



Time-varying predation as a modifier of constant natural mortality for Gulf of Alaska walleye pollock

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ABSTRACT

Although highly variable in time and space, predation remains the greatest source of mortality for juvenile and lower trophic-level fishes. As such, predation can have substantial and long-term effects on the dynamics of these prey. Gulf of Alaska walleye pollock (*Gadus chalcogrammus*) has shown considerable variability in biomass over the past four decades. During this same time, the demersal fish community transitioned from being dominated by pollock to a system comprised primarily of upper trophic-level predators. We estimated time-varying predation mortality to better understand its effects on the population dynamics of pollock in this currently “top heavy” system. Our index of predation accounted for spatiotemporal variation in predator biomass, bioenergetics-based rations, and age-specific proportions of pollock consumed (1990–2019). To evaluate population-level impacts of predation, we included an index of removals as part of the stock assessment model. This formulation allowed for non-annual data inputs and included a proportionality constant with which to scale predation. Age-specific natural mortality was allowed to vary according to a penalized random walk. We found that natural mortality ranged from 37% higher to 17% lower than the long-term mean. Resulting estimates of total pollock biomass differed by as much as 37% relative to a model without time-varying natural mortality, though the maximum difference for exploitable biomass was only 14%. Using an empirically-derived predation index to modify constant natural mortality allows stock assessment scientists to evaluate impacts of time-varying predation on assessed species. This approach provides a relatively simple way of incorporating ecological information into single-species stock assessments and may reduce bias compared to conventional models that do not account for changes in predation mortality. Notably, including predation mortality in single-species assessments may help identify inconsistencies in biomass estimates that warrant further consideration.

1. Introduction

Although highly variable in time and space, predation remains the greatest source of mortality for juvenile and lower trophic-level fishes (Bax, 1991; Schoener, 1983). As such, cumulative effects of predation are likely to have substantial and long-term effects on the dynamics of these prey. While the importance of predation has long been recognized, most stock assessments continue to assume time-invariant natural mortality (Punt et al., 2021). Multispecies modeling approaches have been developed to explore the impacts of predation on population dynamics (e.g., Aydin et al., 2007; Gaichas et al., 2010; Van Kirk et al., 2012). These approaches, however, add model complexity by assuming functional predator-prey relationships or incorporating information about prey availability, thereby introducing parameters that are difficult

to estimate reliably and limiting their utility for providing management advice. Here, we apply a relatively simple approach that integrates predation mortality into the single-species modeling framework. We demonstrate this process in a stock assessment model for walleye pollock (*Gadus chalcogrammus*) in the Gulf of Alaska, an important fisheries resource managed by the North Pacific Fishery Management Council (NPFMC) and the National Marine Fisheries Service (NMFS).

Walleye pollock (hereafter, pollock) is a key component of the continental shelf ecosystem in the Gulf of Alaska (GOA), serving as important prey for several groundfish predators (Aydin et al., 2007; Gaichas and Francis, 2008). The GOA ecosystem has undergone several notable reorganizations, including a well-documented regime shift in 1977 from a shrimp and crustacean dominated system to one dominated by gadids (Anderson and Piatt, 1999). More recently, the gadid-dominated system

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was impacted by substantial increases in the abundance of arrowtooth flounder (*Atheresthes stomias*), a piscivorous flatfish (Duffy-Anderson et al., 2005). Although abundance trends for arrowtooth flounder have stabilized over the past decade, it remains the most abundant species in the GOA shelf ecosystem, with area-swept estimates on the order of 1.0–2.0 million tons (Spies et al., 2019). Arrowtooth flounder is lightly exploited, suggesting that changes in abundance are driven by environmental forcing rather than changes in fishing intensity. These large-scale ecosystem changes highlight the need to evaluate impacts of predation on pollock population dynamics.

Several modeling approaches have been developed to evaluate the impacts of predation in the Gulf of Alaska. These approaches range from augmented single species models, to multispecies and whole ecosystem models. Hallowed et al. (2000) developed a single-species assessment model for GOA pollock where predation is modeled as a type of fishery. Gaichas (2006), Aydin et al. (2007), Gaichas and Francis (2008), and Gaichas et al., (2010, 2011) used Ecopath and other relatively simple ecosystem models to assess energy flow in the Gulf of Alaska. An important outcome of this research was the identification of a suite of highly connected species, namely Pacific cod (*Gadus macrocephalus*), walleye pollock, Pacific halibut (*Hippoglossus stenolepis*), and arrowtooth flounder. This finding suggested that modeling these species would capture key ecosystem dynamics. Subsequent multispecies models found an increase in predation on GOA pollock, but also highlighted tradeoffs between the greater ecological realism and greater uncertainty in estimated parameters that comes from increased model complexity (Van Kirk et al., 2010, 2012).

While there is a rich history of ecological modeling in the Gulf of Alaska, there are pressing research needs to address both tactical and strategic management objectives, particularly in the face of climate change (Hallowed et al., 2019). The objective of this paper is to demonstrate a relatively simple and generally applicable approach for incorporating time-varying predation mortality into the single-species pollock assessment. We employ techniques similar to those used for modeling predation in other stock assessment models (Livingston and Methot, 2000; Hallowed et al., 2000; A'mar et al., 2009; Spencer et al., 2016), but more closely follow methods developed by Moustahfid et al. (2009) where predation (in biomass) is fit directly in the model. We believe that directly modeling predation is simpler and more generally applicable than modeling proxies such as predator biomass. Our approach differs from Moustahfid et al. (2009) in that we use a more flexible approach for modeling time-varying predation mortality, rather than assuming predation mortality is exactly analogous to another fishery. We also note the utility of applying similar techniques to different species and systems as a way of identifying their general applicability.

The data requirements for this approach are relatively modest, but depend on ongoing programs to collect and analyze density and diet data for focal species. Long-term, spatially expansive surveys and advances in spatiotemporal modeling support the use of empirical estimates of predation for Gulf of Alaska pollock in particular. Pollock's major groundfish predators are all commercially valuable and thus have regular stock assessments that produce robust biomass estimates. These same species are amply sampled in time and space by at least one standardized survey. Furthermore, consistent sampling of stomach contents provides valuable information on predator diets and sufficient laboratory data to estimate changing energetic needs (Livingston et al., 2017). We synthesis and use this information in a single-species stock assessment that generates advice on acceptable biological catches (ABCs) to the North Pacific Fishery Management Council and the National Marine Fisheries Service.

2. Material and methods

2.1. Estimating time-varying predation

We estimated pollock predation in biomass for every year with standardized bottom trawl survey data (triennially from 1990 to 1999 and biennially from 2001 to 2019; von Szalay and Raring, 2016). This index accounted for predation by five major groundfish predators: arrowtooth flounder, Pacific cod, Pacific halibut, sablefish (*Anoplopoma fimbria*), and walleye pollock conspecifics. Although sablefish are not generally considered a major predator of pollock, the sablefish stock in the Gulf of Alaska is increasing in abundance. Cumulatively, these species are responsible for more than 80% of total pollock mortality due to predation in the Gulf of Alaska (Gaichas et al., 2015; Dorn et al., 2017). For maximum comparability, we restricted predation indices to the area encompassed by the main stock assessment model for Gulf of Alaska pollock (i.e., west of -140° longitude). We estimated predation $P_{s,a,y}$ for each predator species s , pollock age class a , and year y as follows:

$$P_{s,a,y} = B_{s,y} * rD_{s,y} * \bar{C}_{s,y} * p_{s,y} * A_{a,s,y},$$

where $B_{s,y}$ is total predator biomass (metric tons converted to g) as estimated in the most recent stock assessment, $rD_{s,y}$ is relative predator density (unitless) modeled from fishery-independent survey data (estimated throughout the Gulf of Alaska and summed within the area of the pollock assessment), $\bar{C}_{s,y}$ is mean bioenergetics-based annual rations (g prey per g predator), $p_{s,y}$ is the proportion of pollock (unitless) observed in food habits data, and $A_{a,s,y}$ is the diet-based proportion of each pollock age class (unitless) (Tables S1 and S2). Age classes consisted of juvenile (1 and 2 years) and adult (3 + years) pollock, which were estimated using length-weight and age-length relationships derived from bottom trawl survey data. For each component of the predation index, we restricted predator sizes to those encompassed in stock assessment models: Arrowtooth Flounder ≥ 19 cm (Spies et al., 2019), Pacific Cod ≥ 0 cm (Barbeaux et al., 2019), Pacific Halibut ≥ 82 cm (Stewart and Hicks, 2020), Sablefish ≥ 47 cm (Hanselman et al., 2019), and Walleye Pollock ≥ 35 cm (Dorn et al., 2019). Although using size cutoffs for predators invariably underestimates consumption of a given prey taxa, we do not expect that doing so negatively impacts our conclusions when predation is presented as an index. We summed predator-specific predation to estimate "total" age-specific predation in millions of metric tons ($P_{a,y} = \sum_{s=1}^S P_{s,a,y}$). We then divided age-specific predation by mean weight-at-age for pollock to estimate predation in numbers. Methods followed those developed by Barnes et al. (2020). All data and code necessary to estimate time-varying predation for Gulf of Alaska pollock are publicly available at: <https://github.com/cheryl-barnes/Time-varyingPredation>.

2.2. Modifying the GOA pollock assessment model to incorporate a predation index

2.2.1. Description of the GOA pollock assessment model

The assessment model used for GOA pollock is an age-structured assessment coded in AD Model Builder (Version 10.1), a C++ software language extension and automatic differentiation library (Fournier et al., 2012). Details of the population dynamics and estimation equations are given in Dorn et al. (2019). Here, we describe the basic features of the model before developing the predation-based modifier of constant natural mortality. The pollock assessment covers the period from 1970 to 2019 (50 years) and pollock ages 1–10 years, with age-10 defined as a "plus" group (i.e., all individuals age-10 and older). Population dynamics were modeled using standard formulations for mortality and fishery catch (e.g., Fournier and Archibald, 1982; Deriso et al., 1985; Hilborn and Walters, 1992). Year- and age-specific fishing mortality was modeled as a product of a year effect that represents the full-selection fishing mortality and an age effect representing the selectivity of that age group to the fishery. The age effect was modeled using a

double-logistic function with time-varying parameters (Dorn and Methot, 1990; Sullivan et al., 1997). The model was fit to time series of catch biomass, survey indices of abundance, and estimates of age and length composition from the fishery and surveys (Table 1). Models included parameters for recruitment, fishing mortality, fishery selectivity, survey catchability, and survey selectivity (Table S3). Fishery selectivity and some survey catchabilities were modeled as time-varying using random walk process error. Model parameters were estimated by maximizing the log likelihood of the data, viewed as a function of the parameters. Mean-unbiased log-normal likelihoods were used for survey biomass and total catch estimates. Multinomial likelihoods were used for age and length composition data.

2.2.2. Modeling time-varying M2: the predation element of natural mortality

The current version of the pollock assessment model uses a fixed pattern of age-specific natural mortality. This natural mortality schedule was obtained by taking the average of several approaches, including empirical methods (Brodziak et al., 2011; Lorenzen, 1996; and Gislason et al., 2010) and results from previous models that accounted for predation (Hollowed et al., 2000; Van Kirk et al., 2010, 2012). The ensemble average showed a reasonable pattern of declining natural mortality from 1.39 at age-1–0.34 at age-5, the approximate age at maturity. On average, empirical methods and predation models gave similar results.

For this paper, natural mortality (M) in the pollock assessment model was partitioned into residual mortality (often called M1 in multispecies modeling) and predation mortality (often referred to as M2). Predation mortality was made time-varying according to a random walk. Natural mortality for pollock age *a* in year *y* is given by:

$$M_{a,y} = M_{res} + M_a \exp M_y \quad ,$$

where *M_{res}* is the residual natural mortality (assumed age and year invariant and fixed to 0.05), *M_a* is the additional fixed age-specific natural mortality, and *M_y* is a parameter that quantifies the interannual log-scale deviations in natural mortality. The assumed value for *M_{res}* is close to the value estimated for pollock age-3 and older (Hollowed et al., 2000). Sensitivity runs that halved (0.025) and doubled (0.10) the value for *M_{res}* had results that were almost identical to the model with *M_{res}* = 0.05, indicating a lack of sensitivity to this assumption. The vector of annual *M_y* is specified in ADMB as a zero-sum deviate vector. A random walk process was introduced by assuming changes from one year to the next in *M_y* given an annual error term *e_y*:

$$M_{y+1} = M_y + e_y \quad .$$

The error term is assumed to be normally distributed with a mean of zero and variance σ_{rw} , implying a log likelihood component of:

Table 1

Data sources for the Gulf of Alaska pollock assessment (Dorn et al., 2019). Addition information on each data source is available in Dorn et al. (2019).

Source	Data	Years
Fishery	Total catch (t)	1970–2019
Fishery	Age composition	1975–2018
Shelikof Strait acoustic survey	Biomass (t)	1992–2019
Shelikof Strait acoustic survey	Age composition	1992–2019
Summer acoustic survey	Biomass (t)	2013–2019
Summer acoustic survey	Age composition	2013–2017
NMFS bottom trawl survey	Area-swept biomass (t)	1990–2019
NMFS bottom trawl survey	Age composition	1990–2017
ADF&G large-mesh trawl survey	Delta-GLM index	1988–2019
ADF&G large-mesh bottom trawl survey	Age composition	2000–2018
NMFS bottom trawl survey	Total predation (t)	1990–2019
NMFS bottom trawl survey	Age composition of predation	1990–2019

$$LogLike = -0.5 \sum \left(\frac{M_{y+1} - M_y}{\sigma_{rw}} \right)^2 \quad .$$

Inherent in the assumption of random walk error is that changes in predation are autocorrelated. This is reasonable given that changes in predation are likely driven by changes in the abundance of predators, which are likely to have a high degree of autocorrelation.

2.2.3. Adding a likelihood component for an index of predation

The predicted biomass of annual deaths due to predation \hat{P}_y is given by an adaptation of the familiar catch equation (Beverson and Holt, 1957; Baranov, 1918):

$$\hat{P}_y = \sum_a W_{a,y} N_{a,y} \frac{M_a \exp M_y}{Z_{a,y}} (1 - e^{-Z_{a,y}}) \quad ,$$

where *W_{a,y}* is weight at age from the NMFS bottom trawl survey in year *y*, *N_{a,y}* is population numbers at age, and *Z_{a,y}* = *F_{a,y}* + *M_{a,y}* is total annual mortality.

Pollock predation is related to model predictions using a lognormal likelihood component that includes a scaling term, denoted the predation coefficient *q*, which functions similarly to the catchability coefficient that relates predicted survey biomass to observed survey biomass. This scaling term accounts for the fact that estimated predation does not represent total predation on pollock and allows potential predation to be subject to unquantified biases:

$$LogLike = -0.5 \sum_y \left(\frac{\log(P_y) - \log(q\hat{P}_y) + \frac{\sigma_p^2}{2}}{\sigma_p^2} \right)^2 \quad ,$$

where σ_p^2 is the log scale observation error of predation.

Model behavior was explored by conducting a number of model runs. We compared model runs to the 2019 stock assessment model (Dorn et al., 2019), in which there was no time-variation in predation mortality. In addition to this model, runs included (1) modeling time-varying predation but not including the predation index, (2) a “force-to-fit” scenario in which the predation index is assumed to be very precise (CV = 0.01), and (3) a new base model run in which a more plausible CV of 0.25 is assumed for the precision of the predation index. Uncertainty estimates are not available for the predation index. A coefficient of variation of 0.25 was considered reasonable because is moderately larger than the uncertainty in biomass estimates from the NMFS bottom trawl survey (median CV = 0.16), reflecting the likely greater uncertainty of the predation estimates relative to survey biomass estimates. The model runs described above function as bracketing runs to evaluate the sensitivity to this assumption. Not including the data at all is analogous to assuming the variance is infinite, while the “force-to-fit” scenario assumes very low uncertainty.

The effect of time-varying predation mortality on management reference points was evaluated by calculating the annual *F_{40%}* fishing mortality rate (O’Leary et al., 2020), which is the fishing mortality rate at which spawning biomass per recruit is 40% of the unfished spawning biomass per recruit, using the parameters defined for that year. For Gulf of Alaska pollock, time-varying parameters include estimates of spawning weight at age from the Shelikof Strait acoustic survey, and model-based estimates of time-varying selectivity and predation mortality. The *F_{40%}* fishing mortality rate is used to establish the allowable biological catch (ABC) under Tier 3 of the North Pacific Fishery Management Council’s groundfish tier system used for harvest specification (DiCosimo et al., 2010).

2.2.4. Using predation age composition to inform age-specific predation

The age-specific estimates of predation described above were used to evaluate the feasibility of estimating an age-specific mortality schedule in the assessment model. Model predicted predation by age is given by:

$$\hat{P}_{a,y} = N_{a,y} \frac{M_a \exp M_y}{Z_{a,y}} (1 - e^{-Z_{a,y}}) \quad ,$$

The predation at age estimates were converted to proportions and fit using standard multinomial likelihoods for age compositions (Dorn et al., 2019). Ages 1–3 were fit, with age-3 acting as an accumulator age, that is, all ages 3 and older. The age-specific predation parameters for ages 1–3 were converted from fixed parameters to estimated parameters and subject to a normal Bayesian prior that reflected the variability of the different approaches to estimate an age-specific pattern (CV = 0.41, 0.21, and 0.18 for the age-1, age-2, and age-3 prior respectively). Limiting estimation of age-specific predation to ages 1–3 years recognizes that fact that predation at age data is likely to be informative only about predation mortality for these younger ages. This model used the same configuration of time-varying predation mortality as for the base case described above.

3. Results

3.1. Time-varying predation mortality

Predation mortality was highly variable for Gulf of Alaska pollock (4.14 ± 1.56 mill MT; 26.5 ± 12.2 trillion pollock), ranging from 2.00 mill MT (12.6 trillion pollock) in 2011–7.07 mill MT (61.7 trillion pollock) in 1996 (Fig. 1). In terms of biomass proportions, we found that more adult (age-3 +) pollock were consumed throughout the time series (0.619 ± 0.098), followed by age-2 (0.183 ± 0.082) and age-1 (0.163 ± 0.057) juveniles (Fig. 1A). Age-1 pollock made up more than half of numerical proportions (0.587 ± 0.075), followed by age-3 + (0.244 ± 0.072) and age-2 (0.169 ± 0.069) pollock (Fig. 1B).

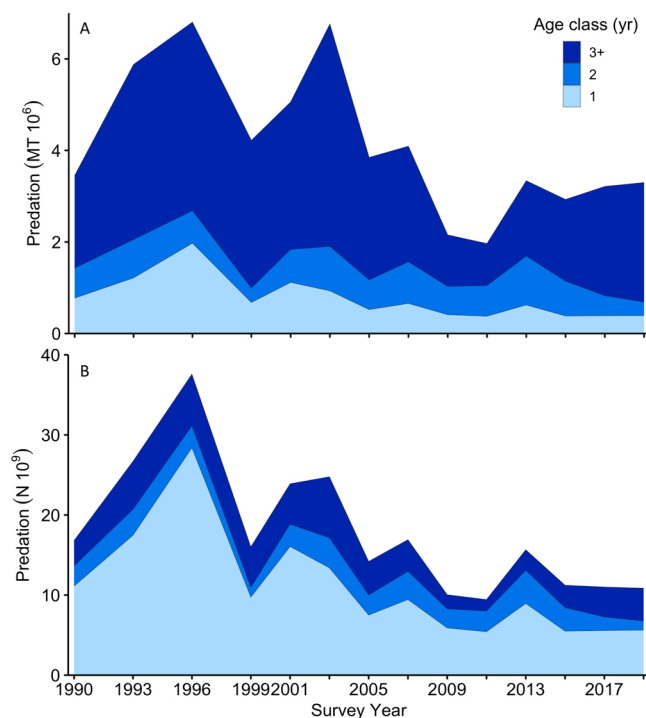


Fig. 1. Predation mortality estimates for walleye pollock in the Gulf of Alaska, 1990–2019. Age-specific predation is shown in A) biomass (millions of metric tons) and B) numbers (trillions) of pollock. Predation mortality includes consumption by all five major groundfish predators: arrowtooth flounder, Pacific cod, Pacific halibut, sablefish, and walleye pollock.

3.2. Modeling predation mortality in the Gulf of Alaska pollock assessment

3.2.1. Model runs to evaluate model behavior when estimating time-varying predation mortality

Model behavior was explored by conducting a number of model runs. An initial run explored a scenario where time-varying natural mortality was allowed, but the predation index was not fit in the model. Even under these circumstances, the model converged with seemingly plausible estimates of time-varying predation and indicated a period of higher predation mortality in the early 2000 s followed by lower predation mortality in the last decade (Fig. 2). These results suggest that other data sets in the assessment model may provide some information about predation, though of course other time-varying processes could be causing this pattern instead. Results are also consistent with those from a previous analysis of time-varying natural mortality for Gulf of Alaska pollock (Dorn, 2004). A second run took the opposite approach and included total predation biomass estimates in the model with a very low assumed CV to compel the model to fit the data. This model run, called “force to fit”, also converged and matched the model’s expected predation nearly exactly. This model had a similar pattern of high predation mortality followed by much lower predation mortality, though the temporal pattern of predation shows considerably more year-to-year variation. Together, the no-data and “force to fit” models identify the extremes in model behavior when allowing for time-varying predation. A new base run was obtained using a more plausible assumption of a CV of 0.25 for predation estimates and gave a result between the two other model runs (Fig. 2). This run indicated a period of high predation mortality for pollock between 1995 and 2010, followed by lower predation mortality after 2010.

Comparison of observed predation indices to model predictions for this set of model runs showed no relationship between observed and predicted for models with constant predation and when predation mortality was allowed to vary but predation index was not fit in the model (Fig. 3). When the index was fit in model, the “force-to-fit” showed a nearly perfect fit, as would be as expected, while the intermediate model showed a weaker relationship between observed and predicted (Fig. 3).

Fig. 4 shows the resulting time series of predation biomass for the different model runs. When the stock itself is highly variable, the conventional assumption of constant natural mortality implies that a nearly constant fraction of the stock is consumed by predators every year. This alone can lead to considerable interannual variation in the biomass consumed. When the stock is at high abundance, it would be reasonable to expect that some targeting of the stock would occur, but predation is likely to saturate according to some functional response. It is interesting to note that the constant predation mortality model had the highest year-to-year variation (CV = 0.54) compared to models with time-

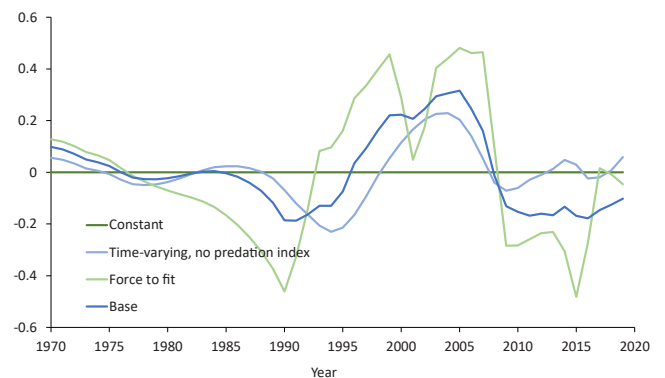


Fig. 2. Estimates of log-scale deviations of time-varying predation mortality for alternative configurations of the Gulf of Alaska pollock assessment model.

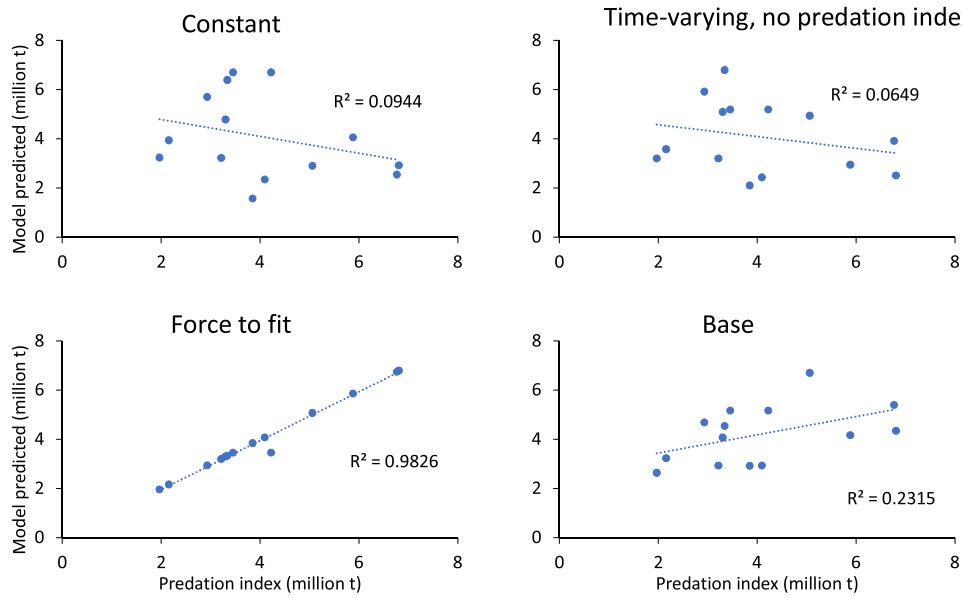


Fig. 3. Comparison of observed predation indices and model predicted indices for alternative configuration of the Gulf of Alaska pollock assessment model. R^2 values are for a linear regression of predicted indices on observed indices (dotted line).

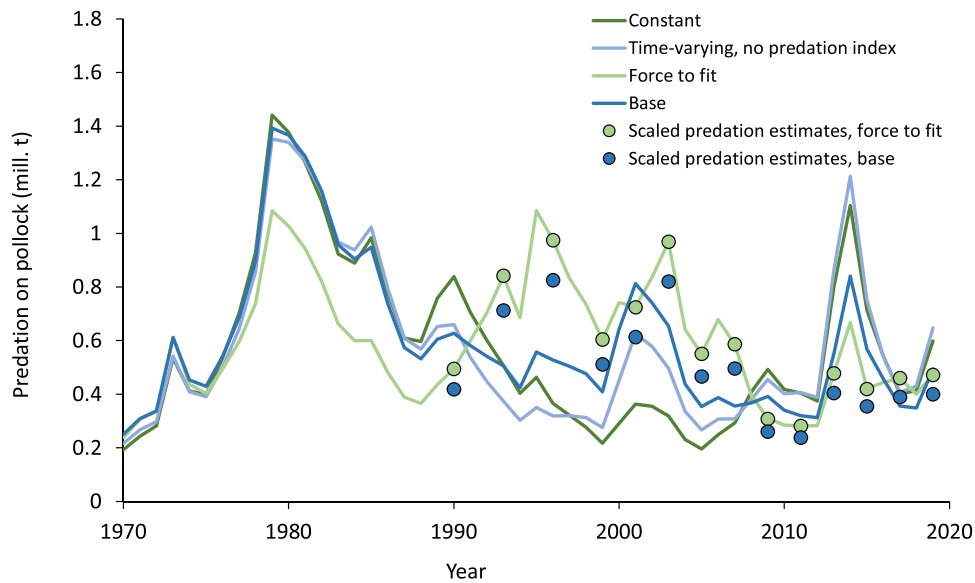


Fig. 4. Model estimates of total predation for alternative configurations of the Gulf of Alaska pollock assessment model. Also shown are the estimates of predation as scaled by predation coefficient for the “force to fit” exploratory model and the base model.

varying predation mortality ($CV = 0.46$). This suggests that some dampening of predation variability occurs when predation mortality is allowed to be time-varying. The 1999 predation estimate seemed to be low and a potential outlier in the data, but the base model was able to achieve an acceptable fit to this estimate. Recruitment was low in 1999 and had been low the two years prior, so there were few pollock in the age range most commonly consumed by groundfish predators, forcing those predators to switch to other prey species.

Examination of the likelihood components of the different models indicated that no input data type consistently fit better or worse when predation mortality was modeled (Table 2). In comparison to the model without time-varying predation mortality, the greatest improvements in fit were from Shelikof Strait survey biomass, age compositions from the Alaska Department of Fish and Game survey, and age compositions from the NMFS bottom trawl survey. Data sets that fit worse were NMFS bottom trawl survey biomass and fishery catch at age. The overall fit

improved (5.03 log likelihood units) after excluding the likelihood components associated with fitting time-varying predation mortality and the predation index, but this would not be considered significant given the additional parameters ($n = 49$) being estimated. The scalar for the proportionality between survey estimated predation and the model predictions were much larger than 1.0 for both the force to fit model ($q = 6.98$, $CV = 0.16$) and the base model ($q = 8.24$, $CV = 0.17$) (Table 2), indicating that predation estimates were larger by a factor of 7–8 compared to model-expected predation.

Examination of model parameter estimates indicated that twenty of the most changed parameter estimates were recruitment deviations, indicating that the model primarily adjusts the year-class strength when accounting for time-varying predation mortality, while only slightly adjusting other model parameters. Comparison of estimated age-1 recruitment between the constant natural mortality scenario and time-varying predation mortality indicate a pattern of increased

Table 2
Log likelihood components for alternative Gulf of Alaska pollock models.

	Constant	Time-varying, no predation data	Force to fit	Base
Total catch	-0.11	-0.08	-0.13	-0.10
Fishery catch at age	-99.72	-97.95	-107.99	-101.38
Shelikof survey biomass	-50.64	-47.44	-41.21	-43.97
Shelikof survey age comp.	-33.06	-30.99	-35.69	-32.24
Trawl survey biomass	-15.50	-15.41	-24.53	-19.06
Trawl survey age comp.	-16.48	-15.26	-14.27	-14.75
Trawl survey size comp.	-3.38	-3.30	-3.20	-3.16
ADF&G survey biomass	-36.17	-36.23	-42.47	-37.80
ADF&G survey age comp.	-30.89	-29.75	-27.42	-28.33
Acoustic age-1 index	-4.80	-4.30	-5.92	-4.51
Acoustic age-2 index	-6.46	-6.27	-8.35	-6.65
Summer acoustic biomass	-3.15	-3.17	-2.00	-2.86
Summer acoustic age comp.	-2.47	-2.48	-2.99	-2.49
Recruitment devs.	-3.49	-3.26	-2.28	-2.82
Fishery selectivity random walk	-13.33	-12.70	-13.48	-12.96
Survey catchability random walk	-28.03	-28.19	-31.12	-29.57
Predation index	NA	NA	-0.35	-11.63
Trawl catchability prior	0.00	-0.01	-0.01	0.00
Predation random walk	NA	-3.56	-38.09	-5.26
Total	-347.68	-340.36	-401.52	-359.52
Predation scalar	NA	NA	6.98	8.24
Average age-1 recruitment (billion)	5.67	5.77	6.33	5.80
Recr. coefficient of variation	1.12	1.14	0.86	0.92

recruitment estimates in periods when predation mortality is higher and reduced recruitment estimates when predation mortality is lower (Fig. 5). Mean recruitment was similar for constant and time-varying predation mortality, but higher for the force to fit model (Table 2). The coefficient of variation of recruitment tended to be lower for models with time-varying predation mortality (Table 2), suggesting that the inclusion of time-varying predation mortality may dampen some of the apparent variability in recruitment.

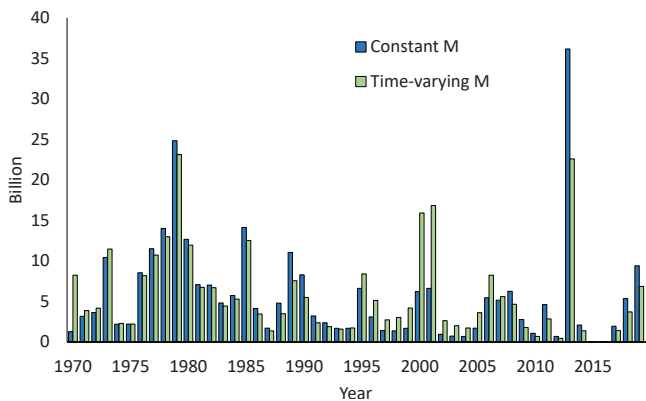


Fig. 5. Comparison of age-1 recruitment estimates for Gulf of Alaska pollock assessment models with constant and time-varying predation mortality.

3.2.2. Potential bias in the stock assessment when not accounting for time-varying predation mortality

If the time-varying predation model is considered correct, assuming constant predation mortality leads to bias in assessment results. Fig. 6 shows a comparison of the exploitable biomass from the base and constant predation models. Exploitable biomass is proportional to the ABC and overfishing limit (OFL), so this comparison is a metric that directly affects the harvest specifications used to manage pollock. The percent difference in exploitable biomass ranged from -13.84-3.99%. The buffer between the OFL and the ABC for Gulf of Alaska pollock is 15.8%, suggesting that a bias of this magnitude would not result in inadvertent overfishing (i.e., exceeding the OFL) when fishing at the ABC level. Higher than average predation mortality tended to result in higher exploitable biomass for the time-varying predation mortality model, though the relationship was quite variable. Percent differences in total biomass were larger between the two models, ranging from -37.47-20.60%. This indicates that time-varying predation mortality more strongly affected total biomass than exploitable biomass.

Fig. 7 shows a comparison of the annual $F_{40\%}$ fishing mortality rate for the constant predation model and the base model with time-varying predation mortality. The annual $F_{40\%}$ fishing mortality rate for the constant predation model varies temporally because both weight at age and selectivity are time-varying in this model. The time-series of annual $F_{40\%}$ fishing mortality rates are highly variable compared to the $F_{40\%}$ calculated using average life history characteristics, with the constant predation model ranging from -23-37% and the time-varying predation model ranging from -30-51%. When time-varying predation mortality is modeled, the annual $F_{40\%}$ fishing mortality rate is strongly correlated with the deviation in predation mortality. As would be expected, annual $F_{40\%}$ is higher when predation mortality is higher and lower when predation mortality is lower.

3.2.3. Estimating age-specific natural mortality

A model that included age-specific predation mortality (M2) was used to estimate the age-specific pattern of natural mortality (M) for ages 1-3 yr. This model successfully converged and produced age-specific estimates of natural mortality (predation mortality + residual

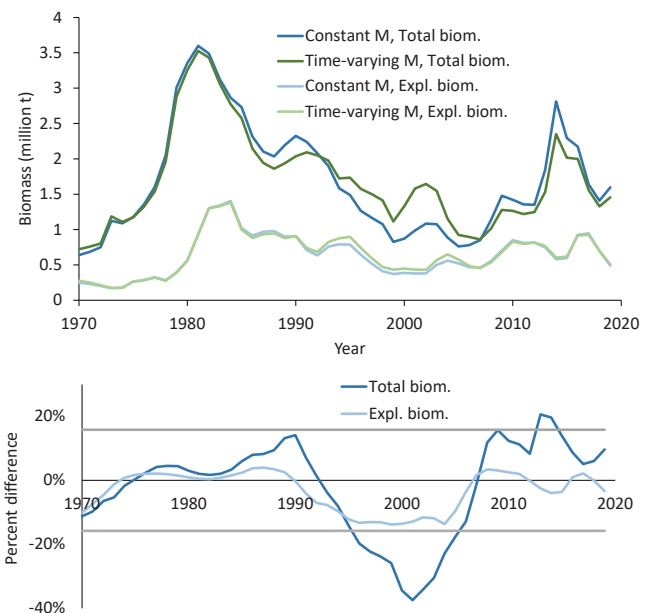


Fig. 6. Comparison of total and exploitable biomass between Gulf of Alaska pollock assessment models with constant and time-varying predation mortality. The lower panel shows the percent difference (constant M relative to time-varying M). Grey lines in the lower panel indicate the 15.8% buffer between the overfishing limit (OFL) and the allowable biological catch (ABC).

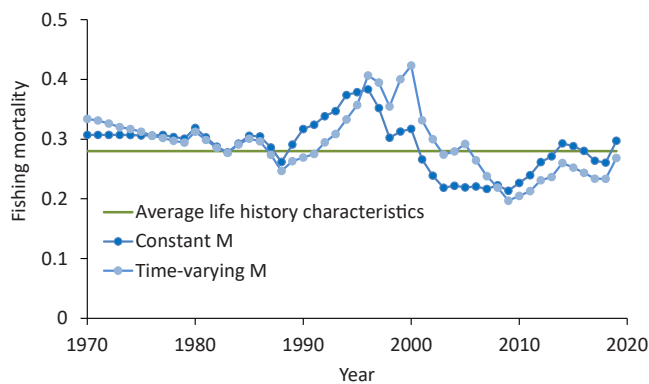


Fig. 7. Comparison of annual F40% estimates between Gulf of Alaska pollock assessment models with constant and time-varying predation mortality. The F40% fishing mortality rate based on average life history characteristics is also shown.

mortality) for ages 1–3 years that were somewhat lower, but well within the bounds of the broad prior (Fig. 8). Estimated natural mortality was reduced at age-1 (0.88 vs. 1.38), age-2 (0.63 vs. 0.69), and age-3 (0.44 vs. 0.48) compared to prior means. These changes had a small effect on the time series of estimated exploitable biomass, with a median decrease of 1.9% for the model with revised natural mortality estimates.

4. Discussion

Our results indicate that predation pressure on pollock can be substantial and temporally variable. Under the common assumption of constant natural mortality, variation in the abundance of pollock would result in changes in the amount of predation, since constant natural mortality implies that a nearly constant fraction of the population is consumed by predators. The lack of ecological realism in this assumption has not prevented it from being used in most stock assessments worldwide (Aldrin et al., 2021). We applied a method that directly incorporates estimates of predation into a single species stock assessment to inform temporal variation in natural mortality. We focused our efforts on a “top heavy” ecosystem (i.e., one that is dominated by predators in terms of biomass; Gaichas et al., 2015) and a prey species that is hypothesized to undergo top-down control (Barnes et al., 2020). Our estimates of predation mortality are based on a relatively long time series of standardized surveys that include consistent stomach sampling of major pollock predators in the Gulf of Alaska. These types of data are

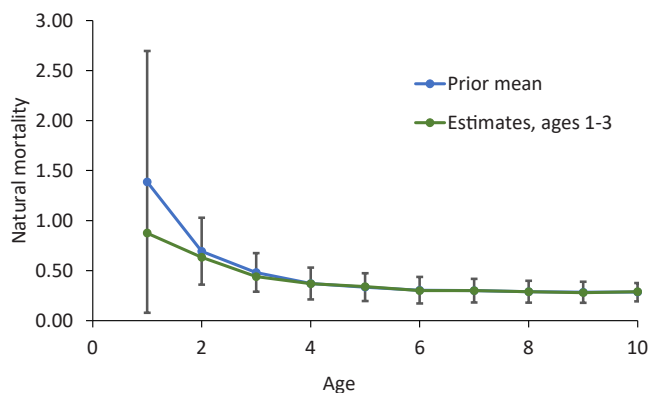


Fig. 8. Estimates of natural mortality based on an ensemble average of different methods independent of the stock assessment (blue) and a Bayesian approach (green) using a stock assessment model that includes age-specific predation mortality. Only natural mortality for ages 1–3 years was estimated. Also shown is the 95% credibility interval based on variability in age-specific natural mortality for different estimation methods in the ensemble.

essential for application of the model described in this paper. This study was made possible due to the foresight of the Resource Ecology and Ecosystem Modeling (REEM) program at the Alaska Fisheries Science Center (NMFS) in instigating and continuing to support food habits data collection in Alaska marine ecosystems.

Although single- and multi-species models that quantify spatiotemporal variation in predation have been around for several decades (Hollowed et al., 2000), only a few models have successfully transitioned from research model to the primary model used for management advice. While the reasons for this slow adoption are not entirely clear, the additional complexity of these models leads to results that are difficult to interpret and are more uncertain. There is also concern that the assumptions used to model predation could distort results in ways that are not yet fully understood. During the course of this research, we had discussions with NPFMC members who expressed interest in incrementally adding ecological information to single species assessments rather than replacing single species models with more complex and less understood multi-species models (S. Madsen, pers. comm. At-sea Processors Association, November 1, 2021). In our view, the interest in finding relatively simple ways to incorporate ecological information into the stock assessment process is well founded, and the approach we describe provides a possible path forward.

Other potentially useful frameworks for incorporating predation mortality within stock assessments are models of intermediate complexity (MICE; Plagányi et al., 2014), which minimize the complexity necessary to incorporate additional biological or ecological processes for tactical fisheries management (e.g., Punt et al., 2016). Another approach for dealing with the complexity of multispecies modeling has become common practice in the North Atlantic International Council for the Exploration of the Sea (ICES) area. This technique involves fitting multispecies models, extracting estimated natural mortality for ecologically or economically important stocks, and using those estimates in single species assessments (ICES, 2020). However, the double use of input data in this procedure makes it difficult to track how uncertainty propagates through the assessment and into management advice.

We have followed the convention typically used in multispecies models where total mortality is split into residual mortality (often called $M1$), which represents the physiological or intrinsic aspects of mortality (such as starvation and aging), and predatory or extrinsic mortality (often called $M2$). This partitioning of natural mortality has the considerable advantage of directing focus toward the more tractable aspects of mortality, such as predation mortality. But it also raises some potentially important issues. It is difficult to justify the initial decision about how large intrinsic mortality should be since information about the causes of intrinsic mortality is often lacking. Given the increased emphasis on understanding effects of climate change on marine populations, it will be necessary to consider ways in which environmental variation can impact both intrinsic and extrinsic mortality. The direct effects of climate change are likely to be on intrinsic mortality; for example, by leading to changes in prey availability or the amount of suitable habitat. Indirect effects of climate change are likely to be on extrinsic mortality via increased metabolic demand of predators in warmer waters (e.g., Holsman et al., 2016) or changes in spatial overlap between predator and prey populations (e.g., Hunsicker et al., 2013). The structure that we have set up accounts for extrinsic forcing by explicitly estimating effects of ambient temperature on predator rations. Nevertheless, we acknowledge that there are advantages to modeling unpartitioned natural mortality. This can be accomplished by modeling time-varying natural mortality as a base mortality multiplied by an annual deviation forced by some covariate such as predator-prey ratios. Such an approach has been suggested as more tractable than making arbitrary decisions about how large intrinsic mortality ($M1$) should be (Plagányi, É., pers. comm. CSIRO, May 17, 2021). We explored models with this formulation and found that the results were nearly identical to our approach. We elected for the simplicity of splitting natural mortality

into residual mortality and predation mortality but acknowledge that alternative approaches are also feasible and may be preferred in some circumstances.

A primary outcome of this research is that estimates of exploitable biomass resulting from a model that ignores time-varying mortality can be moderately biased, but may not result in inadvertent overfishing. In our case, bias in the estimates of total biomass were larger but would not have direct consequences on the management of the stock. Of course, this outcome could not have been known beforehand and may not be transferrable to other stocks in other systems. Our work addressed a concern about the pollock stock that was prompted by long-term increases in the abundance of high-trophic level predators in the Gulf of Alaska, such as arrowtooth flounder. We recommend that our relatively simple and robust modeling approach be considered for other single species assessments because it accounts for temporal variation in predation intensity. It will be especially useful to compare outcomes from models for stocks that represent different roles in the food web and experience varying degrees of predation pressure. Trends in predation mortality reflect changes in the abundance of prey populations, the availability of alternative prey, physiological effects of warming temperatures, and how predator populations respond to changes in pollock abundance. Thus, we expect that continued development of predation-informed assessment models will result in an improvement over the assumption of constant natural mortality. Improvements may be more modest, such as decreasing estimates of uncertainty (as in the case of GOA pollock and [Hollowed et al., 2000](#)). However, they may manifest as changes in exploitable biomass for species with different life histories or positions in the food web. Additional studies will help clarify how generally applicable the technique may be.

Another noteworthy result of this research is that the coefficient used to predict the predation index was approximately 7–8, indicating that index-based estimates of predation were much greater than assessment-estimated values. This is not a new or particularly surprising outcome, since some of the early ecosystem modeling in the Gulf of Alaska (e.g., [Gaichas et al., 2010](#)) had a similar problem of balancing the amount of predation on pollock with the estimated size of the population from the stock assessment. Results from [Hollowed et al. \(2000\)](#) also suggest that relying on external calculations of natural mortality (e.g., those informed by life history characteristics) leads to underestimates of mortality and biomass. Nevertheless, such a disparity between the magnitude of predation and assessment-based estimates of biomass is a stock assessment concern that warrants further investigation.

We have identified a number of factors could have produced what appears to be an extreme value for this coefficient. First, the pollock assessment could rely on input parameters that cause population size to be underestimated. For instance, the scale of the population in the assessment is strongly determined by a prior on catchability (median = 0.8) for the bottom trawl survey ([Monnahan et al., 2021](#)). Although biomass estimates from both the summer and winter acoustic surveys are consistent with the scale of population in the assessment, the possibility of higher abundance of pollock cannot be entirely discounted given uncertainty in survey catchability.

The second possibility is that the abundance of pollock predators is being overestimated by current assessments of those stocks. We focus here on arrowtooth flounder as it is by far the largest contributor to pollock predation. Rather than estimating survey catchability for the NMFS bottom trawl survey, the arrowtooth flounder assessment assumes catchability equals one ([Spies et al., 2019](#)). However, most processes affecting catchability for flatfish tend to result in catchabilities greater than one. For example, trawl efficiency experiments by [Somerton et al. \(2007\)](#) suggest that herding increases catchability for the NMFS bottom trawl net. An additional factor that could produce catchabilities in excess of one is the extrapolation of trawl survey data to the extensive untrawlable areas in the GOA. Species that preferentially inhabit trawlable areas are prone to overestimation, as is likely to be the case for arrowtooth flounder. Expansion of trawl densities to

untrawlable habitat is used as justification for an estimated catchability of 1.82 in the Gulf of Alaska Pacific ocean perch assessment ([Hulson et al., 2021](#)).

Another consideration is that predation estimates rely on estimates of additional processes, such as bioenergetics-based annual rations, whose estimation could be subject to biases. As detailed in [Barnes et al. \(2020\)](#), European plaice were used to estimate bioenergetics parameters for arrowtooth flounder since species-specific information was not available. Predation estimates may have also been biased by the assumption that the predators were feeding at a theoretical maximum consumption rate rather than their realized foraging rates ([Barnes et al., 2020](#)). Though this particular bias is may be minor given that relative foraging rates for arrowtooth flounder appear to be near their theoretical maximum consumption ([Holsman and Aydin, 2015](#)).

Finally, a recent paper on multispecies models for the Gulf of Alaska ([Adams et al., 2022](#)) estimated similar pollock predation as the modeled estimates in this paper (762,000 metric tons in 1997 compared the base model estimate in this paper of 504,000 metric tons). Further comparison among alternative approaches to modeling predation is needed to better understand both the effect of different modeling assumptions and the sources of uncertainty in predation estimates. Regional comparisons using the methods we present here may also shed light on the relative degree of emphasis we should place on conventional assessment-based biomass estimates versus those that include scalars for predation mortality; given that “top heavy” predator-dominated systems are more unpredictable than “bottom heavy” or “beer belly” systems composed primarily of lower and mid trophic level fishes, respectively ([Gaichas et al., 2015](#); [Barnes et al., 2020](#)). Because predation mortality is likely much greater than removals from fishing and other sources, we hypothesize that stocks such as GOA pollock will be most affected by decisions about how to treat predation mortality as part of regular assessments ([Gaichas et al., 2010](#)).

It is straightforward to fit an assessment model for GOA pollock that assumes scalar for predation is one, or includes an informative prior on the scalar for predation. Some experimentation with such models indicates, not surprisingly, that overall scale of the pollock population would need to be much higher to support the level of predation implied by the predation indices. These results should not be given too much credence given unknown biases and uncertainties in predation estimates. Allowing an absolute estimate of predation to determine the scale of the population in an assessment is not advisable in our view until these potential biases and uncertainties can be better addressed. An advantage of the modeling approach presented in this paper is that it allows for these kinds of issues to be addressed in a simple framework that is reasonably transparent and has the added benefit of helping to prioritize research that supports the assessment.

Gulf of Alaska pollock are managed under Tier 3 of North Pacific Fishery Management Council’s groundfish tier system, where reference fishing mortality rates are based on spawning biomass per recruit (SPR) ([DiCosimo et al., 2010](#)). Estimates of annual $F_{40\%}$ for a model with time-varying predation mortality showed a consistent pattern where higher predation mortality resulted in an increase in the harvest rate when fishing at $F_{40\%}$. This was considered an undesirable property of F_{SPR} harvest rates by [Collie and Gislason \(2001\)](#), who argued that “it would be risky and inappropriate to use the formula for calculating $F_{40\%}$ to adjust the BRP (biological reference points) of a given species in response to changes in growth or mortality rates.” [Legault et al. \(2016\)](#) investigated this issue extensively and also criticized the approach of automatically adjusting F_{SPR} values with changes in natural mortality, particularly when the evidence is weak. The modeling approach developed in this paper estimates only the time-varying pattern of predation mortality, such that the overall average predation mortality is unchanged from the model currently used for management advice. For the GOA pollock assessment, life history parameters to calculate F_{SPR} harvest rates have typically been medium to long-term averages ([Monnahan et al., 2021](#)). Considering the modeling results in this paper, in addition

to the recommendations by Collie and Gislason (2001) and Legault et al. (2016), long-term averages of predation mortality may be the best immediate approach for GOA pollock, though continuing to monitor trends in predation mortality is strongly recommended. The “pretty good yield” concept attributed to Alec MacCall (National Marine Fisheries Service, Santa Cruz, California) (Hilborn, 2010) could perhaps be invoked to argue that $F_{40\%}$ would likely perform reasonably well across a range of natural mortalities, though further research is needed to demonstrate this. Recent work by O’Leary et al. (2020) on dynamic F_{SPR} reference points should also be considered for GOA pollock, though dynamic reference points would not completely avoid the undesirable increase in the fishing mortality rate when natural mortality increases.

There are a number of areas where further research is needed to improve the modeling of predation on Gulf of Alaska pollock. First, we lacked estimates of uncertainty for predation mortality. Variance of some components of the predation index are readily available, such as for total predator biomass from stock assessments, model-based predator density, and annual mean rations. However, we did not estimate variances for other components such as proportions of prey consumed. Model-based variances have been estimated from diet data (e.g., Grüss et al., 2020) and could be used to quantify uncertainty for components of the predation index that rely on raw proportions. This would be a beneficial improvement given that proportional diet data can have a considerable impact on predation estimates (Barnes et al., 2020). Overall variances could be estimated using a bootstrap of the components that make up the predation index or some other resampling procedure.

Various components of the predation index can be improved by the future research avenues outlined in Barnes et al. (2020). Among those proposed advancements is to fine-tune the estimates of mean annual rations. The mean annual rations that we used rely on theoretical maximum consumption rates. Relative foraging rates, however, could be used to estimate realized consumption. Additionally, missing information required that bioenergetics parameters be borrowed from related species. Using species-specific information would improve estimates, when possible. Proportions of pollock consumed would be enhanced with year-round sampling. Although von Bertalanffy growth rates were used to integrate physiological and trophodynamic processes throughout the year, predation estimates currently rely only on summer survey data. Additional food habits information during fall and winter would increase our confidence in the relative importance of pollock in the diets of our focal predators. Including dietary information from other predators (e.g., sea birds, marine mammals, all sizes of focal groundfishes) would also increase the accuracy of age-specific predation mortality. Given that arrowtooth flounder represents the dominant pollock predator in the Gulf of Alaska and thereby has the greatest influence on pollock predation mortality, refining any index component for that species (e.g., total biomass, age compositions of pollock prey) would be especially important.

For the assessment model, perhaps the highest priority would be a study that simulates predator-prey dynamics and generates assessment data to estimate time-varying natural mortality. This type of study would elucidate the reliability of time-varying natural mortality estimates and allow for an evaluation of potential assessment errors by comparing simulated and “real” data. More complex models such as those developed by Spencer et al. (2016), which fit predator functional responses, could be tested against the simpler approaches used in our study. Another modeling issue that should be further investigated is whether aggregating predation by all predators in a single index is appropriate. An alternative approach would be to model each predator separately to allow for species-specific estimates of uncertainty. Finally, we need to gain a better understanding about the drivers of food web dynamics in the Gulf of Alaska. For example: Why is there long-term variation in the abundance of species such as pollock and arrowtooth flounder? What drives prey switching for generalist predators? And how will this highly-coupled and productive ecosystem be impacted by climate change in the future?

5. Conclusions

We developed a simple approach to include predation estimates within a stock assessment model as a means of accounting for time-varying natural mortality. The method of modeling predation as an index of removals worked as intended, appeared to be robust, and can be recommended for similar situations. Not accounting for time-varying mortality resulted in potentially biased estimates of total stock biomass, though the bias may not be great enough to cause inadvertent overfishing. There remains a need to better understand various sources of uncertainty in survey-based estimates of predation pressure. Estimated predation on GOA pollock is far greater than can be supported by the current assessment-based estimates of stock abundance. Although other food web studies have found similar disparities between total stock biomass and the biomass of removals estimated from predation, the magnitude of difference remains puzzling. Simulation or estimation testing could demonstrate relative model performance under plausible scenarios with varying predator-prey dynamics. We anticipate that a variety of modeling approaches will be necessary to evaluate ecological and climate forcing on pollock dynamics in the Gulf of Alaska.

CRedit authorship contribution statement

Martin Dorn: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Cheryl Barnes:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2022.106391](https://doi.org/10.1016/j.fishres.2022.106391).

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