Multi-species Stock Assessment for walleye pollock, Pacific cod, and arrowtooth flounder in the Eastern Bering Sea

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Executive Summary

This is a three species stock assessment for walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*) and arrowtooth flounder (*Atheresthes stomias*), from the Eastern Bering Sea (EBS), Alaska updated from Holsman et al. (in press). Results are presented from models estimated and projected without trophic interactions (single-species mode, SSM) and with trophic interactions (multi-species mode, MSM). The main features and settings for this multispecies model include:

- Predation natural mortality was specified to be age specific and annually varying (M2). Residual (non-predation) natural mortality (M1) was age specific but not-annually varying and differs slightly from current assessments for each species (see Table 3 below).
- Predator overlap index was set to 1 for all species (i.e., all prey are available to all predators).
- A Ricker stock recruitment curve is fit a sub-model within CEATTLE by providing point estimates of stock and recruits and estimating parameters for projection purposes. For this assessment, optional environmental covariates were omitted.
- Weights at age were estimated outside of the model using a temperature-dependent von Bertalanffy models using the original series and assume 2012 weight at ages for 2013-2016.
- The acoustic trawl survey selectivity estimates were specified to equal the SAFE report model estimates (earlier versions of the model omitted age composition information from this survey).
- Fisheries selectivity and survey selectivity were specified to be age specific but held constant over time.
- Predator-prey suitability was also age-specific and constant over time.
- Arrowtooth flounder stock was treated as sexes combined (weight at age was estimated separately for males and females and combined using a mortality-based mean).
- Maturity schedules were based on 2012 assessments and differ slightly from 2015 assessments.

Key updates from the original paper include:

- Pacific cod fishery composition data was based on lengths rather than model estimates of catch at age.
- Bottom temperature was based on average survey bottom temperatures (observed) for the Bering Sea and are updated through 2015.
- Projected bottom temperatures were held constant at mean historical values (constant) rather than using climate forecasts.

- Only two harvest control rules are presented here: (1) harvest rate that results in spawning biomass at 40% of unfished biomass (for all three species simultaneously) and (2) aggregate multi-species MSY.
- Bottom trawl survey data now includes 2012-2016 (Holsman et al. *in press* was only through 2011) and was updated for each species based on most recent assessment data.

Results from model runs show that pollock total and spawning biomass remains relatively high and similar to the past 3 years. Multispecies model predictions may indicate a slight decline in total and spawning biomass in 2016. Pacific cod total biomass remains relatively high, although may be slightly lower in 2016 than 2015. Female spawning biomass continues to increase steadily after a low in 2008. Arrowtooth total and spawning biomass estimates suggest declines after a peak in 2008.

Pollock recruitment is down in 2016 for the second year in a row and is lower than estimates for the past ten years (i.e., since 2006). Both single and multi-species models predict that recruitment will increase next year. Pacific cod recruitment is up slightly from 2015, but remains below the 10-year average. Estimates of Arrowtooth flounder recruitment are below average.

For ABC and mMSY estimates the model was projected through the year 2103 (to attain relative equilibrium). This allowed estimating a proxy for $B_{40\%}$ using the approach of Holsman et al. (*in press*) and Moffitt et al. (*in press*) where the model is projected under no fishing (simultaneously for all three species), and then projected under fishing to iteratively solve for the harvest rate that results in and average of 40% of unfished biomass in the last 5 years of the projection (2098-2103).

To derive multispecies MSY (mMSY), we similarly projected the model to iteratively find the harvest rate that maximized aggregate (all species) yield in the last 5 years of the projection (2095-2100).

Summary of assessment results for 2016:

	Walleye pollock		**Pacific cod**		**Arrowtooth flounder**	
Quantity	**SSM**	**MSM**	**SSM**	**MSM**	**SSM**	**MSM**
2016 M (natural mortality age 1)	0.900	2.021	0.340	1.044	0.269	0.897
2016 Average 3+ M (across ages)	0.300	0.317	0.340	0.340	0.226	0.229
2016 total (age 3+) biomass (t)	14,646,800	15,043,940	1,313,105	1,308,296	517,976	513,575
2016 Female spawning biomass; (t)	5,418,040	5,570,280	241,631	239,867	375,576	372,533
**Projected* SSB_0 *(t)*	5,332,960	3,907,090	435,039	413,799	482,457	446,320
**Projected* $SSB_{40\%}$ *(t)*	2,135,160	1,562,800	174,503	165,509	192,974	178,519
***Projected* SSB_{mMSY}	3,016,420	3,665,360	160,413	153,413	3,858	7,902
ABC_{2100} (t)	2,364,920	2,393,050	172,224	174,295	30,941	33,030
**$mMSY_{2100}$ (t)	2,075,700	2,749,000	172,208	176,166	1,658	3,529
$^{\dagger}F_{proxy}$	0.772	1.353	0.334	0.359	0.106	0.121
F_{mMSY}	0.385	0.443	0.367	0.396	0.279	0.287

* SSB is based on the projected SSB at 2100 (~equilibrium).
** mMSY is aggregate multi-species yield
† F_{proxy} is the fishing mortality that reduces the multispecies spawning biomass to 40% of unfished level.

Response to SSC and Plan Team comments

General comments:

Comments specific the Multi-species stock assessment model (CEATTLE)

The BSAI Plan discussed the additive property of the natural (residual) and predation mortalities in the multispecies model. Some Team members felt that the single species model should already incorporate the main components of natural mortality, so there was concern about using these values as base levels in the multispecies model. They felt that the "residual" mortality should be specified at a lower value than the single species assessment, since predation mortality will be explicitly accounted.

The residual mortality inputs in the model were updated to meet this recommendation. For single species mode the residual mortality matches that of current single species assessment models for pollock, Pacific cod, and arrowtooth flounder. The multi-species mode uses the same residual mortality vectors except for the ages 1 and 2 mortality rates for pollock, which were adjusted downward to 0.01 and 0.30, respectively.

The Team also discussed future plans and what other species might best be added. It may be useful to outline short- and long-term utilities of the multi-species approach. The Team discussed whether the predator-prey interaction between fur seals and pollock might be a logical next step for the multi-species approach. There was also a discussion about the possible short-term utility of the model to provide a potential mechanism (predation) to explain why certain cohorts that are initially predicted to be large may fail to materialize in subsequent years.

Sections titled "short-term utility" and "long-term utility" of the multi-species approach" were added to the end of the assessment. These sections discuss potential applications of the multispecies approach for assessment advice.

The Team recommends using a lower (residual) M in the multi-species model for comparisons with the single-species stock assessment values.

As stated above the residual natural mortality values were adjusted downward to meet this recommendation.

The Team also recommends working with MML staff to include fur seals as part of the multi-species model.

In October 2016, MML staff and CEATTLE authors collaborated on a joint proposal to add fur seals to the CEATTLE model. This proposal was submitted and identified as a priority during an internal regional climate action plan request for "shovel ready" projects in October (funding to be determined). A similar proposed study would extend that approach to evaluate drivers of changes in fur seal pup production and is anticipated to be submitted in November as a North Pacific Research Board proposal.

Finally, the Team recommends including the multi-species stock assessment as an Appendix to the EBS Pollock stock assessment in November.

This assessment is included as an appendix to the EBS pollock assessment.

Introduction

MSCAA models for evaluating annually varying M

Multi-species statistical catch-at-age models (MSCAA) are an example of a class of multi-species 'Models with Intermediate Complexity for Ecosystem assessments' (i.e., MICE; Plagányi et al., 2014), which have particular utility in addressing both strategic and tactical EBFM questions (Hollowed et al. 2013; Fogarty 2014; Link and Browman 2014; Plagányi et al., 2014). MSCAA models may increase forecast accuracy, may be used to evaluate propagating effects of observation and process error on biomass estimates (e.g., Curti 2013; Ianelli et al., *in press*), and can quantify climate and trophic interactions on species productivity. As such MSCAA models can address long recognized limitations of prevailing single species management, notably non-stationarity in mortality and maximum sustainable yield (MSY), and may help reduce risk of overharvest (Link 2010; Plagányi et al., 2014; Fogarty 2014). Because multispecies biological references points (MBRPs) from MSCAA model are conditioned on the abundance of other species in the model (Collie and Gislason 2001; Plagányi et al., 2014; Fogarty 2014), they may also have utility in setting harvest limits for multi-species fleets, evaluating population dynamics in marine reserves or non-fishing areas, and quantifying trade-offs that emerge among fisheries that impact multiple species in a food web (see reviews in Pikitch et al., 2004; Link 2010; Levin et al., 2013; Link and Browman 2014; Fogarty 2014).

Depending on their structure, MSCAA models can be used to evaluate climate- and fisheries-driven changes to trophodynamic processes, recruitment, and species abundance (Plagányi et al., 2014). MSCAA models differ somewhat among systems and species, but most use abundance and diet data to estimate fishing mortality, recruitment, stock size, and predation mortality simultaneously for multiple species in a statistical framework. Similar to age structured single species stock assessment models widely used to set harvest limits, MSCAA models are based on a population dynamics model, the parameters of which are estimated using survey and fishery data and maximum likelihood methods (e.g., Jurado-Molina et al., 2005; Kinzey and Punt, 2009; Van Kirk et al., 2010; Kempf 2010; Curti et al., 2013; Tsehaye et al., 2014). Unlike most single-species models (but see Hollowed et al. 2000b; Spencer et al. 2016), MSCAA models additionally separate natural mortality into residual and annually varying predation mortality, and model the latter as a series of predator-prey functional responses. Thus, natural mortality rates for each species in MSCAA models depend on the abundance of predators in a given year and vary annually with changes in recruitment and harvest of each species in the model.

MSCAA models have specific utility in quantifying direct and indirect effects of fisheries harvest on species abundance and size distributions (see reviews in Hollowed et al., 2000a, 2013; Link 2010; Fogarty 2014; Link and Browman 2014; Plagányi et al., 2014), which is important for EBFM and trade-off analyses of various management strategies. Rapidly shifting climate conditions are also of growing concern in fisheries management as changes in physical processes are known to influence individual growth, survival, and reproductive success of fish and shellfish (Hanson et al., 1997; Kitchell et al., 1977; Morita et al., 2010; Hollowed et al., 2013, Cheung et al., 2015). Climate-driven changes in water temperature can directly impact metabolic costs, prey consumption, and somatic or gonadal tissue growth, with attendant indirect effects on survival, production, and sustainable harvest rates (e.g., Hanson et al., 1997; Morita et al., 2010, Cheung et al., 2015). Temperature-dependent predation, foraging, metabolic, and growth rates are common in more complex spatially-explicit food web or whole of ecosystem models such as GADGET (e.g., Howell and Bogstad 2010; Taylor et al., 2007), Atlantis (e.g., Fulton et al., 2011; Kaplan et al., 2012; 2013), and FEAST (Ortiz et al., in press). Temperature functions for growth and predation can also be incorporated into MSCAA models, allowing this class of models to be used to evaluate interacting climate, trophodynamic, and fishery influences on recommended fishing mortality rates.

Numerous studies point to the importance of using multi-species models for EBFM (see review in Link 2010). Multi-species production models produced different estimates of abundances and harvest rates than single species models for Northeast US marine ecosystems (Gamble and Link, 2009; Tyrrell et al., 2011), and MSY of commercial groundfish stocks estimated from aggregated production models are different than the sum of MSY estimates from single-species assessments (Mueter and Megrey, 2006; Gaichas et al., 2012; Smith et al., 2015). Multi-species models have been used to demonstrate long-term increases in yield of Icelandic stocks of Atlantic cod (*Gadus morhua*) and reductions in capelin (*Mallotus villosus*) and Northern shrimp (*Pandalus borealis*) catch associated with short-term decreases in cod harvest (Danielsson et al., 1997). Kaplan et al. (2013) demonstrated the disproportionately large ecosystem impacts of applying the same Fx (e.g., Fx, or the harvest rate that reduces spawning stock biomass to x% of unfished spawning stock biomass, SSB_0; Caddy and Mahon, 1995; Collie and Gislason, 2001) harvest control rule approach to forage fish as is used for groundfish in the northeast Pacific, and trophodynamics in a southern Benguela ecosystem resulted in higher carrying capacity for small pelagic species under fishing (versus no-fishing) scenarios (Smith et al., 2015).

Since natural mortality and recruitment rates in a MSCAA model are conditioned on harvest rates of predators in the model, an ongoing area of research is evaluating MSCAA model analogs to single-species biological reference points (see Moffitt et al., in press), such as harvest rates that correspond to maximum yield (F_{MSY}) or proxies thereof (e.g., F_{proxy}). Other multi-species models have been used to derive and evaluate MBRPs, although these have largely focused on MSY (e.g., Kaplan et al., 2013; Smith et al., 2015). A notable exception is Collie and Gislason (2001), who evaluated a variety of MBRPs using a multi-species, virtual population analysis and found MBRPs to be sensitive to variation in natural mortality (much less so to variability in growth), and as such proposed that fishing mortality reference levels for prey species with high mortality be conditioned on the level of predation mortality. Building on this approach, Moffitt et al. (in press) recently demonstrated a projection approach for using multi-species models to derive a variety of MBRPs for EBFM. This provides a basis for the application of MSCAA models for increased use in tactical and strategic EBFM decision-making across a diversity of management frameworks worldwide.

MSCAA for EBM in Alaska

The eastern Bering Sea (Alaska), is defined by large, climate-driven changes to trophodynamics and species productivity that can vary on annual and multi-annual timescales (see reviews in Aydin and Mueter 2007; Hunt et al., 2011; Stabeno et al., 2012; Baker et al., 2014). Accordingly, fisheries management in Alaska has a long history of using ecosystem information and multi-species models for strategic management advice (e.g., multi-species model-based indices, such as mean trophic level, are regularly reported in the annual Ecosystem Considerations chapter of Alaska Stock Assessment and Fishery Evaluation (SAFE) reports; see review in Livingston et al., 2011). Development of multiple MSCAA models in the region (Jurado-Molina et al., 2005; Kinzey and Punt , 2009; Van Kirk, 2010) has advanced regional management closer to EBFM, facilitating use of estimates from MSCAA models in single-species models used for tactical decisions in the region. For instance, Dorn et al. (2014) recently evaluated predation mortality estimates from a regional MSCAA model developed by Van Kirk (2010) to inform natural mortality for the Gulf of Alaska walleye pollock (*Gadus chalcogrammus*, hereafter “pollock”) stock assessment.

MSCAA models may be most useful for species that exhibit strong trophic interactions (predator and prey species) or contrasting management or biological constraints that require simultaneous evaluation (Link 2010). In the eastern Bering Sea, pollock support one of the largest fisheries worldwide, with over 1.2 million metric tons (t) harvested per year (representing ~99% of the annual quota; Ianelli et al., 2014). Pollock are both predators (adults) and prey (i.e., ages <2; Dunn and Matarese, 1987; Nishiyama et al., 1986) for a variety of species including cannibalistic conspecifics (e.g., Boldt et al., 2012). Variable climate conditions, particularly the spatial extent of winter sea ice, the timing of sea ice spring melt, and subsequent summer bottom temperatures, can differentially promote survival of pollock and their predators and/or modulate predator and prey overlap in the region (e.g., Baily 1989; Zador et al., 2011; Boldt et. al 2012; Hunsicker et al. 2013; Baker and Hollowed 2014). Diet analyses suggest Pacific cod (*Gadus macrocephalus*), cannibalistic adult pollock, and arrowtooth flounder (*Atheresthes stomias*), amongst others, are important predators of pollock populations in the eastern Bering Sea (Livingston 1993; Aydin and Mueter 2007; Mueter et al., 2007).

Multispecies model

Here we present a three species MSCAA model for the Bering Sea (hereafter CEATTLE, for Climate-Enhanced, Age-based model with Temperature-specific Trophic Linkages and Energetics) that includes temperature-dependent von Bertalanffy weight-at-age functions (VBGF; von Bertalanffy, 1938) and temperature-specific, bioenergetics-based predation interactions. CEATTLE, is an example of an "environmentally-enhanced" stock assessment model (*sensu* Link 2010), where temperature-specific algorithms predict size-at-age and predation mortality. The MSCAA is programmed in AD model builder (Fournier et al., 2012), and builds on earlier models that combine catch-at-age assessment models with multi-species virtual population analysis (MSVPA) in a statistical framework (i.e., Jurado-Molina et al., 2005). Abundance and biomass of each cohort is modeled using standard population dynamics equations, accounting for a plus age group (Table 1, Eqs. T1.3, T1.4, T1.5). The initial age-structure is assumed to correspond to unfished equilibrium, and the numbers of each species at age 1 each year are treated as estimable parameters (Eqs. T1.1 and T1.2). Total mortality of each prey species *i*, age *j* (or predator species *p* age *a*) in each year y is the sum of mortality due to predators in the model ($M2_{ij,y}$), fishing mortality ($F_{ij,y}$), and residual mortality ($M1_{ij}$), Eq. T.1.8). Predation mortality (Eq. T2.1) is based on the assumption that the annual age-specific ration of a predator is allocated to prey species of a given age according to predator selectivity (Table 2, Eq. T.2.2). Predator selectivity is based on the suitability function derived by Jurado-Molina et al. (2005) and fit to available data from 1981-2015, while annual ration is a function of temperature-specific allometric relationships between ration and fish weight based on bioenergetics models for each species (Eqs. T2.4 and T2.5; Table 7; see Holsman et al. *in press*, and Holsman and Aydin, 2015 for more detail).

The length-to-weight relationships, predator size and species diet preference, bioenergetics-based, temperature-specific predator rations, and maturity are based on previous studies (Tables 1 and 2; Table 7, Table 8; Holsman et al. Holsman and Aydin, 2015, Holsman et al. *in press*). Size-specific diet compositions for each species were assumed known based on diet data collected during the AFSC bottom trawl survey (i.e., diet data are not included in the objective function) and trophic patterns in survey and fishery-based diet data were used to calculate mean (across years and stations) predator-prey suitability (Eq. T2.2).

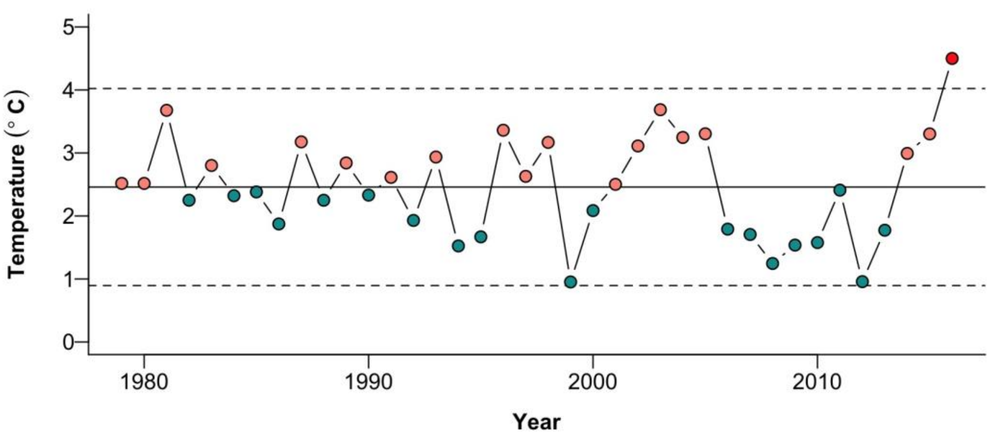

Figure 1. Mean summer bottom temperature for the Eastern Bering Sea; blue and red represent temperatures below or above (respectively) the long-term mean; dashed lines represent 2 standard deviations from the mean.

Temperature specific weight at age

Water temperature is known to directly impact growth through influencing metabolic and digestion rates, which often scale exponentially with body weight and temperature (see Hanson et al., 1997 for an overview). Thus we modified the generalized formulation of the von Bertalanffy growth function (VBGF; von Bertalanffy 1938; Pauly 1981; Temming 1994) to predict temperature-dependent growth by allowing the allometric scaling parameter *d* to increase with temperature. See Essington et al. (2010) and Holsman and Aydin (2015), and Holsman et al. (in press) for descriptions on the derivation and application of the VBGF towards bioenergetics modeling. In this formulation *d* represents the realized allometric slope of consumption, which integrates both the direct effect of temperature on consumption and indirect ecological interactions that scale with temperature and influence relative foraging rates (see Essington et al., 2010; Holsman and Aydin, 2015). We fit the VBGF to otolith-based length- and weight-at-age data (*n* = 21,388, 14,362, and 772, for pollock, Pacific cod, and arrowtooth flounder, respectively) collected during AFSC Bering Sea surveys and analyzed at the AFSC such that:

$$W_{ij,y} = W_{\infty,iy}\left(1 - e^{\left(-K_i(1-d_{i,y})(j-t_{0,i})\right)}\right)^{\frac{1}{1-d_{i,y}}} e^{\varepsilon}, \text{ where } \varepsilon \sim N\left(0, \sigma^2_{d,i}\right) \qquad \textit{Eq. 1}$$

where $t_{0,i}$ is the age at which $W_{ij,y}$ = 0, $W_{\infty,iy}$ is the asymptotic mass which can vary by species *i* and year y (i.e., $W_{\infty,iy} = \left(\frac{H_i}{K_i}\right)^{1/(1-d_{i,y})}$), H_i is the assimilation constant K_i is the energy loss constant (Essington et al., 2010), and ε is a normally and independently distributed random variable with mean 0 and variance $\sigma^2_{d,i}$. Essington et al. (2010) and Holsman and Aydin, (2015) statistically estimated the *d*, *K* and *H* parameters for various species to estimate consumption rates. In particular, Holsman and Aydin (2015) found that the *d* parameter varied between species and regions in Alaska (USA). We further modified this approach to estimate *d* annually for each year *y* in the dataset, as a linear function of temperature T_y such that:

$$d_{i,y} = e^{\left(\alpha_{d,i,y} + \alpha0_{d,i} + \beta_{d,i}T_y\right)} \qquad \textit{Eq. 2}$$

where $\alpha0_{d,i}$ and $\alpha_{d,i,y}$ represent the mean d intercept and $\beta_{d,i}$ is the coefficient for the residual effect of temperature on the d consumption parameter. We chose this formulation based on the empirical relationship between temperature and consumption, assuming that *d* would capture the differential effects of temperature on growth, and that waste rates scale proportionally with weight but do not vary over time with diet or temperature (i.e. *K* is constant but d can vary with temperature). This formulation allows both the slope and asymptotic limit of growth to vary with temperature. Similar approaches, with slightly different modifications to the VBGF, including temperature and prey specific terms for d and k, respectively, have been used elsewhere to evaluate climate impacts on fish growth (e.g., Cheung et al., 2015; Hamre, 2003).

Table 1. Population dynamics equations for species *i* and age *j* in each simulation year *y*. BT indicates the AFSC bottom trawl survey and EIT represents the echo-integrated acoustic-trawl survey. For all other parameter definitions see Table 3.

Definition	Equation		
Recruitment	$N_{i1,y} = R_{i,y} = R_{0,i}e^{\tau_{i,y}}$	$\tau_{i,y} \sim N(0, \sigma^2)$	T1.1
Initial abundance	$N_{ij,1} = \begin{cases} R_{0,i}e^{(-j\,M1_{ij})}N_{0,ij} \\ R_{0,i}e^{(-j\,M1_{iA_i})}N_{0,i,A_i}/\left(1-e^{(-j\,M1_{iA_i})}\right) \end{cases}$	$y=1 \quad 1<j\le A_i$; $y=1 \quad j>A_i$	T1.2
Numbers at age	$N_{i,j+1,y+1} = N_{ij,y}e^{-Z_{ij,y}} \quad 1\le y\le n_y \quad 1\le j<A_i$		T1.3
	$N_{i,A_i,y+1} = N_{i,A_i-1,y}e^{-Z_{iA_i-1,y}} + N_{i,A_i,y}e^{-Z_{iA_i,y}} \quad 1\le y\le n_y \quad j>A_i$		
Catch	$C_{ij,y} = \frac{F_{ij,y}}{Z_{ij,y}}(1-e^{-Z_{ij,y}})N_{ij,y}$		T1.4
Total yield (kg)	$Y_{i,y} = \sum_{j}^{A_i}\left(\frac{F_{ij,y}}{Z_{ij,y}}(1-e^{-Z_{ij,y}})N_{ij,y}W_{ij,y}\right)$		T1.5
Biomass at age (kg)	$B_{ij,y} = N_{ij,y}W_{ij,y}$		T1.6
Spawning biomass at age (kg)	$SSB_{ij,y} = B_{ij,y}\rho_{ij}$		T1.7
Total mortality at age	$Z_{ij,y} = M1_{ij} + M2_{ij,y} + F_{ij,y}$		T1.8
Fishing mortality at age	$F_{ij,y} = F_{0,i}e^{\varepsilon_{i,y}}s^f_{ij}$	$\varepsilon_{i,y} \sim N(0, \sigma^2_{F,i})$	T1.9
Weight at age (kg)	$W_{ij,y} = W_{\infty,iy}\left(1-e^{(-K_i(1-d_{i,y})(j-t_{0,i}))}\right)^{\frac{1}{1-d_{i,y}}}$		T1.10a
	$d_{i,y} = e^{(\alpha_{d,i,y} + \alpha0_{d,i} + \beta_{d,i}T_y)}$		T1.10b
	$W_{\infty,iy} = \left(\frac{H_i}{K_i}\right)^{1/(1-d_{i,y})}$		T1.10c
BT survey biomass (kg)	$\hat{\beta}^s_{i,y} = \sum_{j}^{A_i}\left(N_{ij,y}e^{-0.5\,Z_{ij,y}}W_{ij,y}s^s_{ij}\right)$		T1.11
EIT survey biomass (kg)	$\hat{\beta}^{eit}_y = \sum_{j}^{A_1}\left(N_{1j,y}e^{0.5(-Z_{1j,y})}W_{1j,y}s^{eit}_{1j}q^{eit}_{1j}\right)$	(pollock only)	T1.12
Fishery age composition	$\hat{O}^f_{ij,y} = \frac{C_{ij,y}}{\sum_j C_{ij,y}}$		T1.13
BT survey age composition	$\hat{O}^s_{ij,y} = \frac{N_{ij,y}e^{0.5(-Z_{ij,y})}s^s_{ij}}{\sum_j\left(N_{ij,y}e^{0.5(-Z_{ij,y})}s^s_{ij}\right)}$		T1.14
EIT survey age composition	$\hat{O}^{eit}_{1j,y} = \frac{N_{1j,y}e^{0.5(-Z_{1j,y})}s^{eit}_{1j}q^{eit}_1}{\sum_j\left(N_{1j,y}e^{0.5(-Z_{1j,y})}s^{eit}_{1j}q^{eit}_1\right)}$	(pollock only)	T1.15
BT selectivity	$s^s_{ij} = \frac{1}{1+e^{(-b^s_i\cdot j - a^s_i)}}$		T1.16
Fishery selectivity	$s^f_{ij} = \begin{cases} e^{\eta_{ij}} & j\le A_{\eta,i} \\ e^{\eta_{i,A_{\eta,i}}} & j>A_{\eta,i} \end{cases}$	$\eta_{ij} \sim N(0, \sigma^2_{f,i})$	T1.17
Proportion females	$\omega_{ij} = \frac{e^{-j\,M_{fem}}}{e^{-j\,M_{fem}} + e^{-j\,M_{male}}}$		T1.18
Proportion of mature females	$\rho_{ij} = \omega_{ij}\phi_{ij}$		T1.19
Weight at age (kg)	$W_{ij,y} = W^{\text{fem}}_{ij,y}\omega_{ij} + (1-\omega_{ij})W^{\text{male}}_{ij,y}$		T1.20
Residual natural mortality	$M1_{ij} = M^{\text{fem}}_{ij}\omega_{ij} + (1-\omega_{ij})M^{\text{male}}_{ij}$		T1.21

We used this approach to derive annual temperature-specific coefficients of d for pollock and Pacific cod (combined sexes) and separately for male and female arrowtooth flounder (Table 3; Table 8). For arrowtooth flounder, we then used the age-specific proportions of mature females (ρ_{ij}) and males $(1-\rho_{ij})$ to derive the mean weight-at-age for both sexes combined (Eq. T1.19 and Table 8). Lastly, male and female natural mortality rates (M_{male} and M_{fem}, respectively for arrowtooth flounder only) and age-specific maturity proportions (ϕ_{ij}) from the 2012 stock assessments for eastern Bering Sea pollock (Ianelli et al., 2012), and Bering Sea and Aleutian Islands Pacific cod (Thompson and Lauth, 2012) and arrowtooth flounder (Spies et al., 2012), were used to derive estimates of the proportion of mature females at age (ρ_{ij}; Eq. T1.18).

Table 2. Predation mortality (M2) equations for predators *p* of age *a*, and prey *i* of age *j*.

Definition	Equation	
Predation mortality	$M2_{ij,y} = \sum_{pa}\left(\frac{N_{pa,y}\delta_{pa,y}\overline{S}_{paij}}{\sum_{ij}\left(\overline{S}_{paij}B_{ij,y}\right) + B_p^{other}\left(1-\sum_{ij}\left(\overline{S}_{paij}\right)\right)}\right)$	T2.1
Predator-prey suitability	$\overline{S}_{paij} = \frac{1}{n_y}\sum_{y}\left(\frac{\frac{\overline{U}_{paij}}{B_{ij,y}}}{\sum_{ij}\left(\frac{\overline{U}_{paij}}{B_{ij,y}}\right) + \frac{1+\sum_{ij}\overline{U}_{paij}}{B_p^{other}}}\right)$	T2.2
Mean gravimetric diet proportion	$\overline{U}_{paij} = \frac{\sum_y U_{paij,y}}{n_y}$	T2.3
Individual specific ration (kg kg^{-1} yr^{-1})	$\delta_{pa,y} = \hat{\varphi}_p\alpha_\delta W_{pa,y}{}^{(1+\beta_\delta)} f\left(T_y\right)_p$	T2.4
Temperature scaling algorithm	$f\left(T_y\right)_p = V^X e^{(X(1-V))}$	T2.5
	$V = \left(T_p^{cm} - T_y\right)/\left(T_p^{cm} - T_p^{co}\right)$	T2.5a
	$X = \left(Z^2\left(1+\left(1+40/Y\right)^{0.5}\right)^2\right)/400$	T2.5b
	$Z = ln\left(Q_p^c\right)\left(T_p^{cm} - T_p^{co}\right)$	T2.5c
	$Y = ln\left(Q_p^c\right)\left(T_p^{cm} - T_p^{co} + 2\right)$	T2.5d

Parameter estimation and data

The parameters of the model are either pre-specified or estimated by selecting parameters that minimize the log-likelihood function (Table 9) and include fishing mortality rates ($F_{ij,y}$), fishery and survey selectivity (s_{ij}^{f} and s_{ij}^{s}, respectively), initial (pre-harvest) abundance in year 1979 ($N_{0,ij}$), and annual recruitment ($R_{i,y}$), while the estimable parameter of the likelihood function is the catchability coefficient for the acoustic survey (q_1^{eit}; Table 3; Table 9). We fit the model to available survey and fishery data for the eastern Bering Sea including biomass estimates and age-composition data from the annual AFSC summer bottom trawl survey with the assumption that the survey catchability (q) equals 1—an assumption that differs from the single species assessments, biomass and age-composition data from the AFSC Acoustic-trawl (AT) survey (pollock only), and the total fishery catch and fishery age-composition data collected by AFSC observers and analyzed at AFSC (Hilborn and Walters, 1992; Quinn and Deriso, 1999). Penalties were imposed on the changes over age in fishery selectivity (Table 9). Normal likelihood penalties were applied to the log of annual recruitment and the fisheries mortality deviations, as well as initial abundances. Selectivity for the AT survey was set to previously reported values (Table 9; Honkalehto et al., 2011; Ianelli et al., 2015).

Table 3. Parameter definition (n is the number of parameters for estimated parameters only, type, value (Plk: Pollock; Cod: Pacific cod; Atf: Arrowtooth flounder both sexes; Atf_M: Arrowtooth flounder males; Atf_F: Arrowtooth flounder females), and source. Types: I: Input parameter (assigned); M: model index; E: Estimated parameter; F: fixed parameter P: Derived quantity; D: Data.

Parameter	Definition	Type	Value	Source (see below)
y	Year	M	$[1,2,3 \ldots n_y]$	e
p	Predator	M	$[1,2,3 \ldots n_p]$	e
a	Predator age (years)	M	$[1,2,3 \ldots A_p]$	e
i	Prey	M	$[1,2,3 \ldots n_i]$	e
j	Prey age (years)	M	$[1,2,3 \ldots A_i]$	e
n_i	Number of prey species	I	3	e
n_p	Number of predator species	I	3	e
$R_{0,i}$	Mean Recruitment; n=[1,1,1]	E	≥ 0	e
$\tau_{i,y}$	Annual recruitment deviation; n=[34,34,34]	E	number	e
$N_{0,ij}$	Initial abundance; n=[11,11,20]	E	≥ 0	e
$F_{0,i}$	Mean fishing mortality; n=[1,1,1]	E	≥ 0	e
$\varepsilon_{i,y}$	Annual fishing mort. deviation; n=[34,11,20]	E	number	e
η_{ij}	Fishery age selectivity coef. ; n=[8,8,8]	E	number	e
b_i^s	Survey age selectivity slope; n=[1,1,1]	E	number	e
a_i^s	Survey age selectivity limit ; n=[1,1,1]	E	number	e
$d_{i,y}$	VBGF allometric slope of consumption	P	≥ 0	e
$W_{\infty,iy}$	VBGF max asymptotic weight (kg)	P	> 0	e
ρ_{ij}	Proportion of mature females at age	P	$\in [0,1]$	e
$M1_{ij}$	Residual natural mortality	F	≥ 0	e, h
n_y	Number of simulation years	I	34	e
y_0	Start year	I	1979	e
ω_{ij}	Female proportion of population	F	$\in [0,1]$	c
φ_{ij}	Age-specific maturity proportions	F	$\in [0,1]$	c
$C_{i,y}^*$	Observed total yield (kg)	D	≥ 0	f
$O_{ij,y}^f$	Observed fishery age comp.	D	$\in [0,1]$	f
$O_{ij,y}^s$	Observed BT age comp.	D	$\in [0,1]$	b
$O_{1j,y}^{eit}$	Observed AT age comp.	D	$\in [0,1]$	g
$\beta_{i,y}^s$	Observed BT survey biomass (kg)	D	number	b
β_y^{eit}	Observed AT survey biomass (kg)	D	number	g
T_y	Bottom temperature (º C)	D	number	b
$U_{paij,y}$	Gravimetric proportion of prey in predator stomach	D	$\in [0,1]$	b
B_p^{other}	Biomass of other prey (kg)	D	≥ 0	h
S_{1j}^{eit}	AT survey selectivity	F	$\in [0,1]$	c

Harvest scenarios and reference points

For all future scenarios, we set the bottom temperature in the model to the mean of the historical observed temperatures and mean recruitment (Fig. 1). We used the approach for deriving biological reference points (BRPs) proposed by Moffitt et al. (*in press*) and implemented by Holsman et al. (*in press*); here we evaluated 2 of their 12 harvest scenarios. For each harvest scenario *x* we calculated female spawning stock biomass for species *i* at a given fishing mortality rate F ($SSB_{F,x,i,y}$) by projecting the model forward to 2103 (87 years) under mean recruitment and according to a specified harvest rate (F; $F = 0$ for no fishing scenarios). Here we adopted the current over fishing limit (OFL) for Tier 3 acceptable biological catch ABC and MSY proxies for Bering Sea groundfish stocks; 40% of unfished biomass as the proxy target biomass for the ABC, and 35% as the proxy for B_{MSY} (female spawning biomass corresponding to maximum sustainable yield, MSY, i.e., 35% of $\overline{SSB}_{0,i}$; Punt et al., 2014; NPMFC, 2013; Clark et al., 1991; Brooks et al., 2010).

Table 3 (continued). Parameter definition (*n* is the number of parameters for estimated parameters only, value (Plk: Pollock; Cod: Pacific cod; Atf: Arrowtooth flounder both sexes; Atf_M: Arrowtooth flounder males; Atf_F: Arrowtooth flounder females), and source. I: Input parameter (assigned); M: model index; E: Estimated parameter; F: fixed parameter P: Derived quantity; D: Data.

Parameter	Definition	Type	Value			Source (see below)
			Pollock	Cod	ATF	
A_i	Number of prey ages	I	12	12	21	e
A_p	Number of predator ages	I	12	12	21	e
$\hat{\varphi}_p$	Annual relative foraging rate (d yr^{-1})	I	0.119	0.041	0.125	a
α_δ	Intercept of the allometric maximum consumption function (g g^{-1} yr^{-1})	I	0.119	0.041	0.125	a
β_δ	Allometric slope of maximum consumption	I	-0.460	-0.122	-0.245	a
T_p^{cm}	Consumption maximum physiological temperature (º C)	I	15.00	21.00	34.13	a
T_p^{co}	Consumption optimum physiological temperature (º C)	I	10.00	13.70	19.60	a
T_p^c	Max consumption parameter	I	2.60	2.41	2.18	a
$\alpha 0_{d,i}$	Intercept for VBGF *d* parameter	F	-0.817	-0.375	M: -0.213 F: -0.340	d
$\alpha_{d,i,y}$	Annual intercept for VBGF *d* parameter	F	See Table 5			d
$\beta_{d,i}$	Temperature covariate for VBGF *d* parameter	F	0.009	0.0045	M: -0.0057 F: -0.0115	d
K_i	VBGF energy loss constant (kg kg^{-1} yr^{-1})	F	0.22	0.45	M: 1.08 F: 0.38	d
H_i	VBGF assimilation constant (kg kg^{-d} yr^{-1})	F	16.34	9.30	M: 5.19 F: 5.90	d
$t_{0,i}$	VBGF age when $W_{ij,y}$= 0 (years)	F	0.53	-0.16	M: -1.00 F: -0.28	d
M_i^{fem}	Female natural mortality		NA*	0.37	0.35	c
M_i^{male}	Male natural mortality	F	NA*	0.37	0.20	c

* pollock age-specific M1 residual mortalities from the assessment were used (same values for male and females).

a. Holsman and Aydin 2015
b. Alaska Fisheries Science Center eastern Bering Sea bottom trawl survey
c. Stock assessments (Ianelli et al., 2012; Thompson and Lauth, 2012; Spies et al., 2012)
d. Supplemental materials, this study
e. This study
f. Fishery observer data
g. Alaska Fisheries Science Center echo-integrated acoustic trawl survey
h. Jurado Molina et al., 2005

The corresponding species-specific, acceptable biological catch ($ABC_{x,i,y}$) for each harvest scenario was calculated as the fishery yield for each year *y* of the projection period [1, n_y^{fut}] given a constant fishing mortality rate for the projection period that satisfies each harvest scenario objective ($F^*_{ABC,x,i}$), such that:

$$ABC_{x,i,y} = \left(\sum_{j}^{A_i} \left(\frac{F^*_{ABC,x,i} s^f_{ij}}{Z_{x,ij,y}} \left(1 - e^{-Z_{x,ij,y}}\right) N_{x,ij,y} W_{ij,y} \right) \right)$$

Eq. 3

where $Z_{x,ij,y}$ is the control-rule specific total annual mortality for species i age j in the set [1, 2,… A_i], s_{ij}^{f} is fishery age selectivity, and $N_{x,ij,y}$ and $W_{ij,y}$ are the annual species-specific abundance and weight-at-age for each projection year y. Using this approach, we found the species-specific fishing mortality rate ($F_{x,i}^{*}$) that results in mean female spawning biomass ($\overline{SSB}_{F,i}$) in the target projection period (i.e., last 5 years; 2046-2050) under fishing that is equal to the target proxy percentage (i.e., 40%) of mean unfished female spawning biomass ($\overline{SSB}_{0,i}$; Table 5). To find $F_{ABC,x,i}^{*}$, we iteratively project the model to find the $\overline{SSB}_{F,i}$ that corresponds to a given harvest rate $F_{x,i}^{*}$, adjusting $F_{x,i}^{*}$ downwards if $\overline{SSB}_{F,i}$ is below the target or upwards if $\overline{SSB}_{F,i}$ is above the target, until we achieve $\overline{SSB}_{F,i}$ near or at the proxy of 40% of $\overline{SSB}_{0,i}$. We ran this harvest scenario with the following variations:

- Find the ABC proxy biomass of 40% of unfished spawning biomass, where unfished biomass ($SSB_{0,i}$) is determined from projections where F is set to 0 for all species simultaneously.
- Iterate (i.e., eight iterations of the optimization algorithm) to find the species-specific fishing mortality rates that maximize the total combined yield (i.e., sum of yield for all three species) over the last 5 years of the projection period and where female spawning biomass for each species is not permitted to drop below 35% of the corresponding unfished female spawning biomass.

Results

Model parameterization

The multi-species mode of the model achieved a slightly higher over-all fit to the data (i.e., lower negative log-likelihood with the same number of estimated parameters for both models) for pollock and similar fits to the data for P. cod and arrowtooth. We observed similar fits to survey biomass and age composition data from the single-species (i.e., $M2_{ij,y}$ set to 0, hereafter “single-species model”) and multi-species modes of CEATTLE (see Table 5 for more detail). Although both models predicted similar total and female spawning biomass, inclusion of trophic interactions in the multi-species model resulted in slightly higher estimates of total biomass for pollock (Fig. 3).

Inclusion of predation interactions in CEATTLE improved model fit to observations of survey age composition for pollock, with average annual Pearson correlation coefficient (i.e., R^2) values from CEATTLE model in multi-species mode of 0.85 versus single-species version of CEATTLE model R^2 values of 0.82. The single- and multi-species models performed equally well for the annual Pacific cod and arrowtooth survey age composition data ($R^2 = 0.76$ and 0.65, respectively), and fishery age composition data for all three species ($R^2 = 0.81$, 0.96, and 0.89 for pollock, Pacific cod, and arrowtooth flounder, respectively). The single- and multi-species models fit the survey estimates of biomass with similar accuracy (single- and multi-species R^2, respectively, of 55.5% and 54.5% for pollock, 81% and 81.3% for Pacific cod, and 68.6% and 68.5% for arrowtooth), although the multi-species model fit the survey data slightly better (negative log-likelihood = 351.3 and 350.9 for the single- and multi-species models, respectively). Both models mimicked annual total catch for all three species closely ($R^2 > 0.997$; Fig. 2). Slight differences in total and female spawning biomass estimates between the models partially reflect divergent survey selectivity curves for the two models, with the multi-species model predicting higher survey selectivity for cod (Fig. 13e) and 5+ pollock (Fig. 13d).

Table 4. Correlation coefficients for survey biomass and age composition data from the model run in single-species mode (SSM) and multi-species mode (MSM).

	SSM	MSM
Total survey biomass		
Pollock	0.55	0.54
P. cod	0.81	0.81
Arrowtooth	0.69	0.68
Survey age composition		
Pollock	0.82	0.85
P. cod	0.76	0.76
Arrowtooth	0.65	0.65

Predation mortality varied considerably with changes in predator abundance over time (Fig. 5). Cannibalism was the largest source of predation mortality for pollock (Figs. 6) with older conspecifics exhibiting a high preference (i.e., total pollock suitability >0.75; Fig. 13) for juvenile pollock (ages 1-3; Fig. 13.g). Larger pollock also appear to target small arrowtooth flounder, as evidenced by a slight increase in total suitability of arrowtooth for pollock ages 6-10 (Fig. 13.g). Similarly, younger Pacific cod (ages 2-6) also target arrowtooth flounder (Fig. 13.h). Pacific cod increasingly target pollock prey as they age, and larger, older Pacific cod diets are dominated by age 1 pollock prey. Pacific cod also appear to be cannibalistic from ages 4 through 9. In contrast arrowtooth flounder prefer pollock throughout their lives, with total suitability coefficients (for all pollock ages) between 0.5 and 1.0 for arrowtooth flounder ages 1 through 18 (Fig. 13.i).

Natural mortality ($M1_{ij} + M2_{ij,y}$) was highest for age 1 fish of all three species (Fig. 4), and greatest for pollock (relative to Pacific cod or arrowtooth flounder). Age 1 mortality was estimated to be higher in 2016 (2.02) than it had been in the entire time series (since 1987; Fig. 4). Mortality was lower for age 1 Pacific cod and arrowtooth flounder, with total age 1 natural mortality stable at around 0.68 and 0.64 yr^{-1}, respectively, although both were slightly higher in 2015 and 2016. High predation mortality estimated for 1980-1990 for pollock reflected patterns in combined annual demand for prey by all three predators that was highest in the mid 1980's (collectively 8.97 billion t per year; Fig. 6a), and in recent years (collectively ~ 7.74 billion t per year 2014-2016). The peak in predation mortality of age 1 pollock in 2006 corresponds to the maturation of a large age class of 5-7 year old pollock and 2 year old Pacific cod that dominated the age composition of the two species in 2006. Similarly, the recent peaks in 2011 and 2014 reflect maturation of the large 2008 year class (Fig. 14). In 2016, the high mortality rates observe for pollock and Pacific cod are due to combined impacts of elevated bottom temperatures, which increases individual predator demand for pollock prey, and maturation of cannibalistic conspecific predators.

Pollock are both the dominant predator and a primary prey species in the multi-species model, second only to the 'other prey' category (Fig. 5a, b). After 'other prey' and pollock, the next most dominant prey category consumed is Pacific cod, followed by arrowtooth flounder (Fig. 5b). Pollock are primarily consumed by older conspecifics, and pollock cannibalism accounted for 56% (on average) of total predation mortality for age 1 pollock except for 2006-2008 when predation by arrowtooth flounder exceeded cannibalism as the largest source of predation mortality of age 1 pollock; Fig. 6).

The multi-species version of CEATTLE compensates for elevated predation mortality on younger age classes by increasing estimates of recruitment. Thus, recruitment is higher in the multi-species model than in the single-species model for all three species, especially those with high predation rates (i.e., pollock). The direction of change in annual recruitment estimates from year-to-year was generally the same for both models (i.e., both models increased or decreased recruitment in the same year) with a notable exception; the multi-species model predicted a significant drop in recruitment in recent years for pollock, whereas the single-species model estimated only a slight decline in recruitment (Fig. 7a). Pollock recruitment from the single-species version of CEATTLE was positively correlated with Pacific cod recruitment (R^2 = 0.65) and slightly inversely correlated with arrowtooth recruitment (R^2 = -0.02). Correlations between pollock recruitment and Pacific cod or arrowtooth recruitment were similar between the single- and multispecies versions, although correlations were weaker in the multi-species model for Pacific cod (R^2 = 0.59 and -0.03, respectively).

The single- and multi-species models estimate similar fishing mortality rates for pollock that have remained relatively stable at around 0.13 since the early 1980's (Fig. 8). Both models also estimate low and relatively steady fishing mortality rates for arrowtooth flounder (i.e., ~0.03). Both models estimate higher fishing mortality for Pacific cod (0.24-0.45), with indications of declines in fishing mortality in recent years (Fig.8).

Harvest scenarios and reference points

Projecting CEATTLE forward under mean recruitment produces trajectories of female spawning stock biomass that can be used to derive multi-species biological reference points and attendant fishing mortality rates (Holsman et al. in press). Projections under the Ricker stock-recruitment model lead to over-compensation recruitment dynamics in the first years of the projection (especially for single-species models; Fig. 9; *sensu* Botsford, 1986). However, a long term (>70 year) projection period appeared sufficient for the dynamics to stabilize (Fig. 9).

In general, unfished and harvested female spawning stock biomass ($\overline{SSB}_{0,i}$ and $\overline{SSB}_{F,i}$, respectively) were lower for projections of the multi- than the single-species model (with the exception of harvest scenario 4.3 of mMSY; Fig. 9). Unfished female spawning biomass from the multi-species version of CEATTLE was higher than historical female spawning biomass for Pacific cod and arrowtooth flounder, and approximately equal to recent female spawning biomass for pollock(Fig. 9).

Estimates of $\overline{ABC}_{x,i}$ for pollock were similar but slightly higher for multi-species than single- and models for harvest scenarios with individual species yield targets (scenario 1.1; Fig. 10. In contrast, for pooled yield targets, multi-species yield exceeded single species yield (scenarios 4.3; Fig 10) in the short-term but led to long-term declines in yield due to overharvest of arrowtooth flounder.

Application of MBRPs toward EBFM

Development of diverse multi-species biological reference points (MBRPs) from multi-species models is a necessary step in moving forward with EBFM (Link, 2010; Link and Browman, 2014). Projecting CEATTLE provides proxies for MBRPs that can readily be implemented in current OFL control rules for Alaska fisheries management and demonstrates the range of possible considerations as well as individual strengths and weaknesses of each control rule approach. Proxies for ABCs in multi-species models have been found to be lower compared to single-species counterparts (e.g., Gaichas et al., 2012). That said, Holsman et al. (in press) found that MBRPs do not inherently result in lower harvest recommendations than single-species corollaries (i.e., BRPs); comparative risk of over- or under-harvest depends on the degree of inter-specific predation and cannibalism. They also found that recommended harvest rates were relatively consistent between harvest scenarios, especially if target minimum biomasses are included for individual species. They also found that climate and trophic drivers can interact to affect MBRPs, but for prey species with high predation rates, trophic and management-driven changes may exceed direct effects of temperature on growth and predation. Given this, MSCAA models can readily be used for tactical EBFM decisions under changing climate conditions, if, as suggested by Holsman et al. (in press) and by various authors previously, harvest scenarios used for deriving MBRPs combined a minimum biomass threshold with yield targets to meet biodiversity and yield objectives (Worm et al., 2009; Gaichas et al., 2012). Biomass thresholds will require development of criteria for minimum limits in order represents a necessary advancement of the current approach.

Short-term utility: potential application within current single species assessments

This work demonstrates some alternative applications of multispecies trophic models within a management setting and there may be immediate relevance for current stock assessment models. For example, the estimated historical time series of natural mortality at age over time (M1 + M2) could be used directly within the assessment or used as priors in alternative assessment models with estimated annually varying natural mortality. Similarly, for the case of EBS pollock, the stock recruitment relationship may provide a basis for better estimates or prior distribution specification. It may be that by adding the time series of estimated total natural mortality at age that the estimated stock recruitment relationship may differ substantially given the relative differences in age 1 abundances. Further research on applying alternative stock recruitment relationships is needed as well, especially since the application of the Ricker curve has traditionally been justified due to cannibalistic nature of pollock—a situation that is partially accounted for in this application. In general, monitoring predator trends in a comprehensive way is an important element to link EBFM and climate change research.

Long-term utility: climate- and trophic-specific biological reference points

Because the natural mortality and growth functions are temperature dependent, long-term applications of the CEATTLE model could also include recruitment functions with climate-covariates. In this, the model could be combined with short-term forecasts of physical and lower trophic conditions in the Bering Sea, and used to refine estimates of recruitment and spawning stock biomass under changing conditions. (note that extensive model validation would be needed to evaluate predictive performance and potential utility). Incorporating additional species into the model, such as northern fur seals and Pacific halibut could help provide quantitative estimates of changes in juvenile pollock forage resources associated with different harvest rates of groundfish species in the EBS, as well as refined estimates of predation mortality for prey species in the model under changing conditions. Finally, planned incorporating technical interactions into the model may add realism to projections both for assessment purposes and for research and policy evaluation.

Acknowledgements

Our work is the result of numerous collaborations with researchers at the University of Washington (UW), University of Alaska Fairbanks (UAF), and the NOAA Alaska Fisheries Science Center (AFSC) and Northwest Fisheries Science Center (NWFSC). In particular, Ron Heintz (AFSC), Franz Mueter (UAF), and Elizabeth Siddon (UAF) supported an excellent discussion of the bioenergetics model sub-component of CEATTLE. We thank I. Spies (AFSC), I. Kaplan (NWFSC), and P. Sean McDonald (UW) for providing feedback on previous drafts. Support for the CEATTLE model came from the Alaska Integrated Ecosystem Assessment program (noaa.gov/iea), the Stock Assessment Analytical Methods program under award number 0002, and the North Pacific Research Board (publication number 547). The model was also part of the BEST-BSIERP Bering Sea Project, publication number 165. This effort would not be possible without the help of numerous researchers and volunteers who contribute annually to the collection of biomass, demography, and diet information through Alaska Fisheries Science Center surveys and the NOAA observer program, and the help of those who provide access to fishery-dependent and independent data through the Alaska Fisheries Science Center.

References

Botsford, L. W., 1986. Effects of environmental forcing on age-structured populations: Northern California Dungeness crab (*Cancer magister*) as an example. Can. J. Fish. Aquat. Sci. 43, 2345-2352.

Brooks, E. N., Powers, J. E., and Cortés, E., 2010. Analytical reference points for age-structured models: application to data-poor fisheries. – ICES J. Mar. Sci., 67, 165–175.

Caddy, J. F., Mahon, R., 1995. Reference points for fishery management. FAO Fisheries Technical Paper 347.

Cheung, W.W.L., Brodeur, R. D., Okey, T. A., Pauly, D., 2015. Projecting future changes in distributions of pelagic fish species of Northeast Pacific shelf seas. Prog. Oceanogr. 130, 19–31.

Clark, W. G., 1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. 48, 734–750.

Collie, J. S., Gislason, H., 2001. Biological reference points for fish stocks in a multispecies context. Can. J. Fish. Aquat. Sci. 58, 2167-2176.

Coyle, K. O., Eisner L. B., Mueter F. J., Pinchuk A. I., Janout M. A.,Cieciel, K. D., Farley, E.V., Andrew, A. G., 2011. Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the Oscillating Control Hypothesis. Fish. Ocean. 20(2), 139–156.

Curti, K. I., Collie, J. S., Legault, C. M., and Link, J. S., 2013. Evaluating the performance of a multispecies statistical catch-at-age model. . Can. J. Fish. Aquat. Sci. 70, 470-484.

Danielsson, A., Stefansson, G., Baldursson, F. M., Thorarinsson K., 1997. Utilization of the Icelandic cod stock in a multispecies context. Mar. Res. Econ. 12(4), 329-344.

Dorn, M., Aydin, K., Jones, D., Palsson, W., Spalinger, K., 2014. Chapter 1: Assessment of the Walleye Pollock Stock in the Gulf of Alaska. *In* Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Gulf of Alaska Region, Alaska Fisheries Science Center, National Marine Fisheries Service, Anchorage, AK, p 53−170.

Dunn, J. R. Matarese, A. C., 1987. A review of the early life history of Northeast Pacific gadoid fishes. Fish. Res. 5, 165-184.

Gaichas, S., Gamble, R., Fogarty, M., Benoît, H., Essington, T., Fu, C., Koen-Alonso, M., Link, J., 2012. Assembly rules for aggregate-species production models: simulations in support of management strategy evaluation. Mar. Eco. Prog. Ser. 459, 275–292.

Gamble R. J. and Link, J. S., 2009. Analyzing the tradeoffs among ecological and fishing effects on an example fish community: a multispecies (fisheries) production model. Ecol. Model. 220, 2570-2582.

Gamble, R. J. and Link, J., 2012. Using an aggregate production simulation model with ecological interactions to explore effects of fishing and climate on a fish community. Mar. Eco. Prog. Ser. 459, 259–274, 2012 doi: 10.3354/meps09745

Gislason, H. 1999. Single and multispecies reference points for Baltic fish stocks. ICES J. Mar. Sci. 56, 571-583.

Essington, T., Kitchell J., Walters, C., 2001. The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. Can. J. Fish. Aquat. Sci. 58, 2129–2138.

Fogarty, M. J. 2014. The art of ecosystem-based fishery management. Can. J. Fish. Aquat. Sci. 71, 479-490.

Fogarty, M.J., Overholtz, W. J., Link, J. S., 2012. Aggregate surplus production models for demersal fishery resources of the Gulf of Main. Mar. Ecol. Prog. Ser. 459, 247-258.

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., Nielsen, A., Sibert, J., 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software, 27, 233-249.

Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A.D.M., Smith, D.C., 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish Fish. 12, 171–188.

Hanson, P., Johnson, T. Schindler, D., Kitchell, J., 1997. Fish Bioenergetics 3.0. Madison, WI: University of Wisconsin Sea Grant Institute.

Hamre, J. 2003. Capelin and herring as key species for the yield of north-east Arctic cod. Results from multispecies model runs. Sci. Mar. 67 (Suppl 1), 315-323.

Hilborn, R. and Walters, C. J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York. 570 p.

Hollowed, A. B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J., Rice, J. C., 2000a. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES J. Mar. Sci., 57, 707–719. doi:10.1006/jmsc.2000.0734.

Hollowed, A. B., Ianelli, J. N., and Livingston, P. A., 2000b. Including predation mortality in stock assessments: a case study for Gulf of Alaska walleye Pollock. ICES J. Mar. Sci., 57, 279–293.

Hollowed, A. B., Curchitser, E. N., Stock, C. A., Zhang, C. 2013. Trade-offs associated with different modeling approaches for assessment of fish and shellfish responses to climate change. Climatic Change 119, 111–129 DOI 10.1007/Table 6584-012-0641-z

Holsman, K. K., Ianelli, J., Aydin, K., Punt, A. E., Moffitt , E. A. (in press). Comparative biological reference points estimated from temperature-specific multispecies and single species stock assessment models. Deep Sea Res. II. doi:10.1016/j.dsr2.2015.08.001.

Holsman, K. K. and Aydin, K. 2015. Comparative methods for evaluating climate change impacts on the foraging ecology of Alaskan groundfish. Mar. Ecol. Prog. Ser. DOI 10.3354/mepTable 7102

Honkalehto, T., Ressler, P.H., Towler, R.H., Wilson, C.D., 2011.Using acoustic data from fishing vessels to estimate walleye pollock (*Theragra chalcogramma*) abundance in the eastern Bering Sea. 2011. Can. J. Fish. Aquat. Sci. 68, 1231–1242

Howell, D., Bogstad, B. 2010. A combined Gadget/FLR model for management strategy evaluations of the Barents Sea fisheries. – ICES J. Mar. Sci, 67, 000–000.

Hunsicker, M. E., Ciannelli, L., Bailey, K. M., Zador, S., Stige, L. C., 2013. Climate and demography dictate the strength of predator-prey overlap in a subarctic marine ecosystem. PloS one 8(6), e66025. doi:10.1371/journal.pone.0066025.

Hunt G. L. Jr, Coyle K. O., Eisner L., Farley E. V., Heintz R., Mueter, F., Napp, J. M., Overland, J. E., Ressler, P. H., Salo, S., Stabeno, P. J., 2011. Climate impacts on eastern Bering Sea foodwebs: A synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES J. Mar. Sci. 68(6), 1230–1243.

Ianelli, J. N., Honkalehto T., Barbeaux S., Kotwicki S., 2014. Chapter 1: Assessment of the walleye pollock stock in the Eastern Bering Sea. *In* Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Islands Regions, Alaska Fisheries Science Center, National Marine Fisheries Service, Anchorage, AK, p 55−156.

Ianelli, J. N., Barbeaux, S., Honkalehto, T., Kotwicki, S., Aydin, K., and Williamson, N. 2012. Assessment of Alaska Pollock Stock in the eastern Bering Sea. In Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Islands Regions, pp. 31–124.

Ianelli, J. N., Holsman, K. K. Punt, A. E., Aydin, K. *In press*. Multi-model inference for incorporating trophic and climate uncertainty into stock assessments. Deep Sea Res. II

Jurado-Molina, J., Livingston, P. A., Ianelli, J. N., 2005. Incorporating predation interactions in a statistical catch-at-age model for a predator-prey system in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 62, 1865-1873.

Kaplan, I. C. , P. J. Horne, P. S. Levin., 2012. Screening California Current fishery manamgent scenarios using the Atlantis end-to-end ecosystem model. Prog. Oceanogr. 102, 5-18.

Kaplan, I.C., Brown, C.J., Fulton, E.A., Gray, I.A., Field, J.C., Smith, A.D.M., 2013. Impacts of depleting forage species in the California Current. Environ. Cons. 40, 380–393.

Kinzey, D. Punt, A. E., 2009. Multispecies and single-species age-structured models of fish population dynamics: Comparing parameter estimates. Nat. Res. Mod. 22, 67-104.

Kitchell, J. F., Stewart, D. J. and Weininger, D., 1977. Applications of a bioenergetics model to yellow perch (*Perca flavenscens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34, 1922-1935.

Levin, P. S., Kelble, C. R., Shuford, R., Ainsworth, C., deReynier, Y., Dunsmore, R., Fogarty, M. J., Holsman, K., Howell, E., Monaco, M., Oakes, S., Werner, F., 2013. Guidance for implementation of integrated ecosystem assessments: a US perspective. ICES J. Mar. Sci, doi:10.1093/icesjms/fst112.

Link J. S., 2010. Ecosystem-based fisheries management: confronting tradeoffs, Cambridge University Press, Cambridge.

Link, J. S., Browman, H. I., 2014. Integrating what? Levels of marine ecosystem-based assessment and management. ICES J. Mar. Sci, 71, 1170–1173

Livingston, P. A., Aydin, K., Bolt, J. L., Hollowed , A. B., Napp, J. M., 2011. Alaskan marine fisheries management: advances and linkages to ecosystem research. *In* A Belgrano and W Fowler (eds.), Ecosystem-Based Management for Marine Fisheries: An Evolving Perspective. Cambridge University Press, pp 113-152.

Livingston, P., 1993. Importance of predation by groundfish, marine mammals and birds on walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasi* in the eastern Bering Sea. Mar. Ecol. Prog. Ser. 102(3), 205–215.

Moffitt, E., Punt, A. E., Holsman, K. K., Aydin, K. Y., Ianelli, J. N., Ortiz, I., *In press*. Moving towards Ecosystem Based Fisheries Management: options for parameterizing multi-species harvest control rules. Deep Sea Res. II.

Morita, K., Fukuwaka, M. A., Tanimata, N. and Yamamura, O., 2010. Size-dependent thermal preferences in a pelagic fish. Oikos 119, 1265-1272.

Murawski, S., Matlock G., 2006. Ecosystem science capabilities required to support NOAA's mission in the year 2020. NOAA Technical Memorandum, NMFS-F/SPO-74, Silver Spring, MD.

Mueter, F. J. Megrey, B. A., 2006. Using multi-species surplus production models to estimate ecosystem-level maximum sustainable yields. Fish. Res. 81, 189-201.

Mueter, F. J., Boldt, J. L., Megrey, B. A., Peterman, R. M., 2007. Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts. Can. J. Fish. Aquat. Sci. 64(6), 911-927.

Nishiyama, T., Hirano, K., and Haryu, T., 1986. The early life history and feeding habits of larval walleye pollock *Theragra chalcogramma* (Pallas) in the southeast Bering Sea. Int. North Pac. Fish. Comm. Bull. 45, 177–227.

North Pacific Fishery Management Council (NPFMC). 2013. Fishery Management plan for groundfish of the Bering Sea and Aleutian Islands management area. North Pacific Fishery Management Council, Anchorage, AK.

Ortiz, I, K. Aydin, A. J. Hermann, G. Gibson. In press. Climate to fisheries: Exploring processes in the eastern Bering Sea based on a 40 year hindcast. Deep Sea Res. II.

Pauly, D., 1981. The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforschung 28, 251-282.

Plagányi, É. E., Punt, A.E., Hillary, R., Morello, E.B., Thébaud, O., Hutton, T., Pillans, R.D., Thorson, J.T., Fulton, E. A., Smith, A. D. M., Smith, F., Bayliss, P., Haywood, M., Lyne, V., Rothlisberg, P.C., 2014. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. Fish Fish. 15, 1-22.

Pikitch E. K., Santora C., Babcock E. A., Bakun A., Bonfi, R., Conover, D. O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E. D., Link, J., Livingston, P. A., Mangel, M., McAllister, M. K., Pope, J., Sainsbury, K. J., 2004. Ecosystem-based fishery management. Science 305, 346−347

Punt, A.E., Smith, A.D.M., Smith, D.C., Tuck, G., Klaer, N., 2014. Selecting relative abundance proxies for B_{MSY} and B_{MEY}. ICES J. Mar. Sci. 71, 469-483.

Quinn, T. J., II, Deriso, R. B., 1999. Quantitative Fish Dynamics. Oxford University Press, New York.

Ricker, W. E. (1954) Stock and Recruitment *Journal of the Fisheries Research Board of Canada*, **11**(5): 559–623. doi:10.1139/f54-039

Siddon E. C., Kristiansen T., Mueter F. J., Holsman K. K., Heintz R. A., Farley, E. V., 2013. Spatial Match-Mismatch between Juvenile Fish and Prey Provides a Mechanism for Recruitment Variability across Contrasting Climate Conditions in the Eastern Bering Sea. PLoS ONE 8(12), e84526. doi:10.1371/journal.pone.0084526

Smith, M. D., Fulton, E. A., and Day, R.W. 2015. An investigation into fisheries interaction effects using Atlantis. ICES J. Mar. Sci, 72(1), 275–283. doi:10.1093/icesjms/fsu114

Spencer, PD, **KK** Holsman, S Zador, NA Bond, FJ Mueter, AB Hollowed1, and JN Ianelli. (2016). Modelling spatially dependent predation mortality of eastern Bering Sea walleye pollock, and its implications for stock dynamics under future climate scenarios. ICES Journal of Marine Science; doi:10.1093/icesjms/fsw040

Spies, I. Wilderbuer, T. K., Nichol, D. G. and Aydin, K., 2012. Chapter 6. Arrowtooth Flounder. In Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Islands Regions, pp. 31–124.

Stabeno, P.J., Farley, E.V., Jr., Kachel, N.B., Moor, S., Mordy, C.W., Napp, J.M., Overland, J.E., Pinchuk, A.I., Sigler, M.F., 2012. A comparison of the physics of the northern and southern shelves of the eastern Bering Sea and some implications for the ecosystem. Deep Sea Res. II 65-70, 14-30.

Gouhier, T. C., Guichard, F., Gonzalez, A., 2010. Synchrony and Stability of Food Webs in Metacommunities. Am. Nat., 175 (2), E16-E34

Taylor, L. , Begley, J., Kupca1, V. Stefansson, G., 2007. A simple implementation of the statistical modelling framework Gadget for cod in Icelandic waters. Afr. J. Mar. Sci., 29(2), 223–245

Temming, A., 1994. Food conversion efficiency and the von Bertalanffy growth function. Part II and conclusion: extension of the new model to the generalized von Bertalanffy growth function. NAGA The ICLARM Quarterly, 17(4), 41-45.

Tsehaye, I., Jones, M. I., Bence, J. R., Brenden, T. O., Madenjian, C. P., Warner, D. M., 2014. A multispecies statistical age-structured model to assess predator-prey balance: application to an intensively managed Lake Michigan pelagic fish community. Can. J. Fish. Aquat. Sci. 71, 627-644.

Thompson, G. G., Lauth, R. R., 2012. Chapter 2: Assessment of the Pacific Cod Stock in the Eastern Bering Sea and Aleutian Islands Area. In Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Islands Regions, pp. 31–124.

Tyrrell M. C., Link J. S., Moustahfid H., 2011. The importance of including predation in some fish population models: implications for biological reference points. Fish. Res. 108, 1-8.

Van Kirk, K. F., Quinn II, T. J., Collie, J. S., 2010. A multispecies age-structured assessment model for the Gulf of Alaska. Can. J. Fish. Aquat. Sci. 67, 1135-1148.

von Bertalanffy, L., 1938. A quantitative theory of organic growth. Hum. Biol. 10: 181-213.

Worm B., Hilborn R., Baum J. K., Branch T. A. Collie, J. S., Costello, C., Fogarty, M. J., Fulton, E. A., Hutchings, J. A., Jennings, S., Jensen, O. P., Lotze, H. K., Mace, P. M., McClanahan, T. R., Minto, C., Palumbi, S. R., Parma, A. M., Ricard, D. , Rosenberg, A. A., Watson, R., Zeller, D., 2009. Rebuilding global fisheries. Science 325, 578−585

Zador S., Aydin K., Cope J., 2011. Fine-scale analysis of arrowtooth flounder *Atherestes stomias* catch rates reveals spatial trends in abundance. Mar. Ecol. Prog. Ser. 438, 229-239

Figures

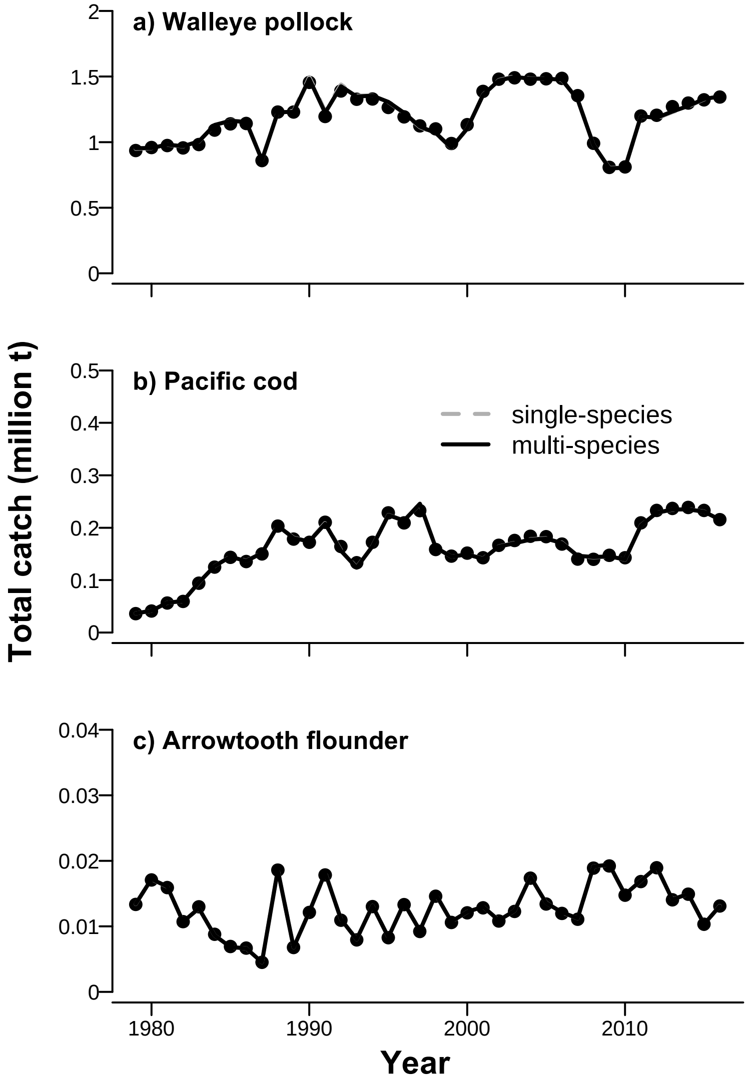

Figure 2.Total observed catch (circles) and model estimates of annual catch (lines) for single- and multi-species models (note that single species lines may not be visible as they overlap with multi-species estimates).

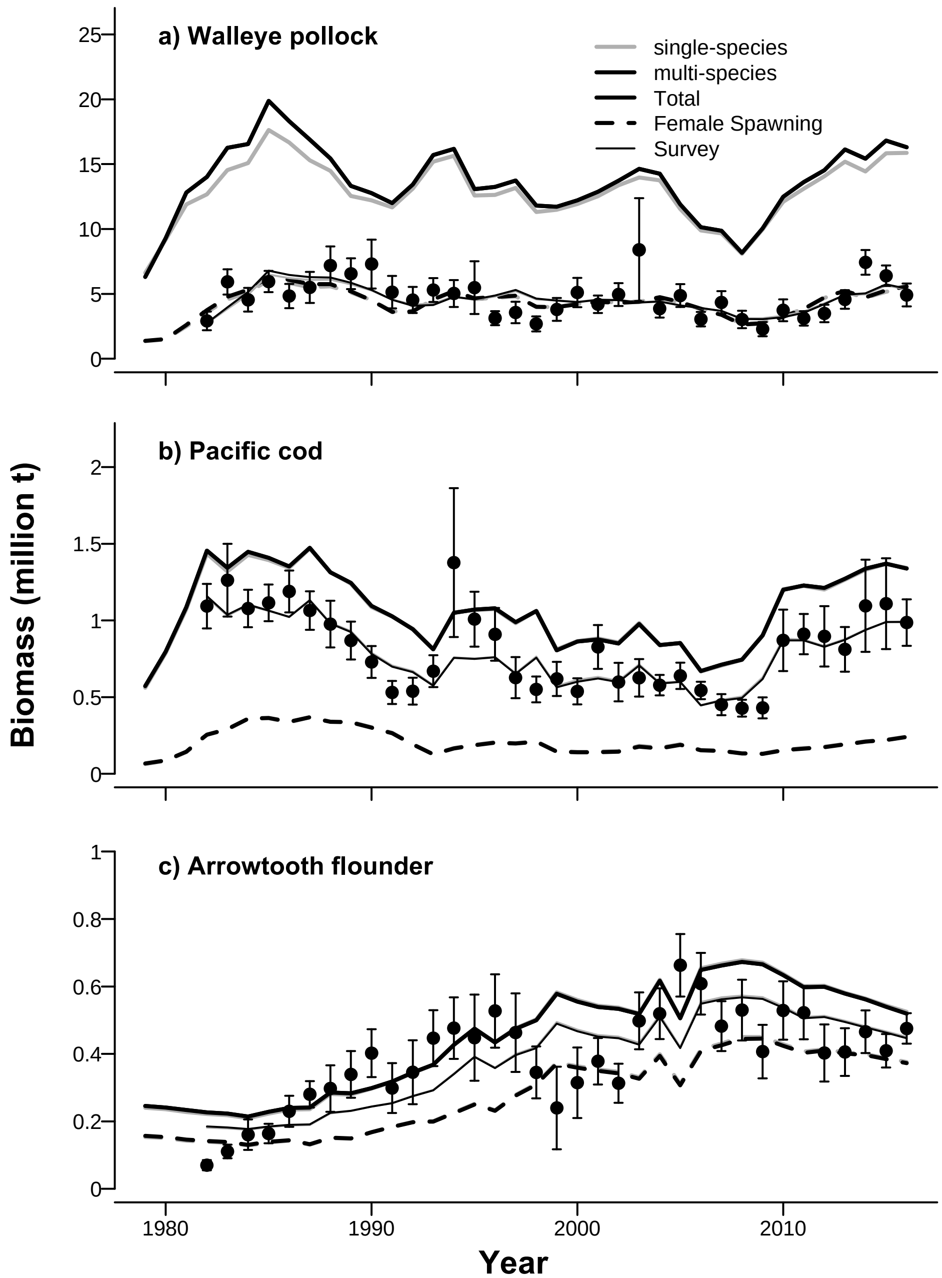

Figure 3. Single- (gray lines) and multi-species (black lines) retrospective model estimates of total (thick solid lines), female spawning (dashed lines), and bottom-trawl survey biomass (thin solid lines). Filled circles represent mean observed groundfish survey biomass and standard errors of the mean (error bars).

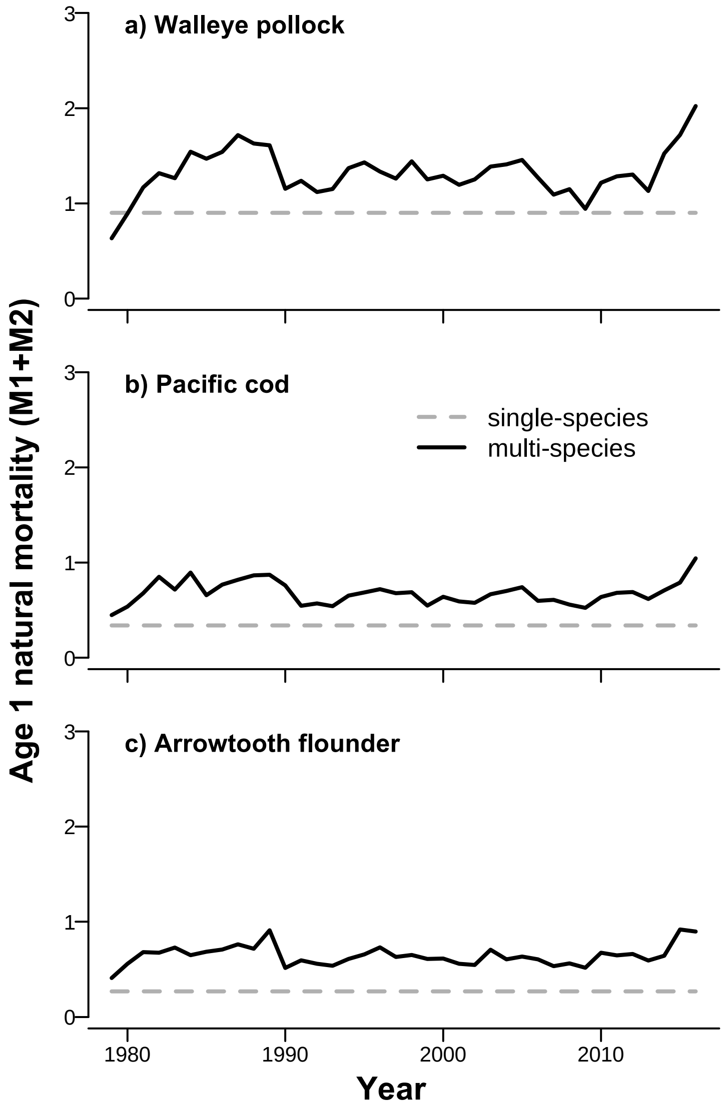

Figure 4. Annual variation in total mortality ($\boldsymbol{M1}_{i1}$+$\boldsymbol{M2}_{i1,y}$) for age 1 pollock (a), Pacific cod (b), and arrowtooth flounder (c) from the single-species models (dashed line), multi-species models with temperature (black line).

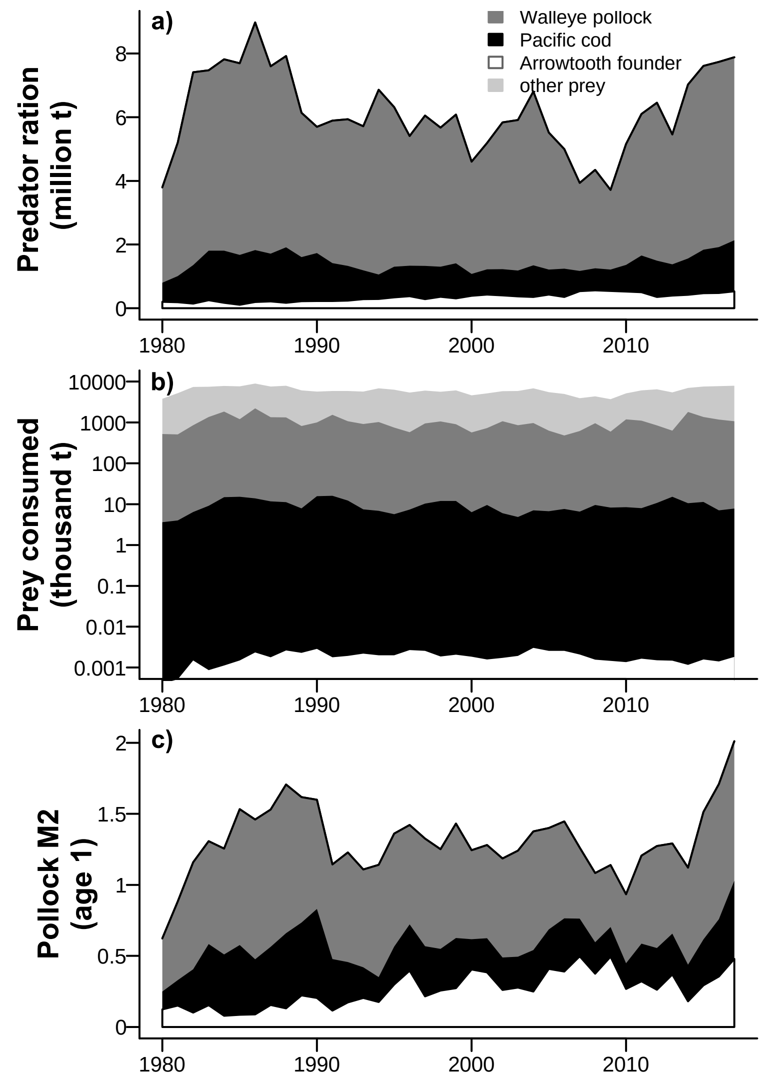

Figure 5. a) Combined total predator ration (all three predators combined) over time grouped by predator. b) Total prey consumed by all three predators combined (note the log scale). c) Pollock predation mortality (M2; age 1 only) consumed by each predator species.

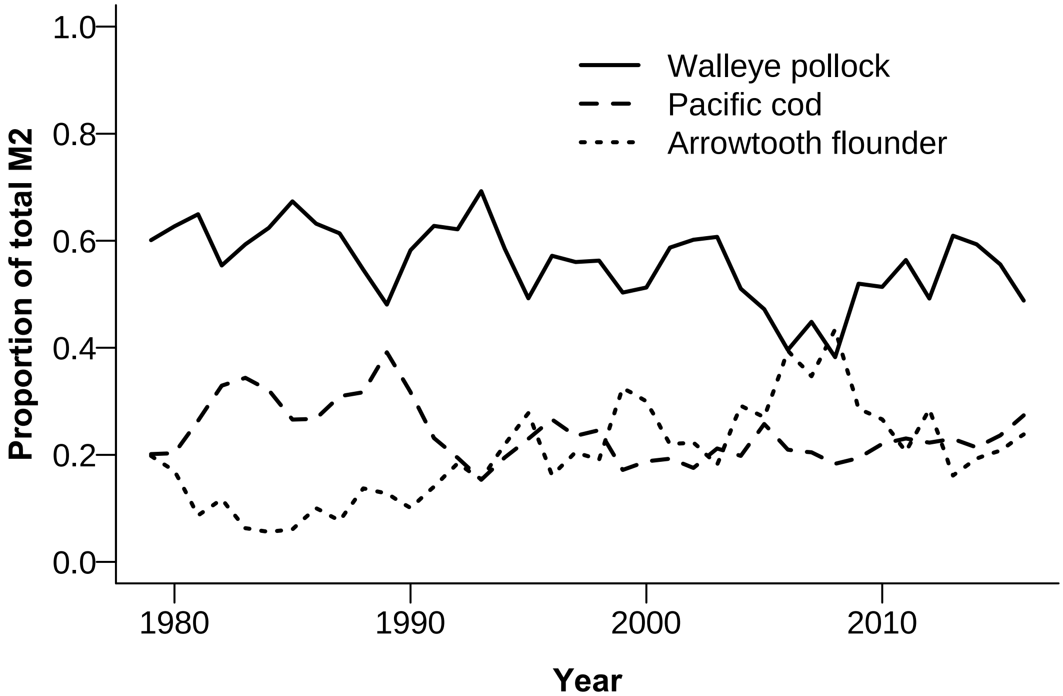

Figure 6. Proportion of total predation mortality for age 1 pollock from pollock (solid), Pacific cod (dashed), and arrowtooth flounder (dotted) predators across years.

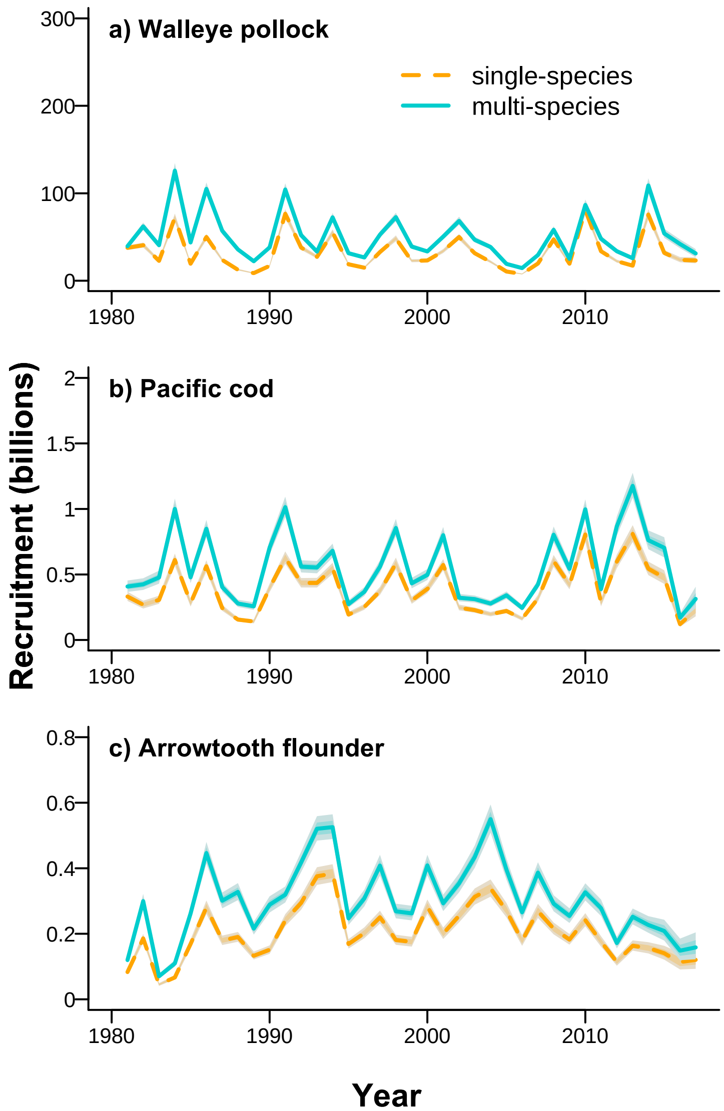

Figure 7. Annual single- and multi-species CEATTLE model estimates of recruitment (age 1) for pollock (a), Pacific cod (b), and arrowtooth flounder (c). Lighter shading represents the 95% CI around mean estimates. Darker shading represents +/- 1 standard error of the mean estimate.

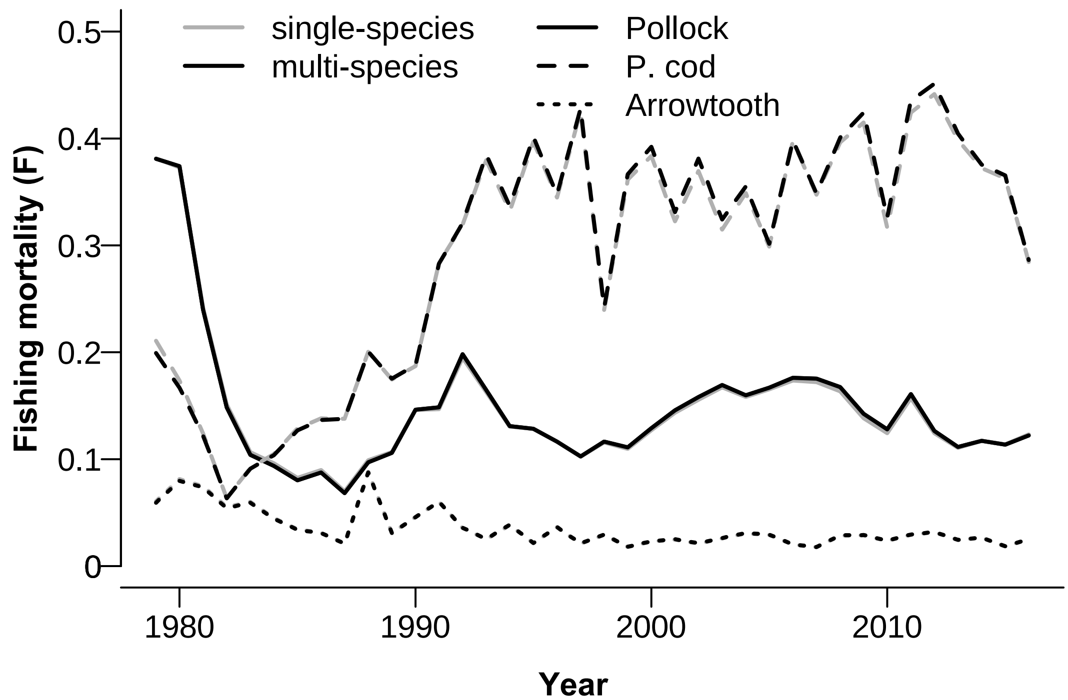

Figure 8. Time-trajectories of single- and multi-species (gray and black, respectively) CEATTLE model estimates of fishing mortality rate for eastern Being Sea walleye pollock (solid lines), Pacific cod (dashed lines), and arrowtooth flounder (dotted lines). Note that the single- and multi-species lines for arrowtooth flounder overlap.

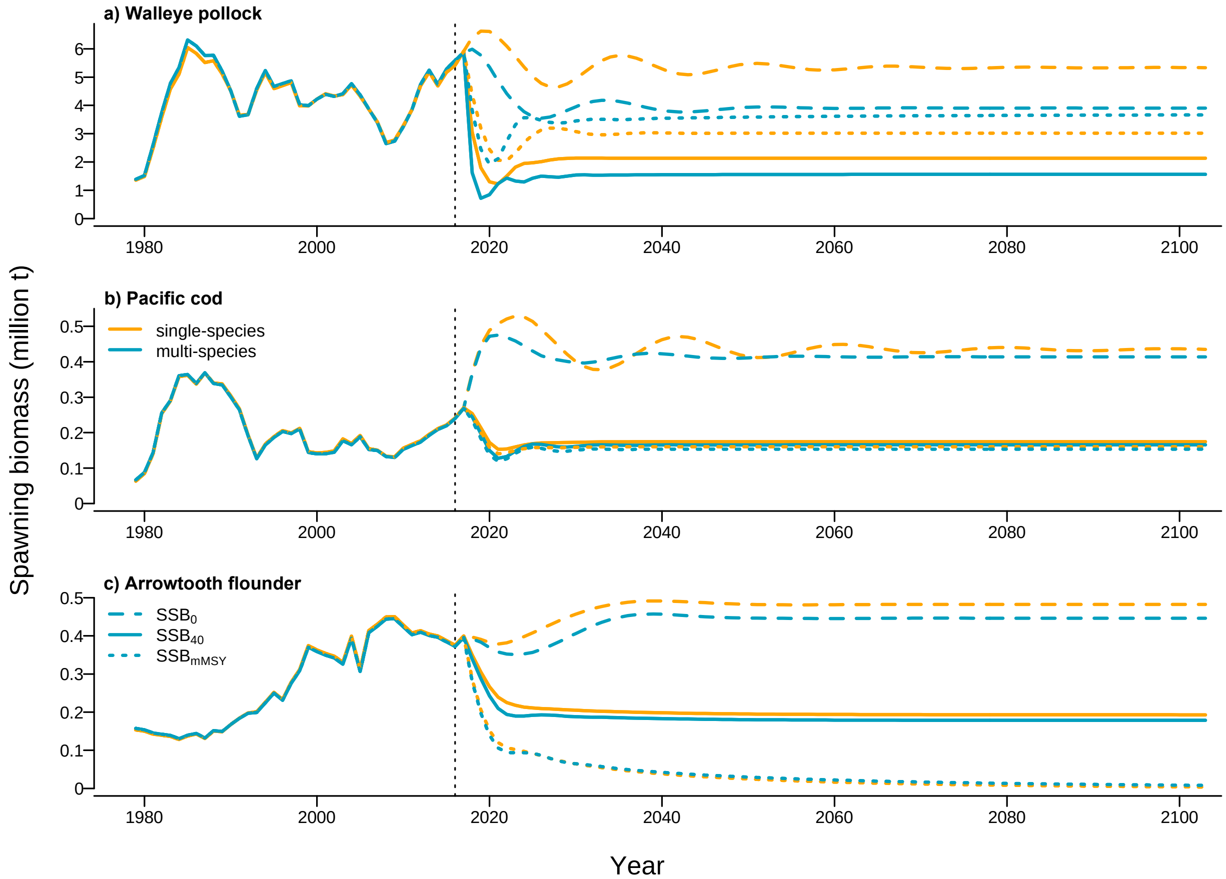

Figure 9. Single- and multi-species (orange and blue, respectively) CEATTLE model projections of unfished (dashed; SSB_0) and fished spawning stock biomass at the harvest rate corresponding with the ABC proxy and aggregate maximum yield (SSB_{40} and SSB_{mMSY}, solid and dotted lines, respectively) for each species.

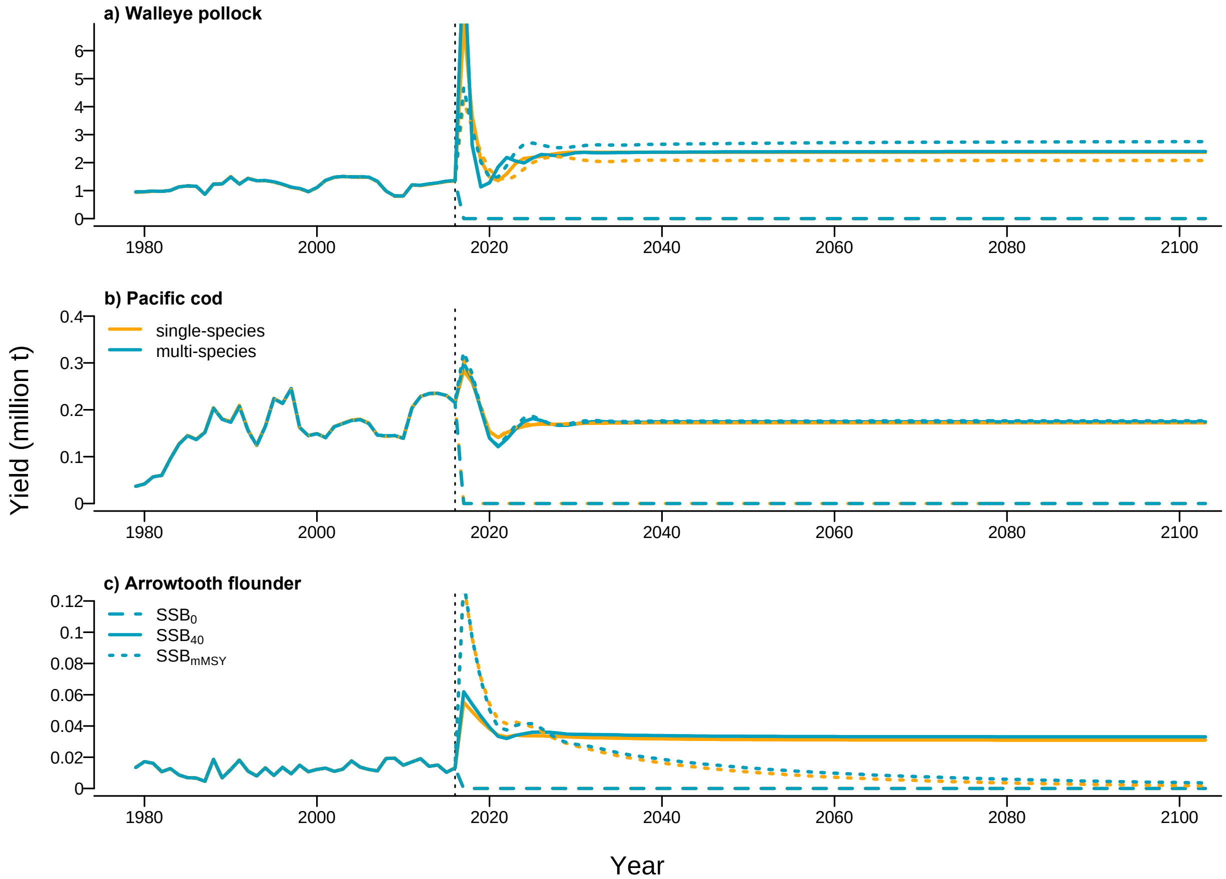

Figure 10. Single- and multi-species (orange and blue, respectively) CEATTLE model projections of annual yield at the harvest rates corresponding with the ABC proxy and aggregate maximum yield (F_{proxy} and F_{mMSY}, solid and dotted lines, respectively) for each species.

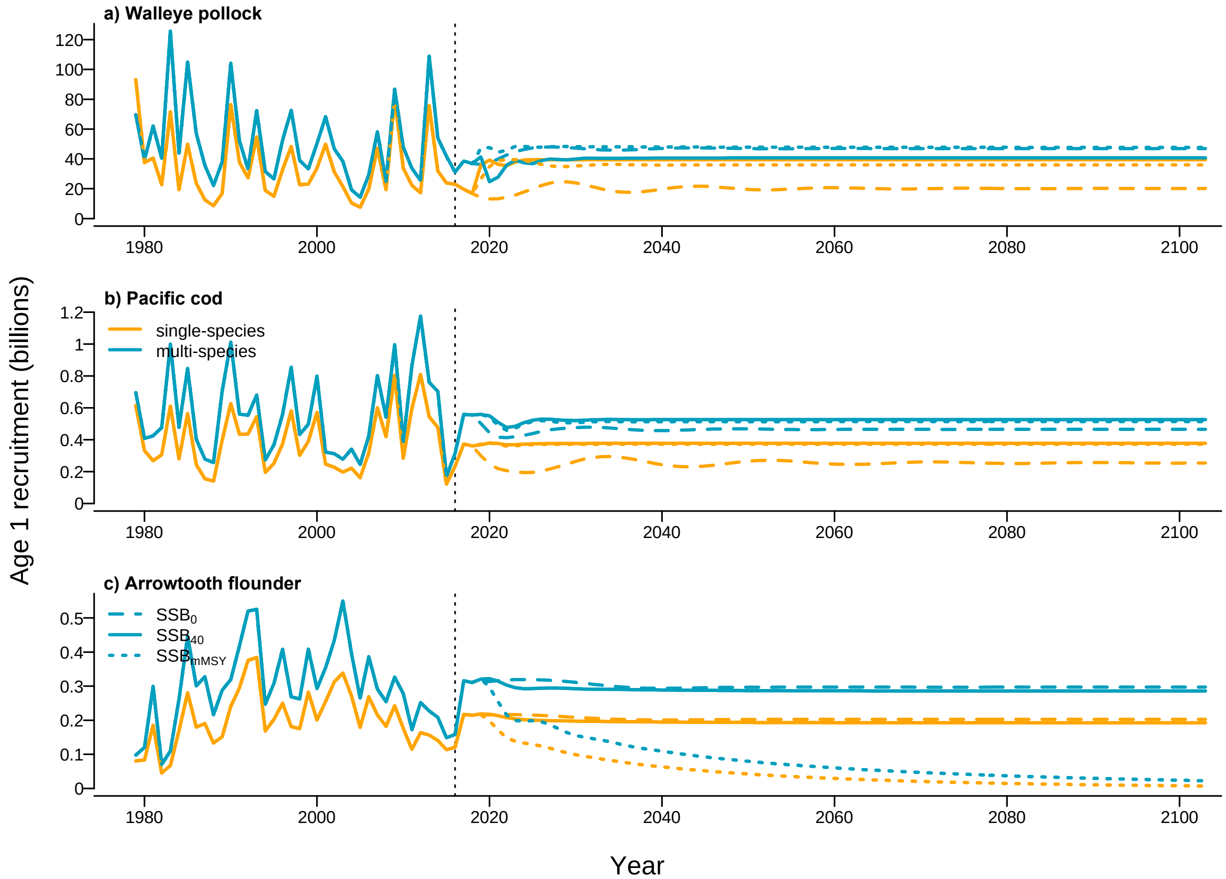

Figure 11. Single- and multi-species (orange and blue, respectively) CEATTLE model projections of age 1 recruitment at unfished spawning stock biomass (dashed; SSB_0) and at fished spawning stock biomass corresponding with the harvest rate at the ABC proxy and aggregate maximum yield (SSB_{40} and SSB_{mMSY}, solid and dotted lines, respectively) for each species.

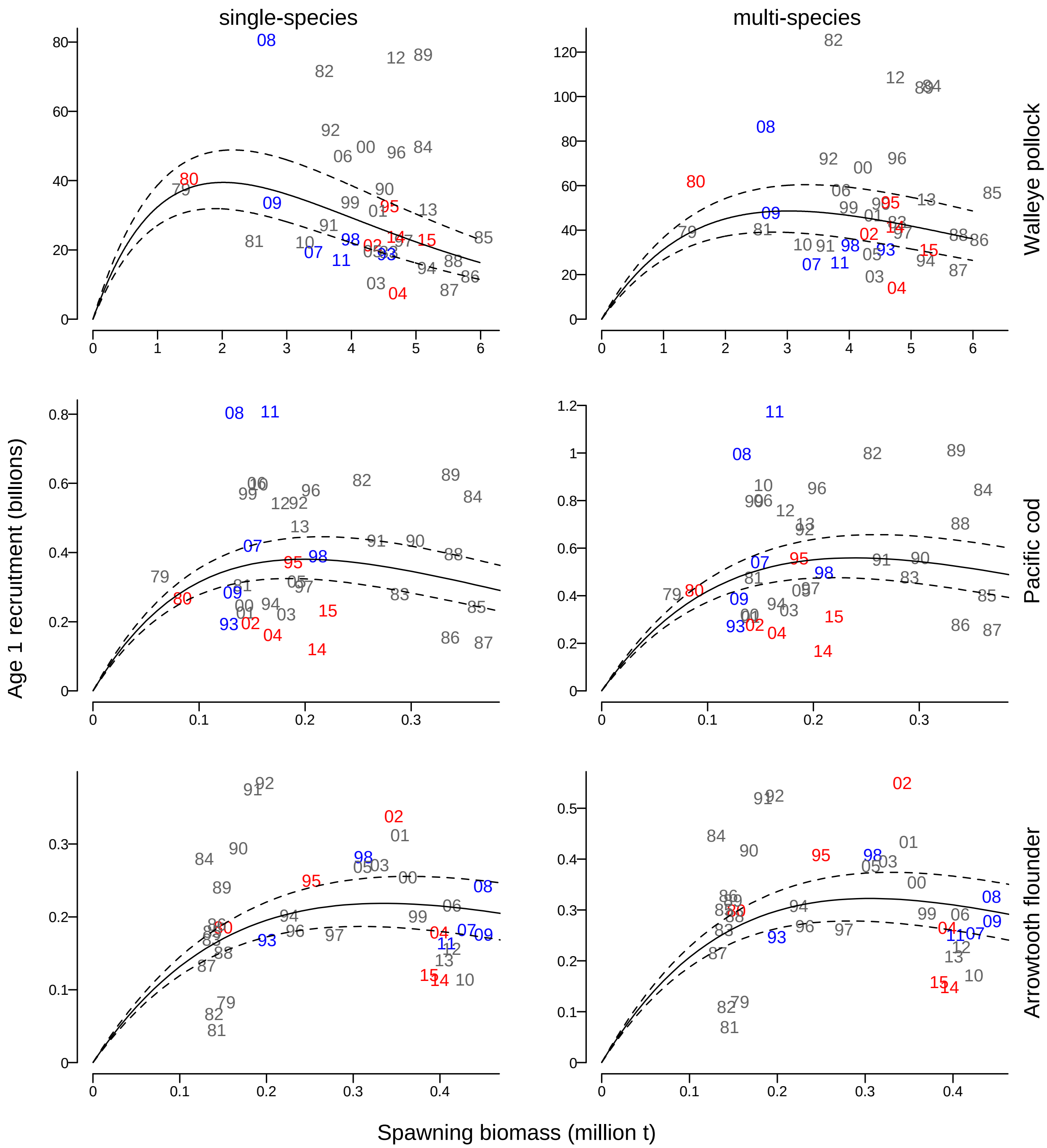

Figure 12. Stock-recruit curves for single- and multi-species models. Red and blue text indicates years where bottom temperature was + or – 1 standard deviation from the mean (respectively)

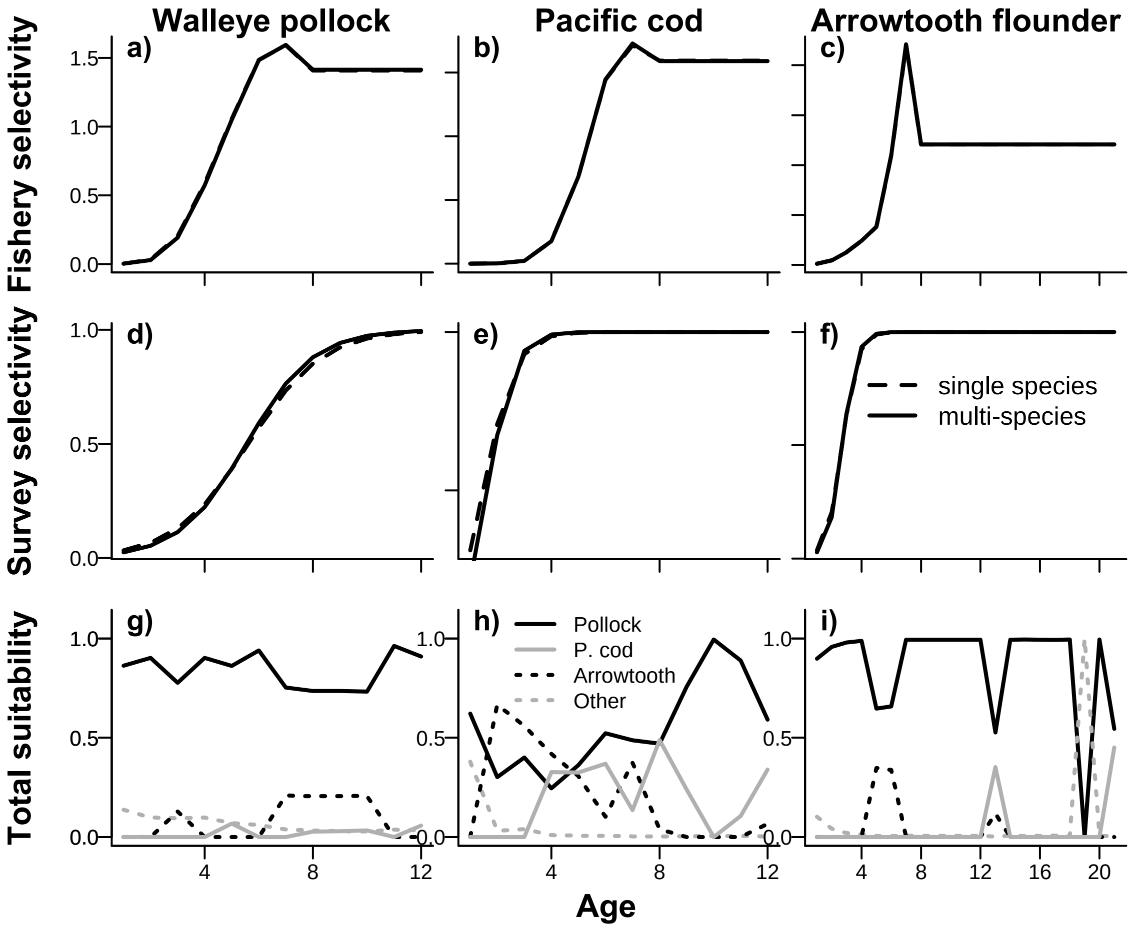

Figure 13. Single-species and multi-species fishery (first row; a-c) or survey selectivity (second row; d-f). Total suitability (across all prey species) for each predator age (third row; g-i).

	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12
1979	0.921	1.505	1.025	0.661	0.604	0.374	0.210	0.182	0.206	0.202	0.174	0.240
1980	0.521	3.476	2.420	1.154	0.559	0.391	0.193	0.100	0.090	0.099	0.096	0.189
1981	0.824	1.540	5.691	2.797	1.005	0.374	0.210	0.096	0.051	0.045	0.049	0.134
1982	1.339	1.284	1.807	6.165	2.055	0.722	0.278	0.138	0.059	0.033	0.029	0.099
1983	2.056	1.143	2.051	2.652	5.787	1.736	0.471	0.172	0.084	0.030	0.015	0.054
1984	0.740	2.251	1.298	2.959	2.431	4.762	1.427	0.401	0.125	0.063	0.032	0.064
1985	2.255	0.780	3.753	1.800	2.719	2.094	4.744	1.207	0.348	0.069	0.041	0.066
1986	0.996	2.017	0.845	5.231	1.432	2.405	1.561	2.688	0.781	0.225	0.063	0.065
1987	0.849	1.077	2.833	1.389	4.309	1.100	1.696	1.100	1.831	0.499	0.130	0.078
1988	0.455	0.518	1.483	3.526	1.227	3.509	0.825	1.203	0.782	1.360	0.409	0.134
1989	0.811	0.309	0.645	1.712	2.922	0.938	2.671	0.588	0.939	0.544	0.928	0.307
1990	1.942	0.655	0.365	0.889	1.532	2.474	0.677	1.892	0.428	0.662	0.413	0.836
1991	0.944	2.780	0.712	0.571	0.753	1.110	1.775	0.472	1.365	0.294	0.416	0.803
1992	0.977	1.409	4.323	1.192	0.544	0.608	0.877	1.248	0.339	0.915	0.216	0.777
1993	1.272	0.824	2.589	6.582	1.046	0.351	0.356	0.488	0.804	0.216	0.595	0.577
1994	0.670	1.858	1.424	3.391	5.595	0.823	0.257	0.295	0.415	0.542	0.151	0.758
1995	0.505	0.512	1.753	1.977	2.354	3.925	0.513	0.182	0.181	0.257	0.345	0.568
1996	1.068	0.418	0.599	3.313	1.761	1.864	2.786	0.384	0.129	0.122	0.175	0.622
1997	1.213	0.949	0.849	1.141	3.585	1.381	1.528	2.172	0.284	0.086	0.084	0.470
1998	0.810	1.237	1.208	0.963	1.157	2.472	0.993	1.005	1.351	0.189	0.057	0.370
1999	0.586	0.575	2.041	2.204	0.813	0.887	1.865	0.697	0.742	0.933	0.130	0.248
2000	0.804	0.564	1.039	3.425	1.938	0.667	0.652	1.288	0.442	0.456	0.692	0.249
2001	1.349	0.855	0.810	1.599	3.300	1.685	0.592	0.487	0.956	0.328	0.324	0.584
2002	0.887	1.569	2.063	1.711	1.535	2.522	1.313	0.422	0.320	0.647	0.219	0.514
2003	0.911	1.108	3.270	2.787	1.651	1.211	1.671	0.775	0.234	0.202	0.394	0.413
2004	0.493	0.762	1.827	4.523	2.352	1.223	0.790	1.017	0.509	0.148	0.130	0.489
2005	0.324	0.326	1.298	2.406	3.259	1.609	0.736	0.482	0.670	0.305	0.097	0.385
2006	0.687	0.243	0.474	1.476	2.021	2.362	1.092	0.476	0.312	0.458	0.237	0.307
2007	1.231	0.652	0.577	0.803	1.453	1.608	1.724	0.711	0.313	0.216	0.286	0.281
2008	0.607	1.056	0.989	0.581	0.654	1.046	1.027	1.056	0.448	0.209	0.138	0.352
2009	1.731	0.617	2.094	1.472	0.528	0.518	0.828	0.775	0.683	0.316	0.136	0.340
2010	1.186	2.373	1.261	3.551	1.337	0.399	0.413	0.541	0.479	0.485	0.200	0.266
2011	0.806	1.225	3.796	1.581	3.234	1.017	0.335	0.280	0.377	0.318	0.332	0.308
2012	0.548	0.646	1.907	5.585	1.322	2.509	0.738	0.194	0.199	0.247	0.223	0.403
2013	2.499	0.438	1.006	2.718	5.211	0.999	1.906	0.539	0.137	0.125	0.163	0.393
2014	1.228	2.847	0.749	1.485	2.103	4.204	0.659	1.267	0.344	0.089	0.090	0.351
2015	0.947	0.898	4.677	1.238	1.645	1.814	3.474	0.577	0.925	0.232	0.065	0.326
2016	0.734	0.530	1.455	6.774	1.096	1.161	1.258	2.074	0.325	0.514	0.151	0.236

Figure 14. Multi-species estimates of total biomass (million t) by age of walleye pollock in the EBS.

Tables

Table 5. Temperature-dependent Von Bertalanffy parameter (parm) estimates, standard deviation in parameter estimates (stdev), and confidence intervals (CI).

	Parm.	Estimate	stdev	lwr 95%ile	Upper						
Pollock	$t_{0,i}$	0.527	0.015	0.498	0.556						
	$\alpha0_{d,i,y}$	-0.817	0.184	-1.175	-0.458						
1990	$\alpha_{d,i,y}$	-0.056	0.183	-0.413	0.301						
1991		-0.007	0.183	-0.363	0.349						
1999		-0.011	0.183	-0.367	0.345						
2000		-0.012	0.183	-0.368	0.344						
2001		-0.017	0.183	-0.373	0.339						
2002		-0.005	0.183	-0.361	0.351						
2003		0.002	0.183	-0.354	0.358						
2004		0.000	0.183	-0.356	0.356						
2005		-0.023	0.183	-0.379	0.333						
2006		-0.009	0.183	-0.365	0.347						
2007		0.014	0.183	-0.342	0.370						
2008		0.020	0.183	-0.337	0.376						
2009		0.036	0.183	-0.320	0.392						
2010		0.048	0.183	-0.308	0.404						
2011		0.020	0.183	-0.336	0.376						
	$\beta_{d,i}$	0.010	0.001	0.008	0.011						
	$log(\sigma)$	-0.919	0.005	-0.928	-0.909						
	$log(K)$	-1.498	0.051	-1.598	-1.398						
	$log(H)$	2.794	0.036	2.723	2.864						
Pacific cod	$t_{0,i}$	-0.157	0.055	-0.265	-0.049						
	$\alpha0_{d,i,y}$	-0.375	0.197	-0.759	0.010						
1993	$\alpha_{d,i,y}$	-0.024	0.196	-0.407	0.358						
1998		0.011	0.196	-0.372	0.393						
1999		-0.006	0.196	-0.388	0.377						
2000		-0.008	0.196	-0.390	0.375						
2001		-0.012	0.196	-0.394	0.371						
2002		-0.019	0.196	-0.402	0.363						
2003		-0.004	0.196	-0.386	0.379						
2004		-0.007	0.196	-0.390	0.375						
2006		0.001	0.196	-0.381	0.384						
2007		0.014	0.196	-0.368	0.397						
2008		0.017	0.196	-0.366	0.399						
2009		0.015	0.196	-0.367	0.398						
2010		0.022	0.196	-0.361	0.404						
	$\beta_{d,i}$	0.005	0.000	0.004	0.005						
	$log(\sigma)$	-0.816	0.006	-0.828	-0.804						
	$log(K)$	-0.796	0.117	-1.025	-0.567						
	$log(H)$	2.230	0.042	2.147	2.313						
	Arrowtooth flounder, male					**Arrowtooth flounder, female**					
	$t_{0,i}$	-1.000	0.000	-1.001	-0.999		$t_{0,i}$	-0.275	0.257	-0.777	0.227
	$\alpha0_{d,i,y}$	-0.213	0.501	-1.189	0.763		$\alpha0_{d,i,y}$	-0.340	0.504	-1.323	0.642
1996	$\alpha_{d,i,y}$	0.001	0.500	-0.974	0.976	1996	$\alpha_{d,i,y}$	-0.005	0.500	-0.980	0.970
2004		-0.001	0.500	-0.976	0.974	2004		0.005	0.500	-0.970	0.980
	$\beta_{d,i}$	-0.006	0.004	-0.014	0.003		$\beta_{d,i}$	-0.011	0.004	-0.020	-0.003
	$log(\sigma)$	-1.003	0.046	-1.092	-0.913		$log(\sigma)$	-1.068	0.031	-1.127	-1.008
	$log(K)$	0.081	0.218	-0.344	0.505		$log(K)$	-0.974	0.369	-1.694	-0.255
	$log(H)$	1.646	0.051	1.546	1.746		$log(H)$	1.784	0.127	1.535	2.032

Table 6. Effective foraging days (Holsman and Aydin, 2015)

Age	Walleye pollock	Pacific cod	Arrowtooth flounder
1	365	365	365
2	365	365	365
3	365	348.66	365
4	365	315.85	365
5	360.41	292.01	359.14
6	347.8	273.87	341.22
7	338.01	259.63	326.9
8	330.18	248.2	315.17
9	323.81	238.88	305.38
10	318.54	231.2	297.1
11	314.13	224.8	290.03
12	307.91	216.75	283.94
13			278.67
14			274.08
15			270.07
16			266.57
17			263.5
18			260.81
19			258.44
20			256.36
21			254.52

Table 7. Relative foraging rate (Holsman and Aydin, 2015).

Walleye pollock	Age										
Year	1	2	3	4	5	6	7	8	9	10	11	12
1979	0.19	0.20	0.20	0.21	0.21	0.22	0.23	0.23	0.24	0.25	0.25	0.26
1980	0.19	0.20	0.20	0.21	0.21	0.22	0.23	0.23	0.24	0.25	0.25	0.26
1981	0.21	0.21	0.21	0.22	0.22	0.23	0.23	0.23	0.24	0.24	0.25	0.25
1982	0.21	0.22	0.22	0.23	0.24	0.24	0.25	0.26	0.27	0.27	0.28	0.29
1983	0.18	0.18	0.19	0.19	0.20	0.20	0.21	0.21	0.21	0.22	0.22	0.23
1984	0.21	0.21	0.22	0.22	0.23	0.23	0.24	0.24	0.25	0.25	0.26	0.27
1985	0.21	0.21	0.22	0.22	0.23	0.24	0.24	0.25	0.26	0.26	0.27	0.28
1986	0.20	0.20	0.20	0.21	0.22	0.23	0.23	0.24	0.25	0.25	0.26	0.27
1987	0.20	0.21	0.21	0.22	0.22	0.23	0.23	0.24	0.24	0.25	0.25	0.26
1988	0.19	0.20	0.20	0.21	0.22	0.22	0.23	0.24	0.24	0.25	0.26	0.27
1989	0.19	0.20	0.20	0.20	0.21	0.22	0.22	0.23	0.23	0.24	0.24	0.25
1990	0.20	0.20	0.20	0.21	0.21	0.22	0.22	0.23	0.23	0.24	0.24	0.25
1991	0.20	0.20	0.21	0.21	0.22	0.23	0.23	0.24	0.25	0.25	0.26	0.27
1992	0.19	0.20	0.20	0.21	0.22	0.22	0.23	0.24	0.25	0.25	0.26	0.27
1993	0.20	0.20	0.21	0.21	0.22	0.23	0.23	0.24	0.24	0.25	0.25	0.26
1994	0.20	0.20	0.21	0.22	0.22	0.23	0.24	0.25	0.26	0.26	0.27	0.28
1995	0.20	0.20	0.21	0.21	0.22	0.23	0.24	0.25	0.25	0.26	0.27	0.28
1996	0.20	0.20	0.21	0.21	0.21	0.22	0.22	0.23	0.23	0.24	0.24	0.25
1997	0.18	0.18	0.19	0.19	0.20	0.20	0.21	0.22	0.22	0.23	0.23	0.24
1998	0.21	0.21	0.22	0.22	0.23	0.23	0.24	0.24	0.25	0.25	0.26	0.27
1999	0.19	0.20	0.20	0.21	0.22	0.23	0.23	0.24	0.25	0.26	0.27	0.28
2000	0.19	0.20	0.20	0.21	0.21	0.22	0.23	0.23	0.24	0.24	0.25	0.26
2001	0.20	0.20	0.21	0.21	0.22	0.22	0.23	0.23	0.24	0.24	0.25	0.26
2002	0.19	0.19	0.19	0.20	0.20	0.21	0.21	0.22	0.22	0.23	0.23	0.24
2003	0.20	0.21	0.21	0.21	0.22	0.22	0.23	0.23	0.24	0.24	0.25	0.25
2004	0.19	0.19	0.19	0.20	0.20	0.21	0.21	0.22	0.22	0.22	0.23	0.24
2005	0.20	0.20	0.21	0.21	0.22	0.22	0.23	0.23	0.23	0.24	0.24	0.25
2006	0.19	0.19	0.20	0.20	0.21	0.22	0.23	0.23	0.24	0.25	0.25	0.27
2007	0.19	0.20	0.20	0.21	0.22	0.23	0.24	0.24	0.25	0.26	0.27	0.28
2008	0.19	0.19	0.20	0.20	0.21	0.22	0.23	0.24	0.25	0.26	0.27	0.28
2009	0.19	0.20	0.20	0.21	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29
2010	0.19	0.20	0.20	0.21	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.30
2011	0.20	0.21	0.21	0.22	0.22	0.23	0.23	0.24	0.25	0.25	0.26	0.28
2012	0.19	0.20	0.20	0.21	0.21	0.22	0.23	0.23	0.24	0.25	0.25	0.26

Table 7. (continued) Relative foraging rate (Holsman and Aydin, 2015).

Pacific Cod	Age											
	1	2	3	4	5	6	7	8	9	10	11	12
1979	0.33	0.35	0.39	0.45	0.55	0.69	0.83	0.97	1.07	1.13	1.16	1.20
1980	0.33	0.35	0.39	0.45	0.55	0.69	0.83	0.97	1.07	1.13	1.16	1.20
1981	0.32	0.34	0.37	0.44	0.53	0.67	0.84	1.03	1.21	1.33	1.38	1.31
1982	0.32	0.34	0.39	0.48	0.61	0.78	0.93	1.03	1.07	1.11	1.20	1.57
1983	0.36	0.38	0.42	0.49	0.59	0.73	0.90	1.08	1.23	1.35	1.42	1.45
1984	0.33	0.34	0.38	0.44	0.53	0.67	0.82	1.00	1.15	1.27	1.33	1.33
1985	0.35	0.36	0.40	0.47	0.57	0.71	0.86	1.00	1.13	1.21	1.26	1.30
1986	0.35	0.37	0.41	0.48	0.59	0.72	0.86	0.99	1.08	1.13	1.16	1.19
1987	0.32	0.34	0.38	0.44	0.54	0.67	0.83	1.00	1.14	1.24	1.29	1.29
1988	0.34	0.35	0.39	0.46	0.56	0.69	0.83	0.96	1.05	1.10	1.13	1.16
1989	0.35	0.37	0.41	0.48	0.59	0.73	0.90	1.07	1.21	1.31	1.36	1.37
1990	0.34	0.35	0.39	0.46	0.56	0.69	0.84	0.98	1.09	1.16	1.19	1.23
1991	0.33	0.35	0.39	0.45	0.55	0.68	0.83	0.96	1.07	1.13	1.16	1.20
1992	0.33	0.35	0.38	0.45	0.55	0.68	0.81	0.93	1.00	1.03	1.05	1.07
1993	0.31	0.32	0.35	0.40	0.46	0.54	0.63	0.73	0.83	0.92	0.99	1.08
1994	0.34	0.35	0.39	0.46	0.57	0.70	0.83	0.95	1.02	1.05	1.07	1.09
1995	0.33	0.35	0.39	0.46	0.57	0.69	0.83	0.94	1.00	1.02	1.02	1.04
1996	0.31	0.32	0.35	0.41	0.51	0.63	0.79	0.95	1.09	1.20	1.25	1.23
1997	0.33	0.34	0.38	0.45	0.55	0.68	0.83	0.97	1.07	1.13	1.17	1.20
1998	0.30	0.32	0.36	0.43	0.54	0.70	0.89	1.08	1.21	1.26	1.21	1.02
1999	0.33	0.35	0.39	0.45	0.55	0.66	0.78	0.88	0.94	0.96	0.95	0.92
2000	0.33	0.34	0.38	0.44	0.53	0.64	0.76	0.88	0.98	1.04	1.08	1.10
2001	0.32	0.34	0.37	0.43	0.51	0.61	0.73	0.85	0.97	1.06	1.12	1.18
2002	0.32	0.33	0.36	0.41	0.48	0.57	0.68	0.80	0.91	1.02	1.11	1.20
2003	0.31	0.33	0.36	0.41	0.50	0.62	0.77	0.94	1.10	1.23	1.30	1.31
2004	0.31	0.32	0.35	0.40	0.48	0.58	0.71	0.84	0.96	1.07	1.15	1.21
2005	0.32	0.33	0.37	0.43	0.53	0.66	0.83	0.99	1.14	1.25	1.30	1.27
2006	0.35	0.37	0.41	0.48	0.59	0.72	0.86	0.97	1.04	1.07	1.07	1.09
2007	0.34	0.36	0.41	0.50	0.63	0.80	0.95	1.04	1.07	1.09	1.14	1.42
2008	0.34	0.36	0.41	0.50	0.63	0.79	0.94	1.01	1.03	1.04	1.10	1.47
2009	0.33	0.35	0.40	0.50	0.64	0.82	0.97	1.04	1.05	1.10	1.25	1.94
2010	0.33	0.35	0.41	0.51	0.68	0.87	1.02	1.07	1.11	1.25	1.66	3.43
2011	0.32	0.34	0.38	0.45	0.56	0.71	0.89	1.08	1.24	1.33	1.34	1.23
2012	0.33	0.35	0.39	0.45	0.55	0.69	0.83	0.97	1.07	1.13	1.16	1.20

Table 7. (continued) Relative foraging rate (Holsman and Aydin, 2015).

Arrowtooth flounder

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1979	0.35	0.34	0.34	0.33	0.33	0.33	0.33	0.34	0.36	0.40	0.45	0.52	0.60	0.68	0.76	0.82	0.86	0.87	0.86	0.83	0.79
1980	0.35	0.34	0.34	0.33	0.33	0.33	0.33	0.34	0.36	0.40	0.45	0.52	0.60	0.68	0.76	0.82	0.86	0.87	0.86	0.83	0.79
1981	0.27	0.26	0.25	0.24	0.22	0.21	0.20	0.20	0.22	0.25	0.30	0.38	0.47	0.57	0.66	0.73	0.75	0.73	0.67	0.60	0.51
1982	0.48	0.48	0.48	0.48	0.48	0.48	0.49	0.51	0.54	0.59	0.66	0.74	0.83	0.93	1.02	1.09	1.15	1.18	1.19	1.18	1.15
1983	0.34	0.34	0.33	0.32	0.30	0.29	0.28	0.29	0.31	0.34	0.40	0.48	0.58	0.68	0.78	0.86	0.90	0.90	0.87	0.82	0.75
1984	0.24	0.24	0.23	0.22	0.21	0.20	0.19	0.19	0.20	0.23	0.26	0.32	0.38	0.46	0.53	0.60	0.64	0.66	0.65	0.62	0.58
1985	0.37	0.37	0.36	0.35	0.34	0.34	0.34	0.35	0.37	0.41	0.47	0.55	0.65	0.74	0.83	0.90	0.94	0.95	0.92	0.88	0.82
1986	0.39	0.39	0.39	0.39	0.39	0.39	0.40	0.42	0.44	0.48	0.54	0.60	0.67	0.75	0.82	0.88	0.92	0.95	0.96	0.96	0.95
1987	0.29	0.29	0.28	0.27	0.26	0.24	0.24	0.24	0.25	0.27	0.31	0.36	0.43	0.50	0.58	0.65	0.71	0.75	0.77	0.77	0.75
1988	0.33	0.33	0.33	0.33	0.32	0.33	0.33	0.35	0.37	0.41	0.45	0.52	0.58	0.65	0.72	0.77	0.80	0.81	0.81	0.79	0.77
1989	0.34	0.34	0.33	0.32	0.30	0.29	0.29	0.29	0.31	0.35	0.40	0.48	0.57	0.66	0.76	0.83	0.88	0.89	0.88	0.84	0.78
1990	0.33	0.33	0.32	0.32	0.31	0.31	0.31	0.32	0.34	0.37	0.41	0.47	0.54	0.62	0.69	0.76	0.80	0.83	0.83	0.82	0.80
1991	0.32	0.32	0.32	0.31	0.31	0.31	0.31	0.32	0.34	0.37	0.42	0.48	0.55	0.62	0.69	0.75	0.79	0.81	0.81	0.80	0.77
1992	0.35	0.35	0.36	0.36	0.37	0.37	0.38	0.40	0.43	0.47	0.51	0.57	0.63	0.69	0.75	0.80	0.84	0.87	0.89	0.89	0.89
1993	0.33	0.32	0.32	0.31	0.30	0.29	0.29	0.29	0.31	0.35	0.40	0.48	0.56	0.65	0.74	0.80	0.84	0.84	0.82	0.78	0.72
1994	0.35	0.36	0.36	0.36	0.37	0.38	0.39	0.41	0.44	0.48	0.53	0.58	0.65	0.71	0.77	0.82	0.86	0.88	0.90	0.90	0.89
1995	0.34	0.34	0.34	0.35	0.36	0.37	0.39	0.41	0.44	0.48	0.52	0.57	0.63	0.69	0.74	0.79	0.83	0.87	0.90	0.92	0.93
1996	0.28	0.28	0.27	0.26	0.24	0.23	0.22	0.22	0.23	0.25	0.28	0.32	0.37	0.43	0.50	0.57	0.63	0.68	0.72	0.74	0.75
1997	0.33	0.33	0.32	0.32	0.31	0.31	0.31	0.32	0.33	0.36	0.40	0.45	0.51	0.58	0.65	0.71	0.77	0.80	0.83	0.83	0.83
1998	0.29	0.28	0.27	0.26	0.25	0.23	0.22	0.23	0.24	0.26	0.31	0.37	0.44	0.53	0.61	0.69	0.75	0.78	0.78	0.75	0.71
1999	0.29	0.30	0.31	0.32	0.34	0.37	0.39	0.42	0.45	0.47	0.49	0.51	0.53	0.56	0.60	0.66	0.73	0.81	0.92	1.04	1.18
2000	0.35	0.35	0.35	0.35	0.34	0.35	0.35	0.37	0.39	0.43	0.48	0.55	0.62	0.69	0.76	0.81	0.85	0.86	0.86	0.85	0.82
2001	0.34	0.34	0.33	0.32	0.31	0.31	0.30	0.31	0.33	0.36	0.41	0.48	0.56	0.64	0.72	0.79	0.84	0.86	0.86	0.84	0.81
2002	0.30	0.30	0.29	0.28	0.27	0.26	0.25	0.25	0.27	0.30	0.34	0.40	0.47	0.56	0.64	0.71	0.77	0.80	0.80	0.79	0.75
2003	0.28	0.28	0.27	0.25	0.24	0.23	0.22	0.21	0.22	0.24	0.27	0.32	0.38	0.46	0.54	0.62	0.69	0.74	0.77	0.78	0.78
2004	0.28	0.28	0.27	0.26	0.25	0.24	0.23	0.24	0.26	0.30	0.37	0.45	0.55	0.65	0.72	0.75	0.73	0.67	0.59	0.49	0.41
2005	0.30	0.29	0.29	0.27	0.26	0.25	0.24	0.24	0.24	0.26	0.28	0.32	0.37	0.42	0.48	0.55	0.61	0.67	0.72	0.75	0.78
2006	0.35	0.35	0.35	0.36	0.37	0.38	0.40	0.42	0.45	0.49	0.53	0.59	0.64	0.70	0.76	0.81	0.85	0.88	0.91	0.93	0.94
2007	0.36	0.37	0.37	0.37	0.38	0.39	0.41	0.43	0.46	0.50	0.56	0.62	0.68	0.75	0.81	0.86	0.90	0.92	0.93	0.94	0.93
2008	0.36	0.37	0.37	0.38	0.39	0.40	0.42	0.45	0.48	0.52	0.56	0.62	0.67	0.73	0.79	0.84	0.89	0.93	0.97	1.00	1.03
2009	0.35	0.35	0.36	0.36	0.37	0.38	0.39	0.41	0.44	0.48	0.54	0.59	0.66	0.72	0.78	0.83	0.87	0.89	0.90	0.91	0.90
2010	0.37	0.37	0.37	0.37	0.37	0.38	0.39	0.41	0.43	0.47	0.52	0.58	0.65	0.72	0.78	0.84	0.88	0.90	0.91	0.91	0.90
2011	0.28	0.28	0.27	0.26	0.24	0.23	0.22	0.22	0.24	0.27	0.32	0.38	0.47	0.56	0.65	0.72	0.76	0.77	0.74	0.70	0.63
2012	0.35	0.34	0.34	0.33	0.33	0.33	0.33	0.34	0.36	0.40	0.45	0.52	0.60	0.68	0.76	0.82	0.86	0.87	0.86	0.83	0.79

Table 8. Proportion mature and residual natural mortality for each species in the model.

Age	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
Proportion mature																					
Walleye pollock	0.00	0.01	0.29	0.64	0.84	0.90	0.95	0.96	0.97	1.00	1.00	1.00									
Pacific cod	0.00	0.02	0.06	0.14	0.30	0.53	0.75	0.89	0.95	0.98	0.99	1.00									
Arrowtooth flounder	0.00	0.00	0.01	0.02	0.06	0.16	0.34	0.59	0.80	0.92	0.97	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Residual mortality (M1): Single-species																					
Walleye pollock	0.90	0.45	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30									
Pacific cod	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34									
Arrowtooth flounder	0.27	0.26	0.26	0.25	0.25	0.24	0.24	0.23	0.23	0.23	0.22	0.22	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21
Residual mortality (M1): Multi-species																					
Walleye pollock	0.01	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30									
Pacific cod	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34									
Arrowtooth flounder	0.27	0.26	0.26	0.25	0.25	0.24	0.24	0.23	0.23	0.23	0.22	0.22	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21

Table 9. Components of the likelihood function for each species *i* of age *j* in year *y*. See Tables 2 and 3 for parameter definitions.

Description	Equation	Data source
Data components		
BT survey biomass	$\sum_i \sum_y \frac{\left[\ln\left(\beta^s_{i,y}\right)-\ln\left(\hat{\beta}^s_{i,y}\right)\right]^2}{2\sigma^2_{s,i}}$	NFMS annual EBS BT survey (1979–2012)
BT survey age composition	$-\sum_i n_i \sum_y \sum_j \left(O^s_{ij,y}+v\right)\ln\left(\hat{O}^s_{ij,y}+v\right)$	NFMS annual EBS BT survey (1979–2012)
EIT survey biomass	$\sum_y \frac{\left[\ln(\beta^{eit}_y)-\ln\left(\hat{\beta}^{eit}_y\right)\right]^2}{2\sigma^2_{eit}},\ \sigma_{eit}=0.2$	Pollock acoustic trawl survey (1979–2012)
EIT age composition	$-n\sum_y \sum_j \left(O^{eit}_{1j,y}+v\right)\ln\left(\hat{O}^{eit}_{1j,y}+v\right)$	Pollock acoustic trawl survey (1979–2012)
Total catch	$\sum_i \sum_y \frac{\left[\ln\left(C^*_{i,y}\right)-\ln\left(C^*_{i,y}\right)\right]^2}{2\sigma^2_C},\ \sigma_C=0.05$	Fishery observer data (1979–2012)
Fishery age composition	$-\sum_i n_i \sum_y \sum_j \left(O^f_{ij,y}+v\right)\ln\left(\hat{O}^f_{ij,y}+v\right)$	Fishery observer data (1979–2012)
Penalties		
Fishery selectivity	$\sum_i \sum_j^{A_i-1} \chi\cdot\left[\ln\left(\frac{\eta^f_{ij}}{\eta^f_{ij+1}}\right)-\ln\left(\frac{\eta^f_{ij+1}}{\eta^f_{ij+2}}\right)\right]^2,\ \chi=\begin{cases}20,\ if & \eta^f_{ij}>\eta^f_{ji+1}\\ 0,\ if & \eta^f_{ij}\le\eta^f_{ij+1}\end{cases}$	
Priors		
	$\sum_i \sum_y \left(\tau_{i,y}\right)^2$	
	$\sum_i \sum_y \left(N_{0,ij}\right)^2$	
	$\sum_i \sum_y \left(\varepsilon_{i,y}\right)^2$	

$v=0.001$.