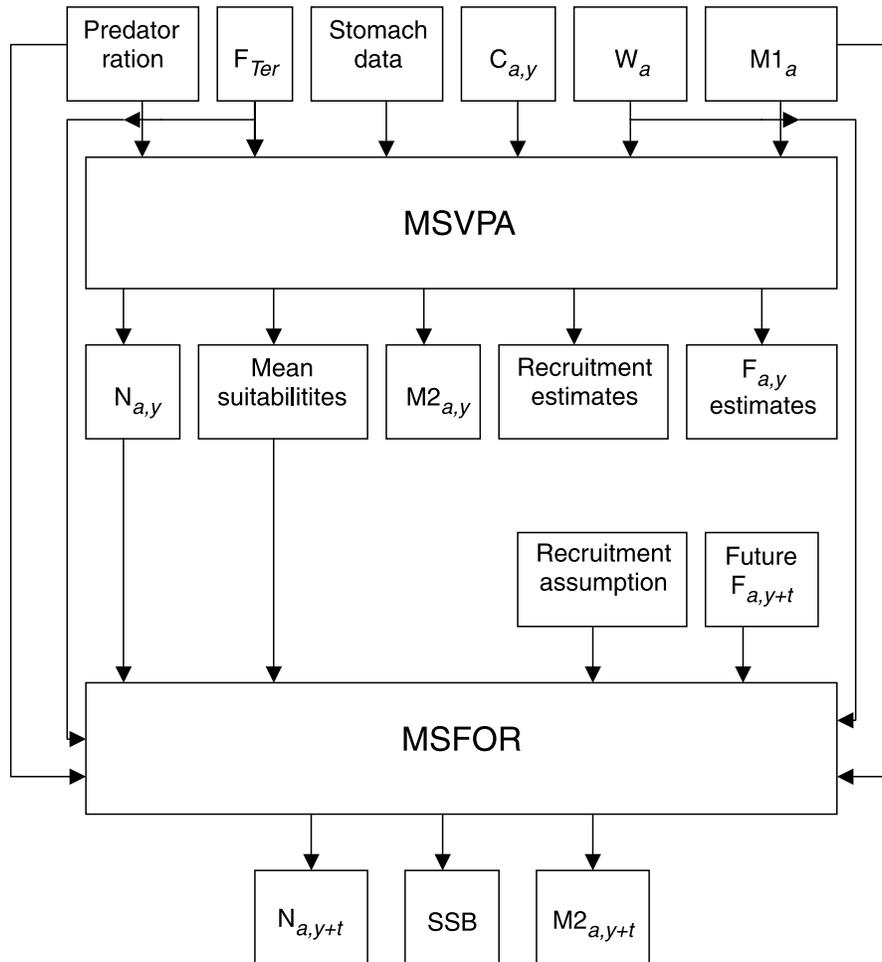
Methods

The assemblage of eight-species from a previous study (Livingston and Jurado-Molina 2000) was used. Walleye pollock, Pacific cod (*Gadus macrocephalus*), Greenland turbot (*Reinhardtius hippoglossoides*), and yellowfin sole (*Pleuronectes asper*) played the role of both predator and prey. Rock sole (*Lepidopsetta bilineata*) and Pacific herring were only considered prey. Arrowtooth flounder and northern fur seal (*Callorhinus ursinus*) were considered external predators. The analysis of the effects of environmental forcing on the dynamics of the groundfish species from the Bering Sea was carried out with stochastic versions of the MSFOR and single-species forecasting (SSFOR) models together with their respective retrospective analysis (MSVPA and VPA).

The multispecies simulation approach uses MSVPA and MSFOR models. MSVPA is an extension of the VPA model (Gulland 1965) that estimates fishing mortality, recruitment, stock size, and predation mortality based on catch-at-age, predator ration, and predator diet information (Fig. 1). In addition to the assumptions and equations from VPA, MSVPA assumes that the natural mortality M is separated in two components, the residual mortality $M1$ and the predation mortality $M2$. $M1$ involves several causes of mortality such as aging, starvation, and diseases and is assumed to be constant for each age class of each species. MSVPA assumes no predation on age-0 organisms in the first two quarters of their first year of life by MSVPA predators. The $M2$ of the prey p of age a is estimated iteratively within the MSVPA with the following equation:

$$(1) \quad M2_{p,a} = \sum_i \sum_j \frac{\bar{N}_{i,j} R_{i,j} S_{p,a,i,j}}{\sum_{p,a} \bar{N}_{p,a} W_{p,a} S_{p,a,i,j}}$$

Fig. 1. Inputs and outputs of the multispecies virtual population analysis (MSVPA) and the multispecies forecasting model (MSFOR); F_{Ter} , terminal fishing mortality; $C_{a,y}$, catch at age in year y ; $M1_a$, residual natural mortality of age- a fish; $N_{a,y}$, population estimates of age- a fish in year y ; $M2_{a,y}$, predation mortality estimates of age- a fish in year y ; $F_{a,y}$, fishing mortality estimates of age- a fish in year y ; t , period of time used in the forecast simulation; SSB, simulated spawning biomass ratio.



$\bar{N}_{i,j}$ represents the average stock size of the predator i of age j . $R_{i,j}$ is the annual ration of the predator and $S_{p,a,i,j}$ is the suitability coefficient for each combination of predator-prey. The suitability coefficient reflects the diet composition of the predators relative to the available food (Sparre 1991). The denominator of eq. 1 represents the total suitable biomass available to the predator. In the denominator, $\bar{N}_{p,a}$ represents the average stock size of the prey p of age a and $W_{p,a}$ represents its weight-at-age. The suitabilities are estimated iteratively in the MSVPA model with the following equation:

$$(2) \quad S_{p,a,i,j} = \frac{U_{p,a,i,j} / (\bar{N}_{p,a} W_{p,a})}{\sum_p \sum_a U_{p,a,i,j} / (\bar{N}_{p,a} W_{p,a})}$$

where $U_{p,a,i,j}$ represents the food composition that is assumed to be equal to the observed stomach content. In the estimation of $M2$, MSVPA uses a weighted average suitability coefficient with the sample size as weight. The number of suitabilities is numerous because there is a value for each age class – predator – prey combination.

The MSFOR is the predictive counterpart of the MSVPA and also uses eq. 1 to estimate $M2$. The average suitability coefficients and the terminal stock sizes are transferred from the MSVPA to MSFOR to carry out the simulation of the future dynamics of the species (Gislason 1991). A schematic of the MSVPA and MSFOR models and associated inputs and outputs are shown in Fig. 1. A more detailed description of the MSVPA and the MSFOR models is found in Sparre (1991) and Magnusson (1995).

The single-species simulation uses the VPA (Gulland 1965) and the SSFOR models. The SSFOR requires an initial run of the VPA providing estimates used as initial inputs to the model. This simulation uses the majority of the inputs and outputs as the multispecies case. However, it assumes constant M and no stomach data is used as input in the VPA.

The single-species and multispecies simulations use a considerable amount of data (Fig. 1). The common input data for the VPA and MSVPA models included catch-at-age, percent of maturity-at-age, and weight-at-age. These data were obtained from the 1998 stock assessments carried out by the National Marine Fisheries Service (NMFS) scientists (NPFMC 1998) with the exception of Pacific herring for which stock assessments were carried out by the Alaska De-

partment of Fish and Game (ADF&G; Fred West, ADF&G, Anchorage, Alaska, personal communication). The terminal fishing mortalities were estimated in a previous work (Livingston and Jurado-Molina 2000). These parameters were chosen to minimize the differences between our population estimates and the ones derived from the stock assessment models used by NMFS and ADF&G scientists during 1979–1998. In particular, MSVPA input included the predator stomach content data (over 40 000 stomach samples) and the residual mortalities. The estimation of $M1$ required an initial run of the MSVPA with $M1 = M$ (M used in the VPA). With this approach, we estimated the average $M2$ of the adult age classes over the model time series. This average was subtracted from the single-species M to get the residual mortality used in the multispecies models. The MSVPA and the VPA models covered the period 1979–1998.

The MSFOR and SSFOR input included the population estimates of 1998, weight-at-age, maturity-at-age, and four levels ($F_{30\%}$, $F_{40\%}$, $F_{50\%}$, and no fishing) of fishing mortality for the majority of the species. The first three fishing mortalities reduce the level of SSB per recruit to the corresponding percentage of the pristine level and are used as harvest guidelines for the North Pacific fisheries. These fishing mortalities were estimated by solving the following equation in the single-species and multispecies cases:

$$(3) \quad \text{SPR} = \frac{\sum_a W_a \% \phi_a e^{-(F_{\text{full}} s_a + M)}}{\sum_a W_a \% \phi_a e^{-M}}$$

where SPR is the remaining percentage of the pristine level of SSB per recruit (30, 40, and 50%). M represents the natural mortality, W_a the individual weight-at-age, $\% \phi_a$ the percent maturity-at-age, F_{full} the full selection level of fishing mortality, and s_a the selectivity-at-age. Given estimates of M and the desired remaining percentage of pristine level of SSB, the F_{full} parameter was estimated by solving eq. 3 iteratively. In the multispecies case, we used $M = M1 + M2$ with $M2$ as the average from the predation mortality estimates from the MSVPA model. Pacific herring is managed with a 20% harvest rate policy. To mimic this policy, we used the F_{ref} that is defined as the average of the fishing mortality estimates from the last 4 years. This approach allowed us to contrast the effects of low, medium, and high fishing mortality.

A stochastic component was introduced into MSFOR in its treatment of recruitment. Groundfish food habit data in the eastern Bering Sea indicates that most predation occurs after 6 months of age (Livingston 1991); therefore, the stochastic MSFOR assumes recruitment of age-0 fish taking place in the third quarter of the year after fish complete the larval phase. However, predation on age-0 groundfish by invertebrates and other fish predators during the first 6 months of life might also be an important source of mortality but is not well sampled. Although recruitment variation during this period might also be influenced by these unmodeled predation effects, we assume here that climate variability is the dominant factor influencing recruitment in the first half year of life. Recruitment is assumed lognormally distributed with a particular mean and variance. The potential effect of cli-

mate regime shifts in the dynamics of the species was simulated through their effects on recruitment. Climate was introduced into the models by assuming that there is a mean level of recruitment and variability associated with each climate regime. Two possible scenarios were presumed. In the first, we assumed that the 1977 climate regime continues in the forecast beyond 1998. In the second scenario, a new climate regime shift in 1989 was assumed to continue in the forecast beyond 1998.

To define the recruitment means and variances associated with each regime shift, we used analysis of variance (ANOVA) to test the hypothesis of different mean recruitment for each regime shift. Recruitment data from MSVPA and single-species VPA (SSVPA) were used in separate analyses. Two periods of time were used to test the hypothesis: the first from 1979 to 1988 and the second from 1989 to 1998. We also used the F test to assess the homogeneity of the recruitment variance in the two time periods. In the case in which the means were not significantly different but the variances were significantly different, we simulated both regimes using the same mean recruitment but different standard deviations for the corresponding time period.

The forecast simulation models (MSFOR and SSFOR) were carried out using Monte Carlo simulations of the medium- and long-term dynamics of the populations of the species. Each forecasting model run included 5000 replicates. In each replicate, new values of recruitment for each year were drawn from the lognormal distributions. We used a correction factor for bias in the simulated recruitment. To calculate this correction factor, we did an initial forecast simulation of the lognormal recruitment. The factor was calculated as the mean of the estimates from MSVPA divided by the mean of the simulated recruitment. This correction factor ensures that the mean of the recruitment estimates from MSVPA equals the mean of the simulated recruitment. We used two sets of correction factors, one for each regime shift. The spawning stock biomass ratio (SSB ratio) in the medium term (year 2015) was chosen as an indicator of change in the system relative to initial conditions and was calculated with the following equation:

$$(4) \quad \text{SSB ratio} = \frac{\text{SSB}(2015)}{\text{SSB}(1998)}$$

The outputs of the forecasting model were the frequency distribution and cumulative frequency distribution of the estimates of the SSB ratio in 2015. In further runs we modified the model to simulate the temporal trend of the median of the SSB ratio. The SSB ratio for each year in each iteration was saved. This calculation is demanding; therefore, we reduced iterations to 300 in each simulation.

Results

MSVPA is not a statistical catch-at-age model and therefore does not use statistical assumptions on observation or process error structure. Thus to validate partially its results, a comparison of the age-3+ fish biomass estimates from MSVPA and the estimates from the statistical assessment models used by fisheries scientists from the Alaska Fisheries Science Center (NPFMC 1998) and the ADF&G (Pacific herring) was made. The estimates of age-3+ biomass ob-

tained with the two methods were similar, although some differences were seen for Pacific herring. The MSVPA was not able to replicate the trend observed in the estimates of the ADF&G stock assessment during the mid-1980s estimating greater SSB for the years 1986 and 1987. However, the age-3+ fish biomass trajectories for the rest of the species were similar between the models (Jurado-Molina and Livingston 2002).

In the multispecies case, we found significant differences between the mean recruitment from the two periods of time for Pacific cod, rock sole, and Pacific herring (Table 1 and Fig. 2). The mean and standard deviation of Greenland turbot were not significantly different. For walleye pollock and yellowfin sole, there was no significant difference between the recruitment means; however, their variances were significantly different (Table 1). Therefore, we used the same average for both regime shifts but different standard deviations. In this case, the standard deviation associated with the 1977 regime shift was calculated using data from 1979 to 1988. The other standard deviation was estimated with data from 1989 to 1998. The ANOVA for the single-species recruitment estimates for 1979 to 1998 did not find any significant differences for the mean recruitment for each regime shift. As Livingston and Methot (1998) pointed out, the climate links to recruitment may not be observable until the historical pattern of juvenile predation mortality is taken into account, which requires a multispecies model. Therefore, to keep consistency, we assigned the same relative changes in the mean and standard deviation of the single-species recruitment for each regime as they were found in the multispecies case (Table 1).

In the following sections, we describe the effects on the SSB ratio caused by fishing mortality and changes in mean recruitment levels in different climate regime shifts in the forecast simulation of the species dynamics.

Fishing mortality

As usual, in the SSFOR simulation, the SSB ratio of all species increased when fishing mortality decreased, corresponding the smallest mean of the SSB ratio to the $F_{30\%}$ level of fishing mortality in each of the two possible scenarios (Table 2). The standard deviations of the SSB ratio followed the same trend.

The medium-term forecast estimates of the means of the SSB ratio of walleye pollock and Pacific cod (cannibalistic species) estimated with MSFOR were larger than the corresponding means estimated with the SSFOR model (Tables 2 and 3). In particular, the means of walleye pollock estimated with MSFOR were considerably larger than the ones estimated in the single-species simulation. For rock sole, the result was the opposite, with larger SSB ratio estimates corresponding to the single-species simulation (Tables 2 and 3).

In the multispecies simulations, most species followed the pattern described for the single-species simulation with the largest means associated with the smaller fishing mortalities. The exception was Pacific herring: in contrast to the single-species results, in the simulation of the 1977 regime shift, the mean of the SSB ratio corresponding to $F_{30\%}$ was bigger than the one corresponding to the fishing levels $F_{40\%}$ and $F_{50\%}$. A similar situation was found in the simulation of the 1989 regime shift (Table 3). The standard deviations of the

Table 1. Results from the analysis of variance, ANOVA ($H_0: \mu_{77-88} = \mu_{89-98}$), for the recruitment of the species of the eastern Bering Sea estimated with the multispecies virtual population analysis (MSVPA) during the periods of time 1979–1988 and 1979–1998.

Species	ANOVA <i>p</i> value	<i>F</i> test <i>p</i> value
Walleye pollock	0.19	0.04
Pacific cod	0.00	—
Greenland turbot	0.11	0.16
Yellowfin sole	0.25	0.00
Rock sole	0.01	—
Pacific herring	0.00	—

Note: Last column shows the *p* values from the *F* test to test the homogeneity of the variances associated with each regime shift.

SSB ratio increased as the fishing mortality decreased, with some exceptions. In the 1989 regime shift simulation, the standard deviations of walleye pollock SSB ratio corresponding to $F_{40\%}$ and $F_{50\%}$ were larger than the standard deviation of the no-fishing case. A decreasing trend of the standard deviation was observed in both regime shifts for Pacific herring.

Climate regime shifts

In the single-species simulations, the effect produced by the change of climate regime assumption on the distributions of the SSB ratio of walleye pollock was minimal. Changes related to climate regime shift were seen for Pacific cod, yellowfin sole, rock sole, and Pacific herring. For the first three species, the change of regime shift assumption produced a lateral displacement to the left of the 1989 cumulative distribution for all levels of fishing mortality in such a way that the mean and the variability of the spawning biomass ratio in 2015 decreased with respect to the results from the 1977 regime shift simulation (Fig. 3 and Table 2). Because of this displacement, two distributions of the Pacific cod SSB ratio originating from different conditions produced similar means and standard deviations (Fig. 3 and Table 2). In the case of rock sole, the displacement produced the overlap of four distributions (Fig. 4). The distribution of the $F_{30\%}$ level of fishing mortality in the 1977 regime shift is similar to the distribution from $F_{40\%}$ in the 1989 regime shift. Similarly, the $F_{40\%}$ – 1977 regime shift distribution overlapped the $F_{50\%}$ – 1989 regime shift distribution (Fig. 4). A smaller displacement was observed for yellowfin sole but no overlap of distributions was observed. In particular, for Pacific herring, the reference fishing mortality F_{ref} was used except in the no-fishing scenario. Therefore, the SSB ratio distribution of Pacific herring was the same, independent of the fishing mortality level used for the rest of the species in the assemblage. The change of climate regime shift assumption produced the same lateral displacement but also a change in the shape of the distribution, but no overlap was observed (Table 2).

The results from the multispecies simulations were more complex. A lateral displacement of the distribution of the 1989 regime shift was found in the simulations of Pacific cod. Because of this displacement, the distribution corresponding to a lower level of fishing mortality ($F_{50\%}$) in the 1989 regime shift was similar to the distribution estimated

Fig. 2. Log-transformed recruitment used in the multispecies forecasting simulations of the dynamics of the species from the eastern Bering Sea: plk, walleye pollock (*Theragra chalcogramma*); cod, Pacific cod (*Gadus macrocephalus*); gtb, Greenland turbot (*Reinhardtius hippoglossoides*); yfs, yellowfin sole (*Pleuronectes asper*); sol, rock sole (*Lepidopsetta bilineata*); her, Pacific herring (*Clupea pallasii*); 77, 1977 regime shift; 89, 1989 regime shift.

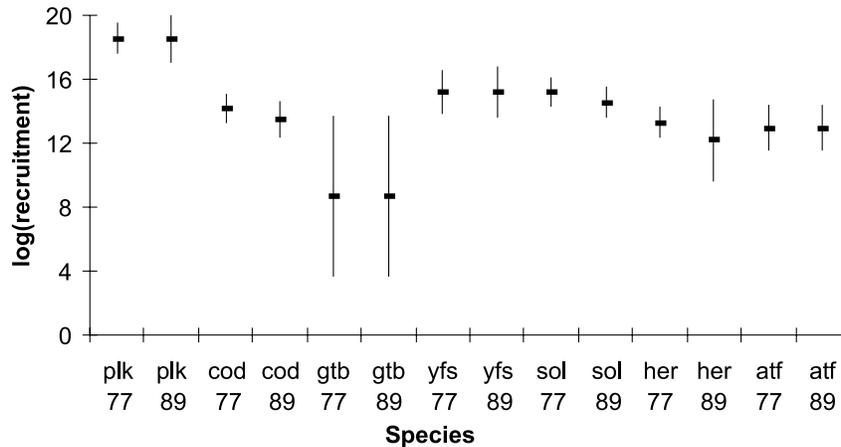


Table 2. Mean and standard deviation of the spawning stock biomass ratio in 2015 estimated with single-species forecasting using four levels of fishing mortality and two assumptions of climate regime shift.

Species	1977 regime shift				1989 regime shift			
	$F_{30\%}$	$F_{40\%}$	$F_{50\%}$	$F = 0$	$F_{30\%}$	$F_{40\%}$	$F_{50\%}$	$F = 0$
PLK	1.1±0.12	1.3±0.17	1.6±0.21	2.9±0.45	1.1±0.13	1.3±0.17	1.6±0.21	2.9±0.45
COD	0.6±0.01	0.6±0.02	0.8±0.02	1.5±0.06	0.4±0.01	0.6±0.01	0.7±0.02	1.3±0.05
GTB	0.3±0.30	0.4±0.25	0.5±0.50	0.8±0.68	0.3±0.27	0.4±0.34	0.4±0.46	0.9±0.70
YFS	1.4±0.05	1.9±0.07	2.3±0.09	4.1±0.19	1.3±0.09	1.7±0.13	2.1±0.16	3.4±0.34
SOL	0.6±0.01	0.8±0.01	1.0±0.02	1.7±0.04	0.5±0.01	0.6±0.01	0.8±0.01	1.5±0.03
HER	1.6±0.11	1.6±0.11	1.6±0.11	2.1±0.14	1.3±0.72	1.3±0.67	1.3±0.63	1.7±0.88

Note: PLK, walleye pollock; COD, Pacific cod; GTB, Greenland turbot; YFS, yellowfin sole; SOL, rock sole; HER, Pacific herring.

Table 3. Mean and standard deviation of the spawning stock biomass ratio in 2015 estimated with the multispecies forecasting using four levels of fishing mortality and two assumptions on climate regime shift.

Species	1977 regime shift				1989 regime shift			
	$F_{30\%}$	$F_{40\%}$	$F_{50\%}$	$F = 0$	$F_{30\%}$	$F_{40\%}$	$F_{50\%}$	$F = 0$
PLK	4.1±1.80	4.8±2.32	5.4±3.00	5.5±3.20	4.7±6.00	5.5±7.58	6.1±8.84	6.6±7.49
COD	1.0±0.04	1.2±0.05	1.5±0.07	2.5±0.11	0.6±0.03	0.8±0.04	0.9±0.04	1.6±0.09
GTB	0.3±0.19	0.4±0.42	0.5±0.44	0.8±0.57	0.3±0.35	0.4±0.34	0.5±0.49	0.8±0.62
YFS	1.4±0.05	1.9±0.07	2.2±0.09	3.5±0.12	1.6±0.12	2.1±0.17	2.5±0.20	4.0±0.29
SOL	0.4±0.01	0.5±0.01	0.6±0.01	1.0±0.02	0.3±0.00	0.3±0.00	0.4±0.00	0.7±0.01
HER	2.4±0.23	2.3±0.21	2.2±0.20	2.5±0.21	1.1±0.55	1.1±0.52	1.0±0.46	1.2±0.49

Note: PLK, walleye pollock; COD, Pacific cod; GTB, Greenland turbot; YFS, yellowfin sole; SOL, rock sole; HER, Pacific herring.

with a higher fishing mortality ($F_{30\%}$) in the 1977 regime shift (Table 3). The simulation of the 1989 regime shift for yellowfin sole produced a small displacement of the distribution that increased the mean and the standard deviation of the SSB ratio compared with the results from the 1977 regime shift simulation. However, no overlap of distributions was observed (Table 3).

In the case of Pacific herring, the change of assumption on climate regime shift caused the same displacement mentioned in previous cases, reducing the mean but increasing the standard deviation (Table 3). No overlapping of distributions was observed. However, in contrast to the single-species results in which the means were almost constant (Table 2),

we observed a slight decrease of the mean of the SSB ratio when the fishing mortality decreased (Table 3). For rock sole, because of the displacement, the distributions corresponding to $F_{30\%}$ – 1977 regime shift and $F_{50\%}$ – 1989 regime shift had similar means (Table 3). The results of walleye pollock were also complex. In contrast to the single-species simulation in which no effect was observed, the assumption of a new regime shift in 1989 produced a change in the shape of the frequency distribution of the SSB ratio producing an increase in the mean and standard deviation of the indicator (Table 3 and Fig. 5). This change of shape in the distributions of SSB ratio caused some SSB ratio distributions to partially overlap and intersect in such a way that

Fig. 3. Cumulative distributions of the spawning stock biomass ratio of Pacific cod (*Gadus macrocephalus*) in 2015 estimated with two levels of fishing mortality (no fishing and $F_{40\%}$) and two assumptions on climate regime shifts in the single-species forecast: —, $F_{50\%}$ 1977 regime shift; - - -, $F_{50\%}$ 1989 regime shift; —, $F_{40\%}$ 1977 regime shift; - - -, $F_{40\%}$ 1989 regime shift.

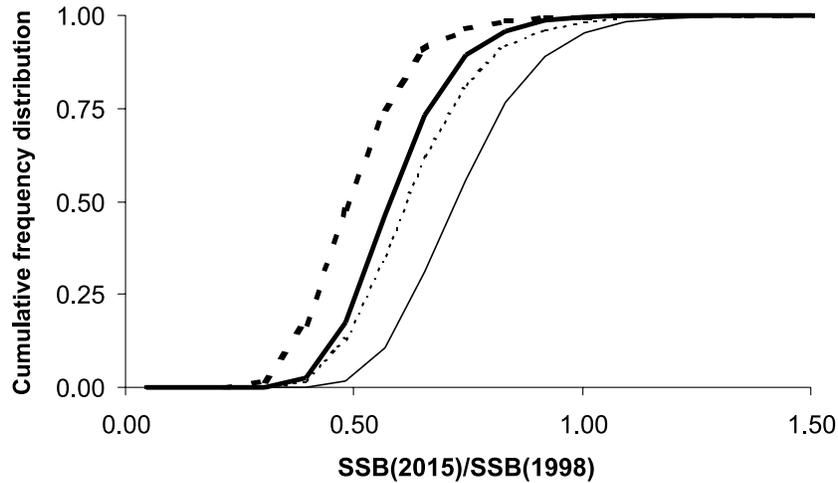
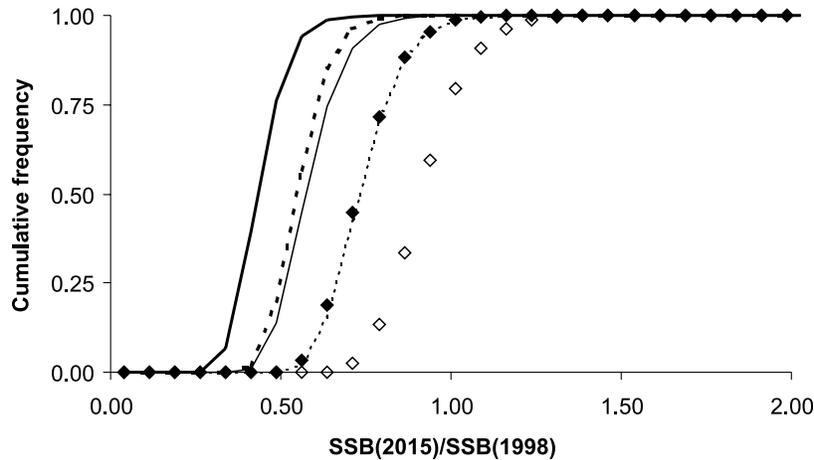


Fig. 4. Cumulative frequencies of spawning stock biomass ratio of rock sole (*Lepidopsetta bilineata*) in 2015 from the single-species forecast simulation assuming two climate regime shifts (1977 and 1989) and three levels of fishing mortality ($F_{30\%}$, $F_{40\%}$, and $F_{50\%}$): \diamond , $F_{50\%}$ 1977 regime shift; \blacklozenge , $F_{50\%}$ 1989 regime shift; - - -, $F_{40\%}$ 1977 regime shift; —, $F_{40\%}$ 1989 regime shift; - - -, $F_{30\%}$ 1977 regime shift; —, $F_{30\%}$ 1989 regime shift.



the means associated with two different combinations of fishing mortality and climate regime shifts were similar. For example, the means of the distributions associated with $F_{30\%}$ in the 1989 regime shift and the distribution from the $F_{40\%}$ level in the 1977 regime shift were comparable. Similarly, the means of the distributions from no fishing in the 1977 regime shift and the distribution from $F_{40\%}$ in the 1989 regime shift were close (Fig. 5).

The temporal trends of the SSB ratio of walleye pollock confirmed the results described previously. The temporal trend showed an increasing SSB together with an oscillating trend of the median of the SSB ratio in the medium term for all levels of fishing mortality (Fig. 6). Different levels of fishing mortality produced different amplitudes and frequencies of the temporal trend of the median of the SSB ratio, corresponding the biggest amplitude and the lowest frequency to the no-fishing case in both regime shift scenarios. The differences in amplitude and frequency produced an intersec-

tion of the trajectories of the medians in the medium term in both scenarios (1977 and 1989 regime shifts; Fig. 6). After stock levels reached equilibrium, the order of the medians is what would be typically expected, with the largest median corresponding to the no-fishing case and the smallest corresponding to the $F_{30\%}$ fishing level (in stochastic simulation models, “reaching equilibrium” means a stable frequency distribution of the SSB ratio). To explain the possible origin of the strong oscillations of the median of the SSB ratio in the simulations, we show the temporal trend of age-0 to age-2 and age-3+ biomass of walleye pollock (Fig. 7).

The rest of the species reached equilibrium faster; therefore, the trajectories of the median of the SSB ratio did not overlap in the medium- and long-term projections. The results of the simulations with both regime shift assumptions suggest an increasing trend for Pacific cod and yellowfin sole. For Greenland turbot and rock sole, the median of the SSB ratio corresponding to all levels of fishing mortality

Fig. 5. Cumulative frequency distributions of spawning stock biomass ratio of walleye pollock (*Theragra chalcogramma*) corresponding to no fishing and $F_{40\%}$ and two assumptions on climate regime shifts estimated with the multispecies forecast simulation: —, $F_{40\%}$ 1977 regime shift; - - -, $F_{40\%}$ 1989 regime shift; —, $F = 0$ 1977 regime shift; - - -, $F = 0$ 1989 regime shift.

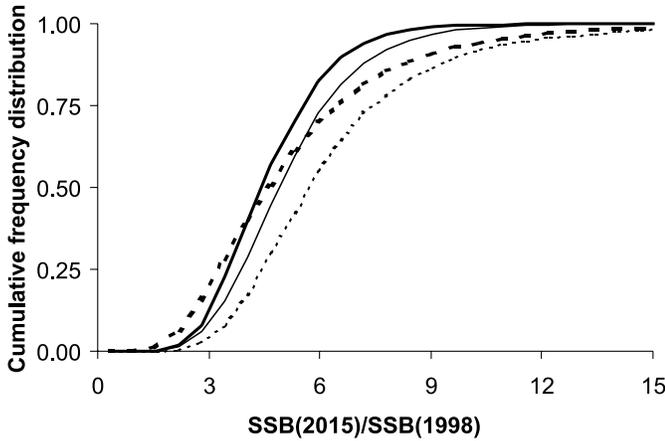
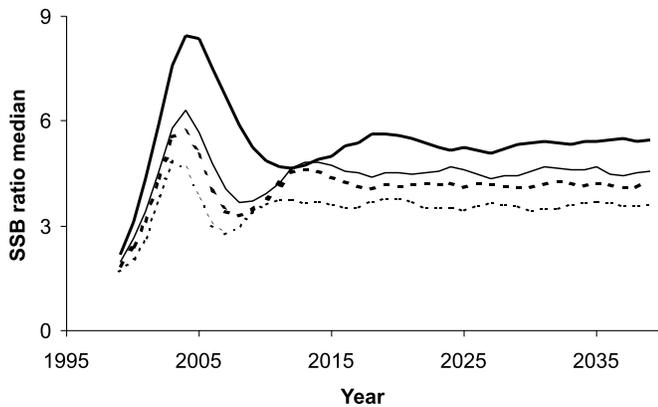


Fig. 6. Temporal trend of the median of the spawning stock biomass ratio of walleye pollock (*Theragra chalcogramma*) simulated with four levels of fishing mortality ($F_{30\%}$, $F_{40\%}$, $F_{50\%}$, and no fishing) during the 1977 regime shift: —, $F_{50\%}$; - - -, $F_{40\%}$; - · - ·, $F_{30\%}$; —, $F = 0$.

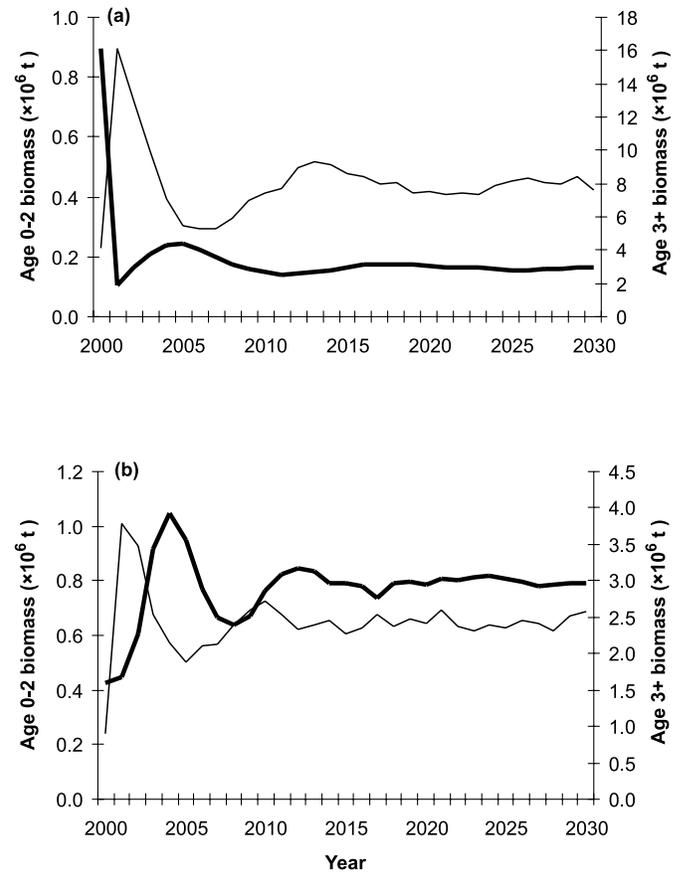


was smaller than 1.0, suggesting that the probability of a decreasing SSB ratio was at least 50%. In contrast to single-species and some multispecies results, the no-fishing scenario in the case of rock sole and Greenland turbot suggested the possibility of a decreasing SSB ratio in the long term with a probability of at least 50% in both regime shifts. For Pacific herring, in the multispecies simulations, we observed that the median of the SSB ratio increased in the long term for all levels of fishing mortality. However, in contrast to the single-species results, the median corresponding to the highest fishing mortality ($F_{30\%}$) was bigger than the medians associated with lower levels of fishing mortality ($F_{40\%}$ and $F_{50\%}$).

Discussion

The goal of this paper was to adopt a holistic approach to simulating the population dynamics of some species of the

Fig. 7. Median biomass trajectories of walleye pollock (*Theragra chalcogramma*) juveniles (age 0 to age 2) and adults (age 3+) from the multispecies scenario of the 1977 regime shift under two different levels of fishing: (a) $F_{30\%}$ and (b) $F = 0$: —, age 0 to age 2; —, age 3+.



eastern Bering Sea to obtain a better understanding of species interactions relative to fishing and climate influences. The MSVPA and MSFOR simulation models are useful frameworks, allowing the inclusion of predation interactions. We hope that this approach will provide useful information to improve fisheries management. In our analysis, the possible effects of climate regime shifts were included in the MSFOR model. We did not include explicit mechanisms between physical factors and recruitment such as SST and wind speed (Niebauer and Day 1989), air temperature and ice cover (Echeverria 1995; Quinn and Niebauer 1995), the influence of fronts on the distribution of age-0 walleye pollock, or factors influencing the transport of larvae (Wespestad et al. 2000). We did not include a spawner–recruit relationship because of the lack of data in different regimes sufficient to parameterize a spawner–recruitment curve in each regime time period. Instead, we took a simple approach by assuming that a climate regime shift produced a change in the variability and mean level of recruitment of some species. This approach allowed us to maintain the MSFOR model in a relatively simple form. In this way, the two factors, oceanographic conditions influencing survival and recruitment in the first 6 months of life and predation primarily influencing survival in the juvenile phase, were analyzed in a multispecies context.

In the single-species context, fishing mortality in conjunction with the regime shift assumption were the most important factors driving the dynamics of the species. As expected, fishing mortality decreased the SSB ratio of all species. Changes in mean recruitment levels associated with the 1977 and 1989 regime shifts produced important effects. Most species experienced a reduction of the mean of the SSB ratio when the 1989 regime shift was compared with the 1977 regime shift results. In contrast, the standard deviation of the same indicator of some species increased. These changes were a direct result of the changes in recruitment assumptions associated with the regime shift scenarios. Thus, forecasts of single-species dynamics can be influenced greatly if regime shift changes in recruitment can be estimated and incorporated into the projections.

Multispecies results showed greater complexity. Fishing was an important factor driving the dynamics of all species. Once again, an increase in fishing mortality caused a decrease in the mean SSB in most species. However, for Pacific herring, the opposite trend was observed even though its fishing mortality was held constant (20% harvest rate). This trend was due to predation interactions. As the fishing mortality of Pacific herring predators increased, their abundance decreased, producing a reduction in Pacific herring $M2$ and thus an increase in its mean SSB ratio. This fact shows how fishing changes on predator populations in combination with predation interactions have the potential to cause unintended changes in prey populations.

Similar effects produced by predation were found in the no-fishing scenario. As usual, the single-species simulations suggested an increase in the SSB of most species in all scenarios when fishing stopped (except for Greenland turbot). The multispecies simulations showed different results for some species. For example, in the single-species simulation, the mean SSB ratio of walleye pollock from the no-fishing scenario was 88% larger than the mean corresponding to the $F_{50\%}$ level of fishing mortality. In the multispecies simulations, this difference was reduced to 1% in the 1977 regime shift scenario and 10% in the 1989 regime shift simulation. This attenuation is due to cannibalistic interactions increased in the absence of fishing. As Livingston (1993) suggested, if predation interactions are taken in account in models of walleye pollock, the absence of fishing mortality produces an increase of the survival of adult walleye pollock and, consequently, an increase in the predation mortality of juvenile pollock. The result is the possible damping of recruitment at high adult stock sizes. This result was also seen in these simulations: the initial effect of a no-fishing regime on pollock in the multispecies forecast is a strong buildup of adult biomass and the depression of juvenile pollock biomass. The attenuation of the increase of the SSB ratio of walleye pollock can also be explained by the increased consumption of walleye pollock by the rest of the predators in absence of fishing (Jurado-Molina and Livingston 2002).

Predator-prey theory predicts that population densities in a predator-prey system may show damping oscillations before reaching equilibrium. This scenario has been recognized as the most realistic (Pianka 1983) because it assumes that the rate of increase of the predator population has an upper limit and that the growth of the prey population in the absence of the predator is density dependent (Poole 1974). All

species in our medium-term forecasts exhibited these oscillations for the median of the SSB ratio. The highest amplitudes of oscillation were found for walleye pollock. For this species, the trajectory of the median of the SSB ratio (no-fishing case) is characterized by a lower frequency and higher amplitude than the trajectories of the medians that included fishing. This characteristic is probably due to the strong feedback mechanism (cannibalism) originating from the initial large buildup of adult walleye pollock biomass when fishing pressure was removed. The lack of an explicit stock-recruitment function in generating recruitment values in this model is also likely responsible for the strong depression of juveniles at high adult walleye pollock stock sizes. Future refinements for this model should include stock-recruitment relationships for walleye pollock under different climate regimes. However, there are not yet enough historical observations of stock and recruitment to derive these relationships for each climate regime.

For rock sole, predation interactions also had an important effect. The multispecies simulation of no fishing under the two regime shift assumptions predicted a decreasing SSB ratio (<1). The decreasing trend of the SSB ratio is likely due to increased predation mortality caused by an increase in the population of rock sole's predators (walleye pollock and Pacific cod) when fishing stopped. This result contradicts the trend found in the single-species simulation in which spawning biomass increased in absence of fishing.

For Pacific cod and rock sole, the results from the multispecies simulation suggest that the effect caused by the change of climate regime shift on the SSB ratio was similar to the one observed in the single-species simulation. All results suggested the overlap of the cumulative distributions of a low-fishing policy under recruitment assumptions of a 1989 regime shift with the distribution of a more intensive fishing policy under the assumptions of the 1977 regime shift in the medium term. The extreme case corresponded to rock sole in the multispecies simulation in which a low-fishing policy ($F_{50\%}$) under recruitment assumptions of a 1989 regime shift would produce similar effects on the SSB ratio to the ones produced by heavier fishing in the 1977 climate regime shift.

In contrast to single-species results, for walleye pollock, there was partial overlap of the cumulative distributions of the SSB ratio in different scenarios of fishing and climate regime shift. Again, similar effects on the SSB ratio were produced by different fishing policies depending on the climate regime assumed. Sometimes the effect of the predation interactions was more important than the change of regime shift assumption. Therefore, discriminating among environmental, predation, and fishing effects on this species will continue to be a challenge. Similarly, the design of multispecies or ecosystem-based management strategies that attempt to balance human and predator needs for walleye pollock are complicated by these cannibalistic interactions that are confounded with fishing and environmental factors.

In summary, the effects of fishing, predation interactions, and climate could be considered similar because they produce changes in the SSB ratios of the same order of magnitude. Fishing always reduces the biomass of the target species in single-species forecasts. On the other hand, the effects of predation and fishing in multispecies forecasts cannot be generalized and depend on the species, the complexity and

magnitude of the predation interactions, and the species' position in the food web and its response to climate variability.

MSVPA and MSFOR models are a first step in taking a more holistic approach in fisheries management. However, some aspects in this approach can be improved. The incorporation of climate regime shifts in the model will require a better understanding of the mechanisms involving changes in physical environment and their effects on recruitment success during a climate regime. The recognition of the 1977 regime shift was made in the early 1990s and there is a belief that that event was not exceptional but the latest in a sequence of regime shifts (Hare and Mantua 2000). Therefore it is necessary to have a reliable way to identify regime shifts based on biological and (or) physical indices. Hare and Mantua (2000) suggested that monitoring indices in the Bering Sea ecosystem might allow for an earlier identification of regime shifts. This identification, in combination with a sufficient number of stock and recruitment data points in different regimes, will allow a more detailed specification of recruitment of the Ricker or Beverton–Holt form for each regime shift. Long-term monitoring is required to recognize and quantify the effects of regime shifts on marine ecosystems. This recognition and the improved understanding of the influence of multispecies interactions will help resource management better adapt to current or future environmental conditions. The multispecies models used do not take into account uncertainty. This could be improved through the development of a multispecies statistical catch-at-age model. This type of model would be based on similar foundations as the state-of-the-art single-species stock assessment models but with the addition of predation interactions. The present model does not include the possible changes in species spatial overlap and resulting predation that may occur in different climate regimes. Refinement of our understanding of the interaction between physical factors and prey availability is required along with a spatially explicit modeling framework. As shown, improvement in observation and modeling will help us to move toward ecosystem-based management.

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