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# A simple predation pressure index for modeling changes in natural mortality: Application to Gulf of Maine northern shrimp stock assessment

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ABSTRACT

This paper describes a method for incorporating varying predation pressure in stock assessment that does not require estimation of consumption rates or absolute consumption by predators. The method is applied to assessment of northern shrimp *Pandalus borealis*, an important forage species in the North Atlantic Ocean and the target of major fisheries. A predation pressure index (PPI) was developed using data collected during resource surveys in Gulf of Maine northern shrimp habitat areas during 1968–2013. Predators were identified based on the percent frequency of occurrence (PFO) of Pandalid shrimp in their diets. The PPI for each year was the weighted sum of the biomass indices of 21 identified predators, where the weights were the time-series average PFO for each predator. The PPI thus reflected the effects of both the biomass of each predator and its importance as a predator of shrimp. The PPI time series was used to scale an assumed average natural mortality rate ($M$) that replaced a constant $M$ assumption in the stock assessment model. Use of the PPI-scaled $M$ improved the overall fit of the model and reduced a retrospective pattern in the constant $M$ model by nearly 60%. The PPI approach allows time-varying predation to be accounted for in an assessment model without requiring estimates of absolute abundance of predators and their total consumption, quantities which may be unavailable or difficult to estimate accurately.

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## 1. Introduction

The importance of accounting for species interactions in fishery management has been recognized for decades (e.g., McHugh, 1959, 1988; Mercer, 1982; Tyler et al., 1982; Fogarty, 2014), yet most fisheries continue to be managed based on information about the target species only. The foundations for more holistic approaches to fishery management have been accumulating with increasingly sophisticated observation systems, ecological understanding and modeling capabilities (Murawski, 2007). However, parameterizing complex multi-species and ecosystem models can be a substantial challenge (Fulton et al., 2003) and simpler approaches are also needed (Murawski, 2007; Fogarty, 2014). This paper describes a simple approach to including species interactions in stock assessment by accounting for predation on an important forage species in the North Atlantic Ocean.

The northern shrimp *Pandalus borealis* is distributed across a wide latitudinal range (~42°N –70°N; Shumway et al., 1985; Bergström, 2000) in the North Atlantic Ocean and is the target of important fisheries. It is also a key component of food webs that support demersal fish, including Atlantic cod *Gadus morhua* (Parsons, 2005a). A meta-analysis of nine northern shrimp populations found that cod predation was a structuring force in most regions. However, in the Gulf of Maine (GOM), cod did not appear to exert a controlling influence (Worm and Myers, 2003). The GOM has a complex food web (Overholtz and Link, 2009) and a broader suite of predators than the more northern systems. Thus, the overall impact of predation is probably not well represented by only a single predator. A subsequent study identified ten fish species that consistently prey on Pandalid shrimp in the GOM (Link and Idoine, 2009).

Management of the GOM northern shrimp fishery is guided by annual stock assessments that have used Collie-Sissenwine catch-survey analysis (CSA; Collie and Sissenwine, 1983; Cadrin et al., 1999) for almost two decades. However in recent years the CSA developed a retrospective pattern (Mohn, 1999; Legault, 2009) that suggested biomass was overestimated and fishing mortality

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**Table 1**
Sources of data for estimating PPI and inputs to the CSA models. PFO is percent frequency of occurrence of Pandalids in predator stomachs; CSA is Collie–Sissenwine Analysis (Collie and Sissenwine, 1983).

| Data type | Estimated quantity | Source | Years | Comments |
|---|---|---|---|---|
| Food habits | PFO for each predator | NEFSC spring, fall surveys | 1973–2011 | Aggregated over season and years |
| Survey indices | Predator biomass index | NEFSC fall surveys | 1963–2012 | Used to estimate PPI |
| Survey indices | Shrimp abundance index | ASMFC shrimp surveys | 1984–2012 | Recruit and post-recruit indices for CSA |
| Survey indices | Shrimp abundance index | NEFSC fall surveys | 1984–2012 | Aggregate abundance index for CSA |

**Table 2**
Species of Pandalid predators included in the PPI, number of stomachs examined, average PFO of Pandalids in each predator's diet (1973–2011), and proportion of the total PPI accounted for by each species on average. CV is inter-annual coefficient of variation of PFO for each species during 1977–2012.

| Predator scientific name | Predator common name | Number stomachs sampled | Average PFO | CV (PFO) | Average percent of PPI |
|---|---|---|---|---|---|
| *Sebastes fasciatus* | Acadian redfish | 2375 | 6.6 | 117% | 20.6% |
| *Urophycis tenuis* | White hake* | 6924 | 15.5 | 61% | 17.3% |
| *Squalus acanthias* | Spiny dogfish | 6825 | 3.5 | 106% | 15.2% |
| *Gadus morhua* | Atlantic cod* | 5311 | 12.9 | 55% | 15.1% |
| *Merluccius bilinearis* | Silver hake* | 14,157 | 7.5 | 64% | 7.5% |
| *Amyblyraja radiata* | Thorny skate* | 1888 | 8.6 | 80% | 6.4% |
| *Urophycis chuss* | Red hake* | 5111 | 13.1 | 59% | 5.1% |
| *Pollachius virens* | Pollock* | 1905 | 6.4 | 76% | 3.8% |
| *Melanogrammus aeglefinus* | Haddock | 1985 | 2.8 | 110% | 3.0% |
| *Clupea harengus* | Atlantic herring | 4527 | 1.9 | 119% | 1.5% |
| *Hippoglossoides platessoides* | American plaice | 5284 | 1.2 | 134% | 0.8% |
| *Lophius americanus* | Goosefish | 2414 | 2.9 | 80% | 0.8% |
| *Malacoraja senta* | Smooth skate | 751 | 20.8 | 56% | 0.7% |
| *Myxocephalus octodecemspinosus* | Longhorn sculpin* | 1782 | 9.6 | 70% | 0.6% |
| *Dipturus laevis* | Barndoor skate | 28 | 35.7 | 26% | 0.6% |
| *Leucoraja ocellata* | Winter skate | 344 | 4.4 | 249% | 0.3% |
| *Hippogrossus hippoglossus* | Atlantic halibut | 192 | 12.5 | 60% | 0.3% |
| *Hemipterus americanus* | Sea raven* | 1487 | 4.3 | 100% | 0.2% |
| *Leucoraja erinacea* | Little skate | 493 | 11.0 | 100% | 0.1% |
| *Paralichthys oblongus* | Fourspot flounder* | 337 | 5.0 | 80% | 0.0% |
| *Scophthalmus aquosus* | Windowpane* | 213 | 1.4 | 264% | 0.0% |
| *included in Link and Idoine (2009) | Total | 64,333 | | | |

underestimated, clearly a concern for fishery management. Further eroding confidence in the CSA, consumption of Pandalid shrimp by fish in the GOM was estimated to equal or exceed the population size of northern shrimp estimated by the CSA (Link and Idoine, 2009). CSA continued to be used for the assessment, assuming higher rates of natural mortality to account for the apparent underestimation of population size. However, in a 2014 benchmark assessment review (NEFSC, 2014), all models put forth for the northern shrimp assessment were rejected for use in management because of poor performance on diagnostic measures, including retrospective patterns. The modeling approaches were considered appropriate for the assessment, but required further development to resolve diagnostic issues.

To explore a potential cause for the retrospective patterns in the CSA, we devised a simple index-based method for incorporating time-varying natural mortality due to predation. The approach uses diet data and predator trend data from research surveys, but avoids the need for estimates of absolute numbers of northern shrimp consumed. In this paper we describe the method and its application to assessment of GOM northern shrimp.

## 2. Methods

The general approach was to first identify predators and quantify their relative importance to shrimp using food habits data. Trends in biomass of each predator were then estimated and a weighted sum calculated where the weights were each predator's importance as a source of shrimp predation. The weighted sum was taken as an annual index of predation pressure on northern shrimp and was used to track interannual trends in assumed natural mortality ($M$) in the CSA. CSA model estimates and diagnostics were compared for runs with constant and variable $M$ to evaluate whether incorporating predation pressure improved model performance. Table 1 summarizes the data that were used in the study.

### 2.1. Sampling methods for predators

Food habits and predator biomass data used to calculate the predation pressure index (PPI) were collected during spring and autumn bottom trawl surveys conducted annually since the 1960s by the Northeast Fisheries Science Center (NEFSC). Sampling is conducted according to a stratified random sampling design, with strata defined by depth and latitude, and sampling effort (number of stations) proportional to stratum size. Details of survey design, operations and gear specifications can be found in Grosslein (1969), Azarovitz (1981) and Miller et al. (2010). Operating procedures have followed a standard protocol since the inception of the survey. However, a major change occurred in 2009 that included replacement of the research vessel and modernization of the net design (Miller, 2013). Calibration coefficients estimated from experimental tows (Miller et al., 2010) were applied to adjust survey catch data for predators for these changes (see Section 2.2). Approximately 40 stations in GOM northern shrimp habitat were visited during each survey (Fig. 1).

Food habits data collected during 1973–2011 NEFSC spring and autumn surveys in northern shrimp habitat areas were used to identify fish predators and estimate the prevalence of Pandalids in their diets. Typically, stomach contents were identified for a subsample of individuals of predator species at each station up to a maximum number per species per stratum. Food habits sampling was distributed across geographic regions, and the number of samples per station was limited to ensure that sampling was distributed across strata. After 1980, sampling was also stratified by length class within predator species. Data collected included prey species identification, volume or weight of each prey species, prey number,

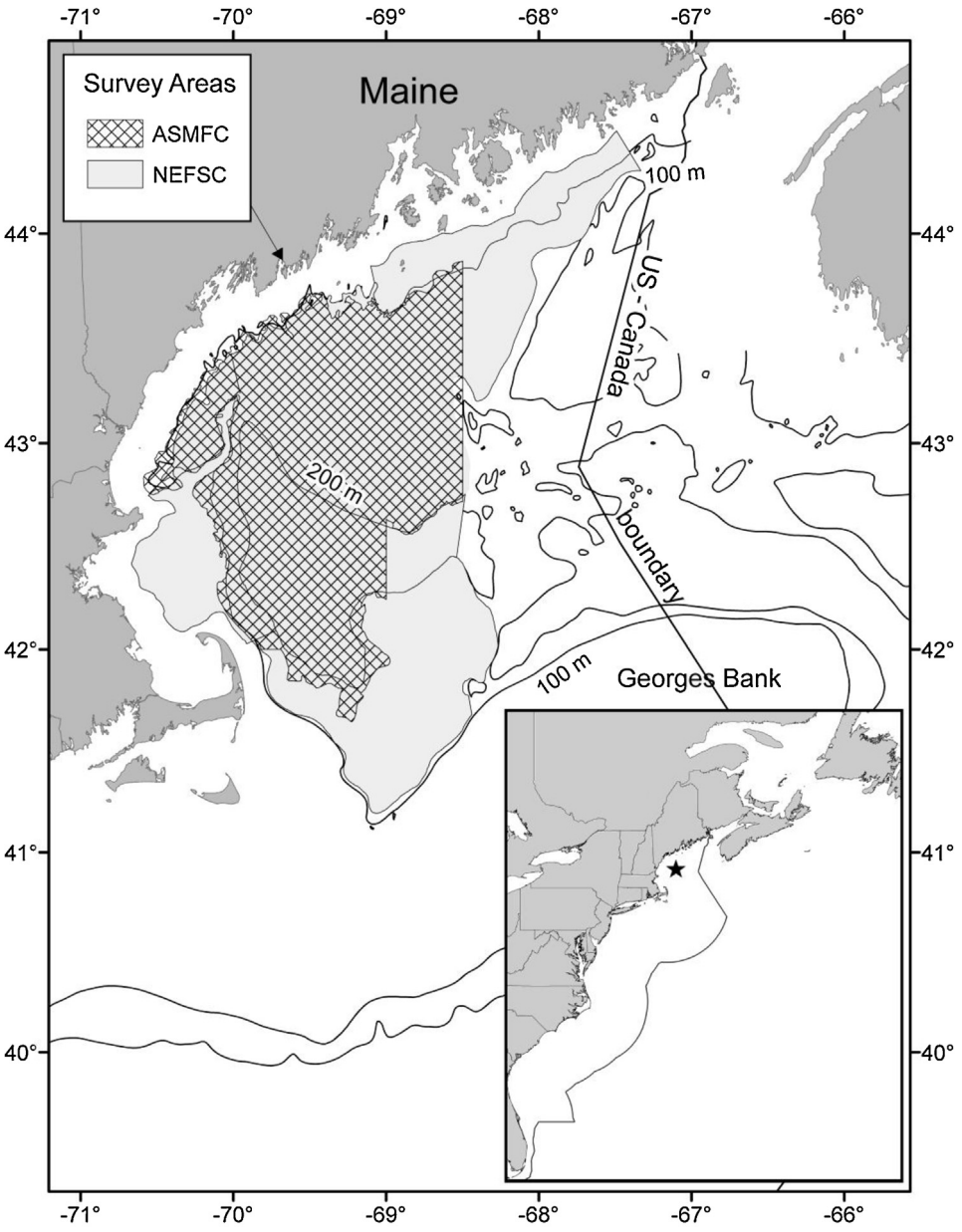


**Fig. 1.** Map of the study area in the Gulf of Maine. NEFSC surveys were used for food habits data, predator biomass indices and northern shrimp population data; ASMFC shrimp surveys were used for northern shrimp population data. Inset shows location of Gulf of Maine (star) in the northwest Atlantic Ocean.

total stomach volume or weight, and prey length when possible. Sampling became more systematic and expanded over time, particularly after 1976 and 1994, to include more species and broader geographic coverage. Further detail on methods for food habits sampling is given in Link and Almeida (2000), and an overview of results of the food habits sampling program is in Smith and Link (2010).

### 2.2. Predation pressure index

Predators were included in the analysis of northern shrimp predation if the percent frequency of Pandalids in their diet averaged over all years and both seasons was at least 1%. Prey taxonomic resolution in stomach contents was at the level of family (Pandalidae) and included *P. montagui, P. propinquus, Dichelopandalus leptocerus*, and unidentified Pandalids as well as northern shrimp. Northern shrimp is the dominant Pandalid in survey catches, accounting for 86% of the Pandalid biomass during fall and 74% in spring survey catches on average during years when all shrimp species were identified (fall 1991–2012, spring 1991–2004). For each predator, the average percent frequency of occurrence (PFO) of Pandalids in predator stomachs was estimated as the percentage of stomachs containing Pandalids in fall and spring surveys, combined over all years:

$$\mathrm{PFO}_j = \frac{\sum_i S_{i,j}}{\sum_i \mathrm{T}_{i,j}} \times 100 \quad (1)$$

where $i$ is year, $j$ is predator species, $S_{i,j}$ is number of stomachs containing Pandalids, and $T_{i,j}$ is the total number of stomachs examined. Using annual PFO estimates to estimate PPI rather than PFO averaged over years was also explored (Appendix A).

Trends in predator biomass during 1963–2013 were represented by biomass indices (stratified mean kg per tow) from

NEFSC fall bottom trawl surveys in the northern shrimp stock area (Fig. 1). Survey indices were used rather than total biomass estimates because population assessments were not available for all predators and several species had highly uncertain assessments (NEFSC, 2012). Predator biomass trends were represented by fall survey indices because they were considered less likely than spring survey indices to be affected by variable timing of seasonal migrations. The predator biomass indices from 2009–2013 surveys were standardized to account for survey modernization by applying calibration coefficients developed from paired tow experiments for each species (Miller et al., 2010). Calibration for Atlantic halibut *Hipoglossus hipoglossus* and pollock *Pollachius virens* were not available. Therefore, the average coefficient for all flatfish species was used for Atlantic halibut, as in the 2012 stock assessment (NEFSC, 2012), and the coefficient for pollock was assumed equal to one (Miller, 2013). The predation pressure index (PPI) was a weighted sum of predator biomass indices from fall surveys, calculated as:

$$\mathrm{PPI_i} = \sum_j B_{i,j} \times \mathrm{PFO}_j \quad (2)$$

where $B_{i,j}$ is the predator biomass index. The PPI thus took into account both changes in relative biomass and the average importance of each predator.

### 2.3. Application to assessment

Application of CSA to modeling of northern shrimp dynamics was described in detail in Cadrin et al. (1999) and updated in NEFSC (2014). CSA is a stage-based modeling approach for estimating population size from time series of abundance indices and catch data (Collie and Sissenwine, 1983). The modeled population is divided into two groups: shrimp that will grow to harvestable size in the coming year ("recruits") and those that are already large enough at the beginning of the year to be harvested ("post-recruits"). Shrimp that will not reach harvestable size in the coming year do not enter the model. Key assumptions include the rate of natural mortality ($M$) and relative catchability of the survey gear for recruits and post-recruits. CSA has been tested (Cadrin, 2000), reviewed (NEFSC, 2007, 2014), and used for annual GOM northern shrimp assessments since 1997. For the current study, CSA was implemented using software from the NMFS Fisheries Toolbox (CSA ver 4.2; http://nft.nefsc.noaa.gov; NEFSC, 2014). The program used maximum likelihood methods to estimate parameters and allowed multiple survey indices to be included. Further details of the CSA implementation are provided in Appendix B.

The CSA time frame was 1984–2013. The northern shrimp abundance indices for recruits and post-recruits came from dedicated shrimp surveys conducted each summer by the Atlantic States Marine Fisheries Commission (ASMFC) (Fig. 1). This survey follows methods similar to NEFSC bottom trawl surveys, but uses gear designed for capturing northern shrimp (Clark, 1989) and has used the same research vessel and sampling gear since its inception. The net has 1 3/8 inch stretch mesh in the body and 1 inch stretch mesh in the extension piece and codend. No size-sorting grid is used. An additional abundance index for northern shrimp was derived from NEFSC autumn survey data. This was brought into the CSA as an aggregate index (recruits and post-recruits combined). The modernized fall survey (2009–2012) was entered as a separate series because calibration coefficients are not available for northern shrimp. Catch data were obtained from mandatory dealer reports for 1984–1999, and from the greater of mandatory harvester reports or dealer reports for 2000–2013 (NEFSC, 2014). Annual mean weight in the catch was estimated from dockside sampling of commercial landings. Discards are assumed to be zero in the GOM northern shrimp fishery because the fishery takes primarily females which are relatively large and segregate themselves inshore during the hatch (and fishery) period (NSTC, 2014).

Time varying natural mortality was incorporated into CSA by adjusting an assumed average $M$ by annual deviations in the PPI. $M$ was thus scaled up in years with higher than average PPI and down in years with below average PPI:

$$M_i = \frac{M_\mathrm{b} \times \mathrm{PPI}_i}{\overline{\mathrm{PPI}}} \quad (3)$$

where $M_\mathrm{b}$ is the assumed baseline natural mortality ($M = 0.5$; NEFSC, 2014) and $\overline{\mathrm{PPI}}$ is average PPI. We constructed a likelihood profile with baseline $M$ values ranging from 0.3 to 0.8 year$^{-1}$ to evaluate the baseline $M$ assumption.

The retrospective pattern was explored by sequentially removing terminal years (2013–2009) from the analysis and re-estimating population size and fishing mortality. We used Mohn's rho to characterize the retrospective pattern (Mohn, 1999). Markov chain Monte Carlo (MCMC) methods were used to demonstrate the implications of uncertainty in biomass and $F$ estimates for 2008 as years were removed from the models (Legault, 2009). MCMC calculates the objective function at random locations in the parameter space to characterize the shape of the likelihood surface.

## 3. Results

### 3.1. Predation pressure

The stomach contents of 60 fish species contained Pandalidae during 1973–2011 NEFSC spring and fall surveys. Of these, 21 species had greater than 1% PFO of Pandalids in their diet on average and were included in the PPI (Table 2). $\mathrm{PFO}_j$ of these 21 predators averaged over all years ranged from 1.2% (American plaice) to 35.7% (barndoor skate) (Table 2). Inter-annual variation in PFO for individual species (CV = standard deviation/mean) during 1977–2012 ranged from 26 to 264% (median 80%), but ranged from 55 to 119% (median 75%) for the ten predators contributing most to the PPI (Table 2).

Total predator biomass began to increase after the early 1990s and since 2000 has fluctuated around levels approximately three times higher than during the 1980s (Figs. 2 A and 3 ). Before the 1990s, predator biomass was distributed relatively evenly across a number of species, but with declines in thorny skate, Atlantic cod, white hake, and red hake, and increases in spiny dogfish and Acadian redfish, the latter two species now dominate the predator biomass.

Trends in the PPI (Fig. 2B) mirror changes in predator biomass, particularly since the mid-1990s, when predator biomass became dominated by few species. Predator pressure was relatively high prior to the 1980s (average PPI = 849), was lower during the 1980s and 1990s (average PPI = 594), and increased again after 1999 (average PPI = 1083, 2000–2013). Trends in predator biomass and the PPI were more dissimilar prior to the decline of the gadids and thorny skate because the species that declined had higher frequencies of occurrence of Pandalids in their diets than the species that replaced them (Table 2).

### 3.2. Application to assessment

The likelihood profile results for baseline $M$ showed that the objective function was minimized at $M = 0.6$ year$^{-1}$, but differed by less than 2 likelihood units from the objective function at $M = 0.5$ year$^{-1}$ (i.e., the difference was not statistically significant at $p = 0.05$). We selected $M = 0.5$ year$^{-1}$ because it had been used in the most recent stock assessment based on considerations of shrimp biology (maximum longevity 6 years).

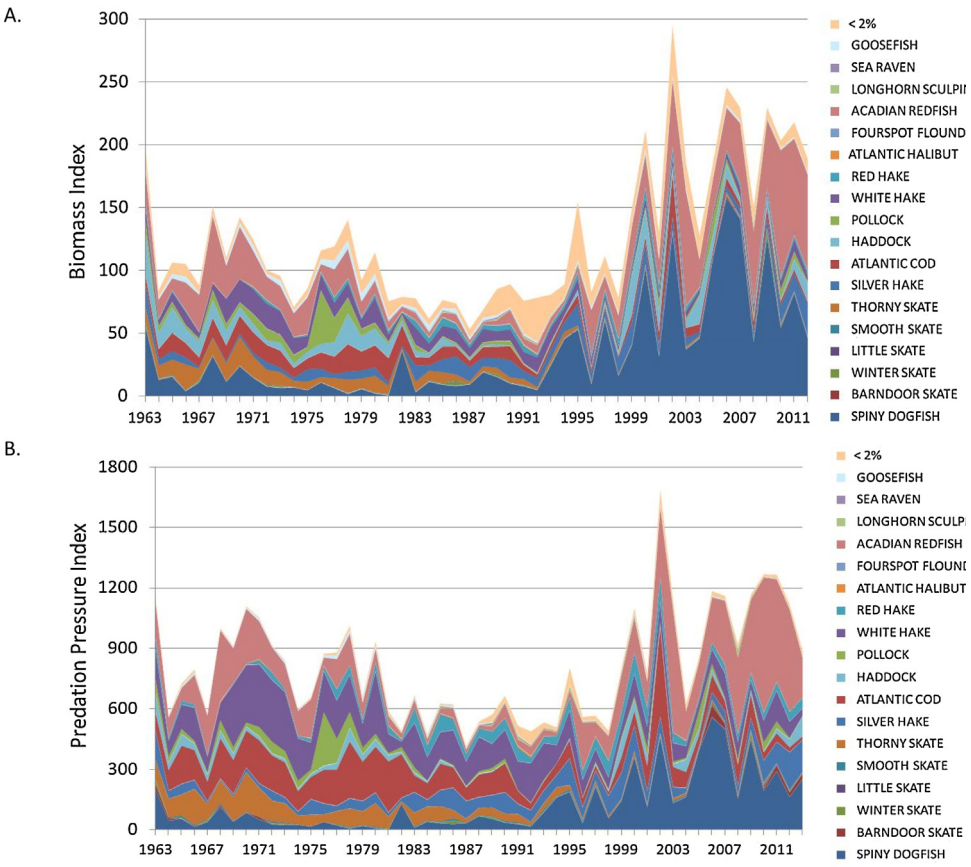


**Fig. 2.** (A) Biomass indices (stratified mean kg per tow) for 21 predators of Pandalids in the western Gulf of Maine from NEFSC fall bottom trawl surveys, 1963–2012. Indices for years after 2008 were adjusted for changes in survey methods instituted in 2009. (B) Predation pressure index showing individual species components for 1963–2013. Predators with average PFO < 2% are combined in the plots.

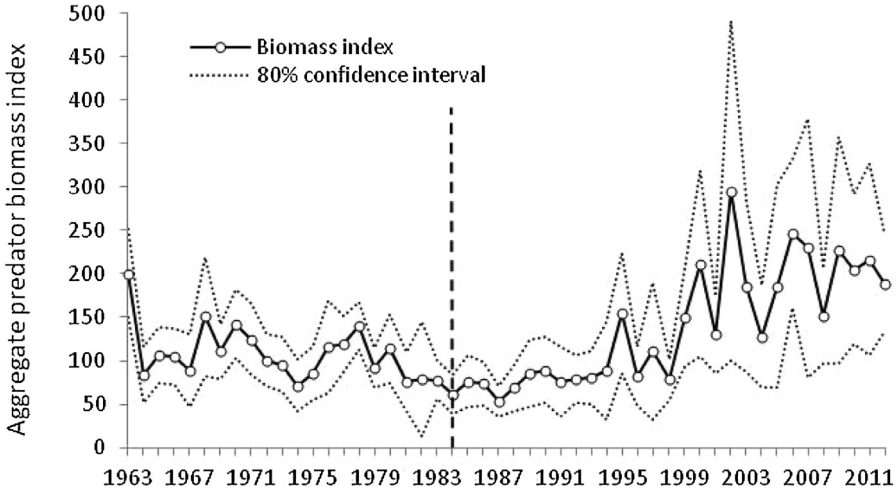


**Fig. 3.** Aggregate biomass index for 21 species of fish predators of northern shrimp; 80% confidence intervals shown. Vertical dashed line indicates beginning of assessment time period.

During 1984–1988, PPI-adjusted $M$ averaged 0.35 year$^{-1}$ and the annual estimates were generally lower than the assumed constant $M = 0.5$ year$^{-1}$ (Fig. 4). After 1988, PPI-adjusted $M$ was much higher than during the earlier period (average $M = 0.67$ year$^{-1}$) and typically remained above the constant $M = 0.5$ year$^{-1}$.

The overall fit of the CSA improved significantly (8.7 likelihood units) when PPI-scaled $M$ replaced constant $M$ (Table 3, Fig. 5). However, the largest improvement in model diagnostics was in the retrospective patterns (Fig. 6). Mohn's rho, which reflected the terminal five years, was reduced by 57% on average when $M$ was scaled by the PPI (Table 4). In addition, retrospective stability improved in all years for all estimates. For the constant $M$ model, 90% of samples from the MCMC posterior distributions fell within the range 32–136 kt for biomass and 0.02–0.09 year$^{-1}$ for $F$; for the PPI model, 90% were within the relatively narrow ranges 22–47 kt and 0.06–0.13 (F) (Fig. 7).

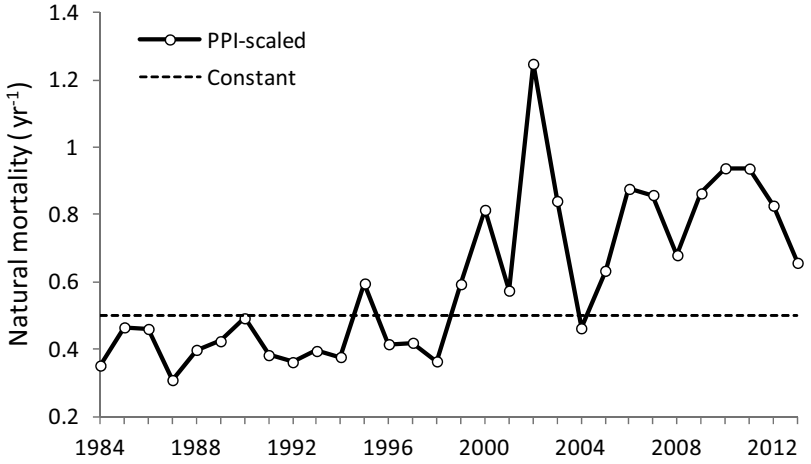


**Fig. 4.** Annual natural mortality rates used in CSA for constant the *M* model and the PPI-adjusted *M* model.

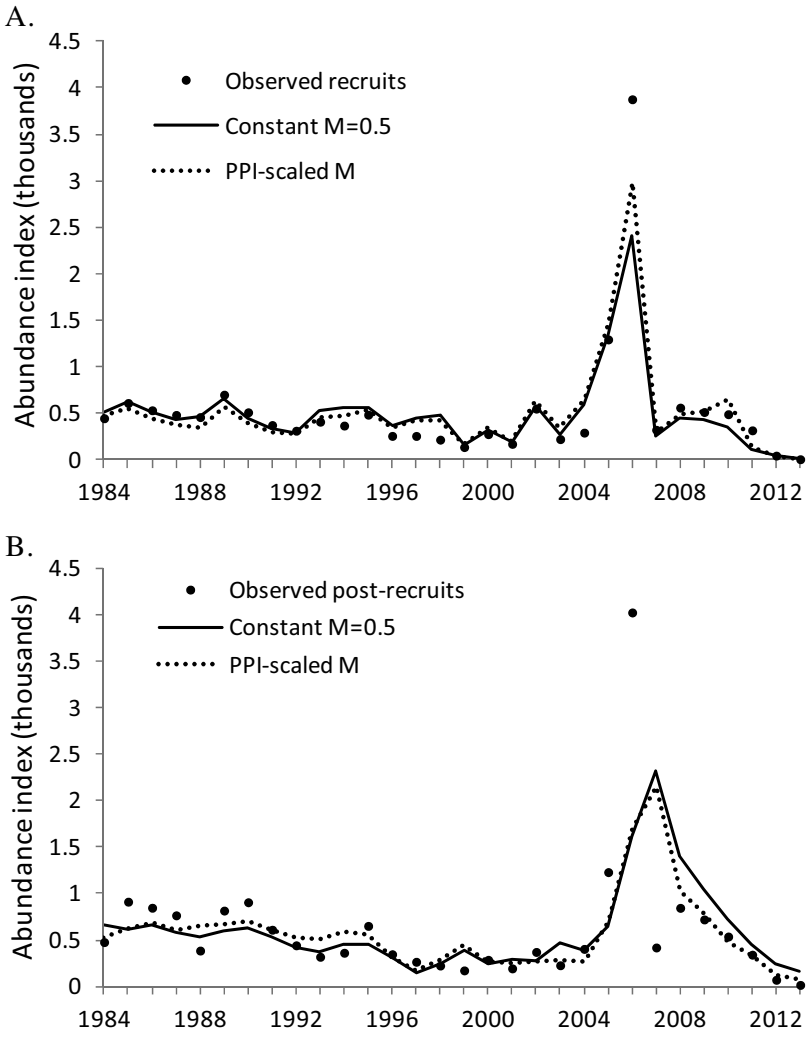


**Fig. 5.** Model fits to observed abundance indices of northern shrimp recruits (A) and post-recruits (B) using constant *M* and PPI-adjusted *M* model configurations.

## 4. Discussion

Adjusting natural mortality inputs to account for estimated predation pressure improved model fits and reduced a severe retrospective problem in the assessment for GOM northern shrimp. The simple approach was data-driven, allowed inclusion of predators for which estimates of total abundance (e.g., from stock assessment models) were not available, and did not require estimation of additional parameters within the model.

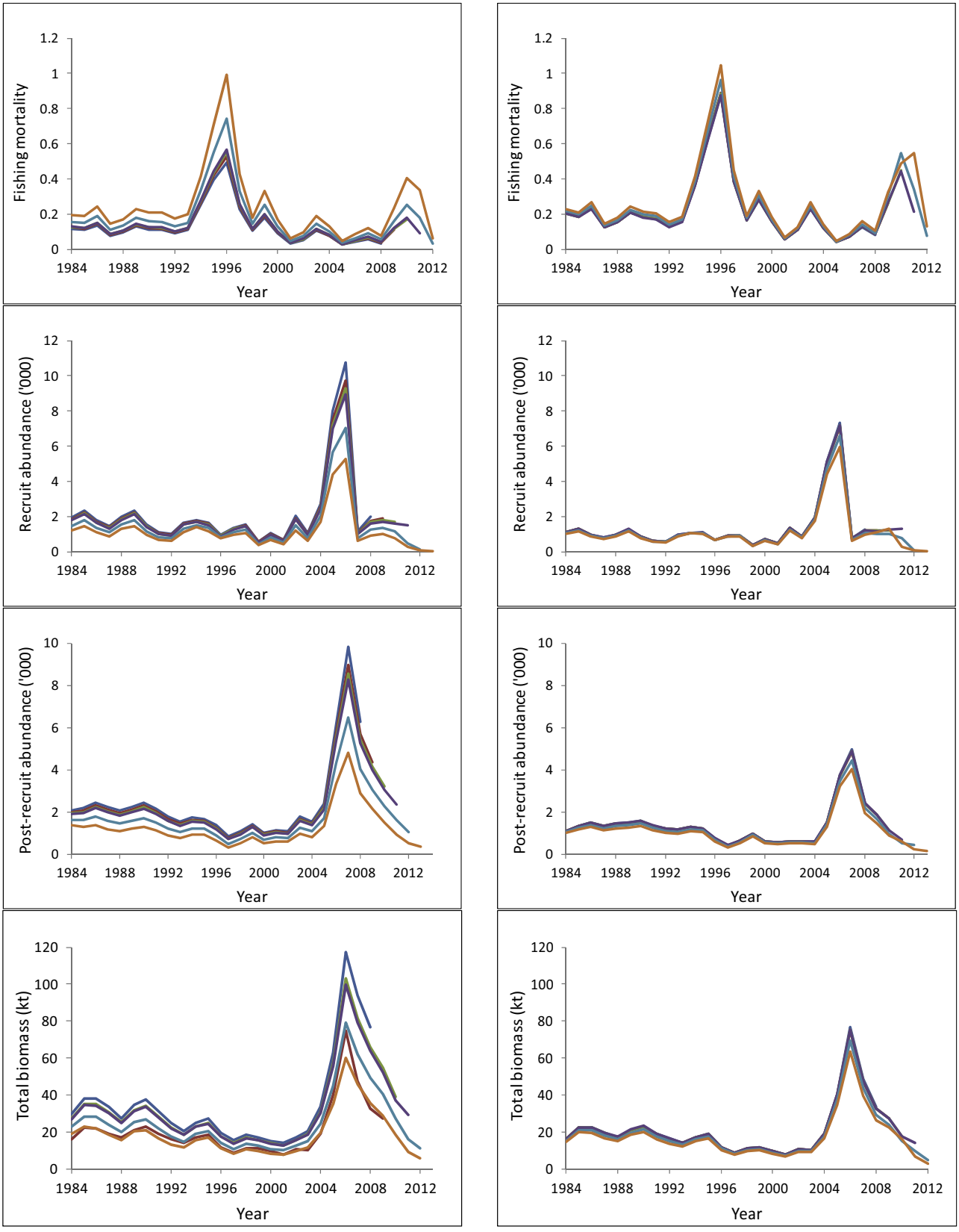


**Fig. 6.** Results of retrospective analysis (sequentially omitting five terminal years) using the CSA model for northern shrimp. Left column shows results assuming constant $M = 0.5\ \text{year}^{-1}$, right column shows results using PPI-adjusted annual $M$.

Analytical approaches to including predation in single species assessments often involve estimates of per-capita consumption rates or total consumption by predators (e.g., Sparre, 1991; Hollowed et al., 2000; Moustahfid et al., 2009). Such approaches account for time-varying species interactions, but consumption estimates are data-intensive and the required data may be unavail-

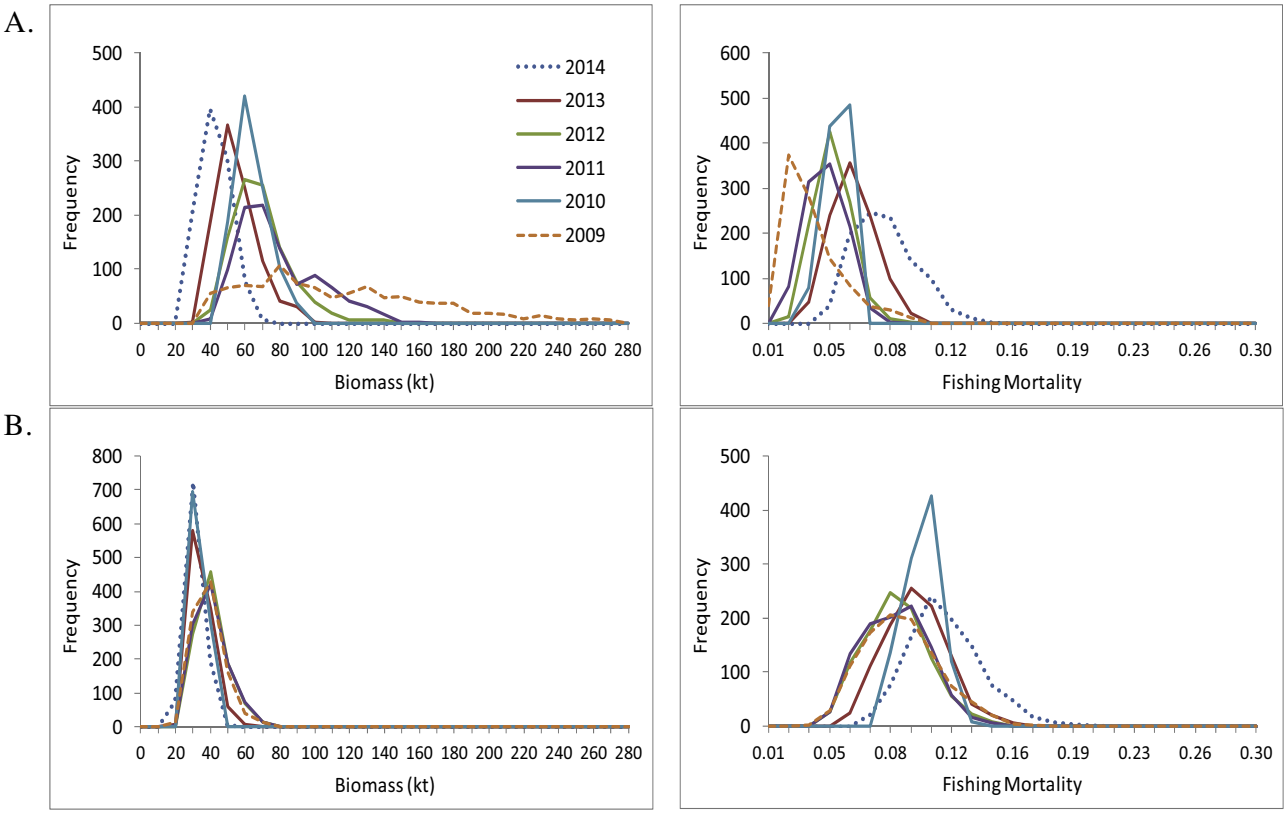


**Fig. 7.** MCMC distributions of biomass (left column) and fishing mortality (right column) estimated for 2008 from retrospective analysis with CSA models. (A) Constant $M = 0.5\ \text{year}^{-1}$, (B) PPI-adjusted $M$.

**Table 3**
Goodness of fit statistics for CSA models assuming a constant natural mortality rate ($M = 0.5\ \text{year}^{-1}$) or PPI-scaled $M$. Lower values of negative log-likelihood indicate better fit.

| Component | Negative log-likelihood | |
|---|---|---|
| | $M = 0.5$ | PPI-scaled $M$ |
| Shrimp survey recruits | −21.2 | −22.7 |
| Shrimp survey post-recruits | 4.0 | −3.4 |
| Fall survey abundance | −6.0 | −5.7 |
| Catch | −89.8 | −89.8 |
| Objective function | −112.9 | −121.6 |

**Table 4**
Mohn's rho for quantities estimated by CSA assuming a constant natural mortality rate ($M = 0.5\ \text{year}^{-1}$) or PPI-scaled $M$. Percent reduction in Mohn's rho is relative to the CSA model with constant $M = 0.5\ \text{year}^{-1}$. Mohn's rho is positive for overestimates and negative for underestimates.

| Parameter | $M = 0.5$ | PPI-scaled $M$ | Reduction |
|---|---|---|---|
| Fishing mortality | −0.57 | −0.31 | 46% |
| Recruit abundance | 1.68 | 0.85 | 49% |
| Post-recruit abundance | 1.18 | 0.36 | 69% |
| Total biomass | 1.28 | 0.48 | 63% |
| Average | | | 57% |

able or highly uncertain. Consumption estimates are subject to many potential sources of error, beginning with estimation of diet using 'bulk' methods (e.g., volumetric percent diet composition), which can be difficult even with extensive sampling (Lilly et al., 2000; Baker et al., 2014). When extrapolated to population level estimates of consumption, diet composition error is compounded by uncertainty in quantities such as gastric evacuation rates and predators' total population size. In short, estimating consumption is a worthy goal, but the potential for error is large. This is an important consideration for stock assessments because including consumption in assessment models can strongly influence parameter estimates and implied management targets (Hollowed et al., 2000; Moustahfid et al., 2009).

In contrast, the PPI method depends only on the simplest metric of diet (PFO) and indices of predator biomass. PFO is a relatively crude diet metric, based only on the presence or absence of a prey item in individual predators' stomach contents. However PFO has some distinct advantages despite its simplicity. Presence/absence data are comparatively easy to collect, readily interpretable, and the resulting estimates avoid some of the pitfalls of volumetric diet estimation (Baker et al., 2014). PFO was relatively stable in our study, with interannual variation (median CV for all species) of 80%, while interannual CV for shrimp abundance indices was 120% (NEFSC, 2014). Using annual PFO estimates to calculate PPI (Appendix A) did not improve model fits or retrospective patterns compared to using time-averaged PFO. This suggests that the PPI method might be applicable in some relatively data-poor situations where annual diet estimates are not available. PFO has received relatively little attention in diet studies (Baker et al., 2014), but deserves further study and development of applications.

Several causes of retrospective patterns have been identified in simulation studies with age-structured models, including systematic changes in natural mortality, growth, the amount of catch accounted for, and survey catchability (Legault, 2009; Hurtado-Ferro et al., 2015). These can act together to cause retrospective patterns, making it difficult to determine the underlying problem(s). However, information external to the model can provide clues (Legault, 2009). A change in $M$ was an obvious hypothesis to explore for northern shrimp given its importance as a forage species and major changes in the GOM demersal fish community (Fig. 2; EAP, 2009). In contrast, there was no evidence to implicate

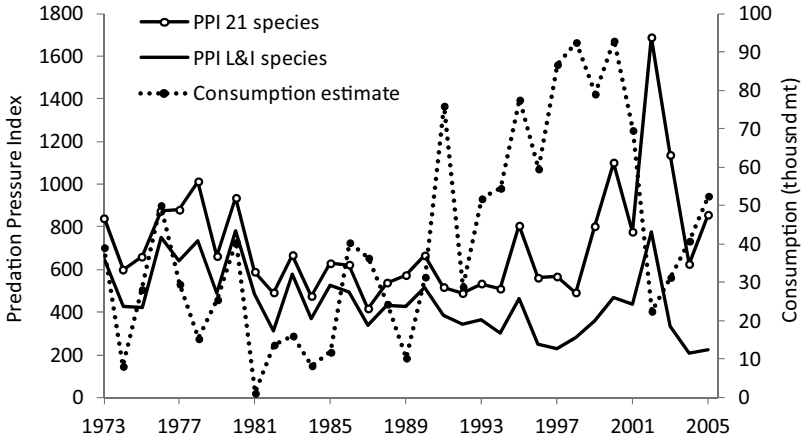


**Fig. 8.** Comparison of predation pressure index (PPI) (open dots) with estimates of annual Pandalid consumption from Link and Idoine (2009) (dotted line) and PPI calculated using only the 10 species included in Link and Idoine (2009) (solid line). L&I: Link and Idoine (2009).

trends in catchability. Survey data did not show shifts in distribution of northern shrimp that might affect catchability (NEFSC, 2014), and the vessel, fishing gear and methods used in the shrimp survey were consistent throughout the time series. Systematic changes in the proportion of catch reported may have occurred with increasingly strict reporting requirements (NEFSC, 2014). Sensitivity runs that adjusted for hypothesized under-reporting showed an additional 14–17% reduction in Mohn's rho (R.A. Richards, unpublished) beyond the nearly 60% reduction when changes in predation pressure were accounted for. Growth mis-specification is another potential cause of retrospective patterns (Hurtado-Ferro et al., 2015) that should be examined in future GOM northern shrimp assessments.

One approach to identifying the cause(s) of a retrospective pattern is to introduce time-varying parameters and observe the model response. If a particular manipulation reduces the retrospective pattern, plausible explanations are sought to explain the time varying change and model inputs are altered accordingly (Hurtado-Ferro et al., 2015). This 'model-down' approach can be informative, but if the underlying problem has not been identified correctly, improvements may be short-lived (Legault, 2009). 'Data-up' approaches such as the PPI-scaled *M* avoid the circular process of building hypotheses based on model output and then using these to modify the model inputs. However, it remains to be seen whether improvements based on data-up methods will be persistent, including whether the improvement in northern shrimp CSA retrospective patterns will hold over time.

Although northern shrimp are recognized as important components of North Atlantic ecosystems, quantifying their ecological importance has not been easy. Estimates of consumption of northern shrimp are generally accompanied by strong caveats, and vary widely with time, region, and predator (Parsons, 2005a), making it difficult to evaluate the impact of northern shrimp population dynamics on productivity of fish populations. Similarly, the influence of predation on northern shrimp productivity has been widely recognized (Berenboim et al., 2000; Koeller, 2000; Lilly et al., 2000; Worm and Myers, 2003; Parsons, 2005b; Wieland et al., 2007), but rarely included in assessment models for North Atlantic stocks. Trends in predator biomass are sometimes reported in northern shrimp stock assessments. However, only one northern shrimp stock assessment outside the GOM presently includes a model that directly accounts for variation in predation (NIPAG, 2014). The development of simple methods such as those described here may facilitate attempts to directly account for predation in shrimp stock assessment models.

Trends in the PPI from our study did not match trends in estimated consumption of GOM northern shrimp from earlier work (Link and Idoine, 2009; Fig. 8). However the two studies are not directly comparable for several reasons. Most importantly, (1) they used different representations of diet (percent diet composition vs. PFO) and predator population trends (abundance vs. biomass) and (2) several important predators (redfish, spiny dogfish, Atlantic herring, haddock) were not included in the consumption estimates due to sampling gaps early in the time series. When PPI was calculated without these four predators, the recent (post-mid-1990s) estimates of PPI were much lower and the PPI time series trend was flat rather than increasing. These results suggest that simple methods that account for a broader range of predators may be more informative than complex estimates for fewer predators.

Despite accounting for increasing *M* in recent years, shrimp abundance estimated from the CSA using PPI-adjusted M remained substantially lower than the estimated numbers of shrimp consumed. Understanding these discrepancies will require further work with both CSA and the consumption estimates.

Natural mortality rates are influenced by factors other than predation pressure, however for populations of forage species such as shrimp, predation is undoubtedly an important structuring force. Ignoring time-varying *M* when it exists has been shown to bias assessment results (Fu and Quinn, 2000; Deroba and Schueller, 2013) in addition to potentially contributing to retrospective problems (Legault, 2009). The simple and parsimonious approach described here for accounting for predation pressure could be applied in many assessments which otherwise would be obliged to assume constant natural mortality.

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## Appendix A.

This Appendix explores sensitivity to the use of time-invariant (average) PFO versus annual estimates of PFO in calculating the PPI.

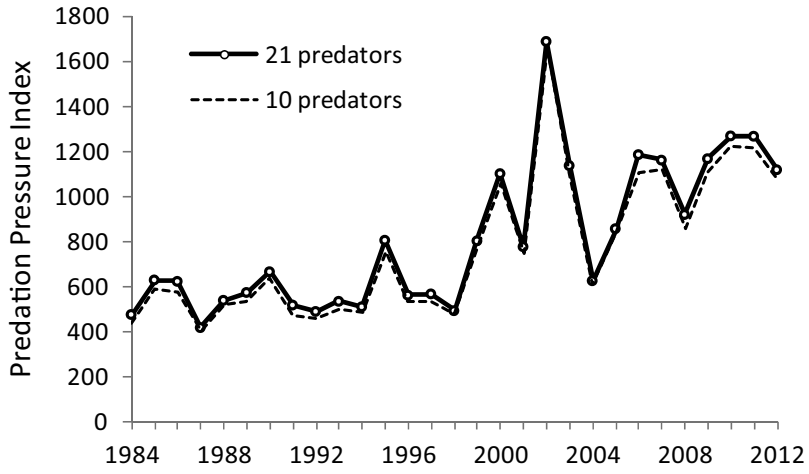


**Fig. A1.** Comparison of PPI based on full suite of 21 identified predators vs. only the 10 predators that contributed more than 1% on average to the PPI.

This analysis includes only the ten most important predators (those that contributed more than 1% to the PPI score on average, Table 1). The calculations to produce annual PFO for each species are labor intensive and inclusion of the minor predators would have had little effect (Fig. A1).

The PPI based on annual PFO and fall survey data for predators was calculated as:

$$\mathrm{PPI}_{Ai} = \sum_{j} B_{i,j} \times \mathrm{PFO}_{i,j} \quad \text{(A.1.1)}$$

**Table A1**
Annual PFO of Pandalids in diets of predators that contributed at least 1% on average to the PPI during 1973–2011. Number of sampled stomachs in parentheses; shaded cells were estimated (Eq. (A.1.2)) due to low sample size or missing data. CV is interannual coefficient of variation.

| Year | Acadian redfish | White hake | Spiny dogfish | Atlantic cod | Silver hake | Thorny skate | Red hake | Pollock | Haddock | Atlantic herring |
|---|---|---|---|---|---|---|---|---|---|---|
| 1984 | 0 (0) | 8.8 (136) | 0.9 (106) | 9.7 (31) | 0 (58) | 0.9 (13) | 4.2 (118) | 5.8 (36) | 0 (11) | 1.3 (0) |
| 1985 | 3.3 (61) | 3.6 (139) | 1.3 (157) | 5.4 (203) | 0.6 (650) | 2.8 (106) | 1.9 (159) | 2.2 (46) | 0 (21) | 1.3 (0) |
| 1986 | 0 (29) | 9.0 (266) | 1.6 (125) | 5.6 (216) | 2.2 (543) | 1.1 (87) | 4.4 (136) | 7.4 (46) | 1.7 (3) | 0 (20) |
| 1987 | 0 (35) | 6.2 (257) | 0 (84) | 4.5 (132) | 1.8 (506) | 0 (23) | 8.2 (73) | 2.4 (41) | 0 (11) | 0 (11) |
| 1988 | 0 (32) | 13.6 (323) | 1.1 (94) | 2.5 (275) | 5.2 (521) | 4.1 (74) | 12.7 (229) | 2.0 (50) | 2.1 (1) | 1.3 (5) |
| 1989 | 0 (13) | 6.4 (233) | 0.5 (211) | 7.8 (281) | 3.2 (624) | 3.4 (118) | 9.2 (185) | 1.5 (67) | 0 (25) | 1.3 (0) |
| 1990 | 0 (15) | 9.6 (312) | 2.5 (198) | 11.3 (300) | 4.3 (488) | 4.5 (133) | 17.2 (174) | 2.6 (78) | 2.9 (2) | 0 (5) |
| 1991 | 12.7 (0) | 23.2 (633) | 2.6 (418) | 15.4 (279) | 9.7 (722) | 6.0 (150) | 21.7 (263) | 6.9 (72) | 5.3 (2) | 1.3 (21) |
| 1992 | 9.1 (1) | 14.4 (521) | 1.2 (813) | 14.4 (236) | 5.9 (881) | 8.0 (138) | 19.3 (223) | 2.5 (81) | 3.8 (1) | 1.6 (316) |
| 1993 | 11.6 (0) | 15.8 (594) | 2.8 (431) | 21.7 (217) | 10.6 (933) | 16.5 (127) | 16.4 (214) | 4.4 (90) | 4.8 (1) | 0.9 (580) |
| 1994 | 15.9 (0) | 22.4 (416) | 6.1 (309) | 24.4 (119) | 10.7 (829) | 24.1 (79) | 25.0 (196) | 8.3 (24) | 6.6 (2) | 1.0 (311) |
| 1995 | 16.6 (0) | 28.9 (474) | 3.3 (690) | 22.5 (306) | 15.5 (1131) | 8.3 (121) | 22.0 (440) | 7.1 (56) | 0 (10) | 2.3 (564) |
| 1996 | 10.9 (0) | 19.9 (141) | 6.4 (203) | 19.1 (209) | 6.1 (491) | 2.7 (37) | 12.3 (171) | 6.8 (39) | 4.5 (0) | 3.1 (259) |
| 1997 | 8.0 (0) | 8.0 (150) | 2.0 (248) | 21.3 (141) | 9.7 (431) | 11.1 (36) | 8.5 (201) | 14.7 (68) | 3.3 (5) | 1.2 (164) |
| 1998 | 11.6 (5) | 23.0 (200) | 5.1 (450) | 13.3 (181) | 11.6 (757) | 15.4 (65) | 14.4 (284) | 13.8 (94) | 4.1 (73) | 0.7 (566) |
| 1999 | 14.5 (173) | 23.0 (152) | 7.0 (302) | 16.0 (175) | 11.5 (445) | 23.3 (30) | 18.6 (210) | 3.8 (78) | 3.2 (125) | 0.5 (183) |
| 2000 | 8.0 (125) | 18.1 (171) | 5.0 (200) | 16.2 (142) | 9.9 (314) | 8.9 (45) | 12.3 (171) | 3.8 (53) | 1.9 (107) | 3.1 (159) |
| 2001 | 7.2 (167) | 4.5 (133) | 0.5 (201) | 12.4 (113) | 11 (300) | 3.1 (32) | 6.2 (130) | 5.8 (93) | 0 (126) | 0.8 (125) |
| 2002 | 9.7 (124) | 7.1 (99) | 3.0 (166) | 7.7 (104) | 6.6 (273) | 0 (21) | 5.8 (104) | 6.3 (48) | 1.1 (90) | 8.7 (115) |
| 2003 | 0.7 (148) | 8.7 (69) | 6.1 (148) | 7.3 (110) | 7.2 (236) | 11.3 (53) | 1.1 (88) | 7.7 (52) | 3.6 (111) | 3.3 (122) |
| 2004 | 9.2 (141) | 21.3 (61) | 5.1 (99) | 10.6 (66) | 9.9 (203) | 5.0 (20) | 10.9 (55) | 6.5 (31) | 6.0 (84) | 2.8 (106) |
| 2005 | 14.4 (139) | 20.7 (58) | 18.8 (112) | 11.7 (94) | 11.1 (153) | 20.0 (20) | 16.7 (54) | 16.2 (68) | 7.7 (91) | 6.9 (102) |
| 2006 | 15.3 (176) | 27.2 (92) | 9.5 (158) | 17.2 (128) | 7.0 (186) | 12.0 (25) | 12.6 (111) | 8.6 (58) | 5.5 (146) | 3.7 (108) |
| 2007 | 6.3 (144) | 13.2 (76) | 2.3 (129) | 12.9 (101) | 2.5 (203) | 3.8 (26) | 2.9 (105) | 5.6 (36) | 3.9 (77) | 1.5 (132) |
| 2008 | 2.3 (172) | 11.8 (93) | 4.1 (122) | 5.8 (103) | 5.1 (236) | 0 (24) | 7.3 (110) | 1.8 (56) | 2.0 (49) | 0 (113) |
| 2009 | 6.5 (200) | 15.5 (129) | 7.5 (106) | 13 (131) | 8.5 (293) | 12.7 (79) | 14.7 (109) | 8.8 (34) | 5.3 (95) | 4.1 (170) |
| 2010 | 2.9 (171) | 5.5 (146) | 7.0 (115) | 5.5 (91) | 5.7 (211) | 10.4 (67) | 6.1 (49) | 20.0 (40) | 0 (85) | 1.6 (192) |
| 2011 | 1 (208) | 9.8 (133) | 4.4 (113) | 12.5 (72) | 3.4 (267) | 6.7 (60) | 7.0 (71) | 6.7 (45) | 0 (98) | 0.6 (159) |
| 2012 | 1.3 (240) | 5.6 (124) | 3.2 (155) | 3.6 (110) | 4.2 (330) | 3.6 (83) | 5.3 (132) | 4.3 (46) | 0.7 (151) | 0.5 (222) |
| Mean PFO | 6.9 | 14.0 | 4.2 | 12.1 | 6.9 | 7.9 | 11.2 | 6.7 | 2.8 | 1.9 |
| CV PFO | 83% | 53% | 89% | 50% | 56% | 86% | 58% | 67% | 85% | 104% |

**Table A2**
Relationships used to fill data gaps in annual PFO during 1984–1998.

| Predator | Number of years | Regressor (x) | Relationship | $R^2$ |
|---|---|---|---|---|
| Acadian redfish | 9 | PFO in all other predators | $y = 1.01x - 2.0$ | 0.68 |
| Thorny skate | 1 | PFO in all other predators | $y = 1.38x - 4.59$ | 0.55 |
| Pollock | 4 | Shrimp recruitment index | $y = 0.01x + 5.74$ | 0.18 |
| Haddock | 9 | PFO in all other predators | $y = 0.42x - 0.89$ | 0.47 |
| Atlantic herring | 5 | Mean shrimp carapace length (mm) | $y = -1.97x + 44.17$ | 0.72 |

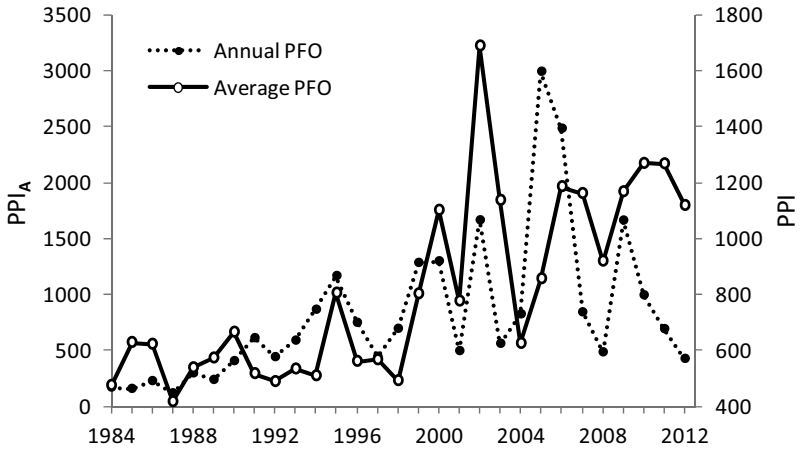


**Fig. A2.** Comparison of PPI calculated using average PFO of Pandalids in diet for each predator (PPI) vs. using annual PFO ($PPI_A$).

where symbols are as for Eqs. (1) and (2). Data to estimate $PFO_{ij}$ was missing for some years (Table A1). These gaps were filled using species-specific regression relationships estimated from years with complete data (1999–2010):

$$\mathrm{PFO}_{ij} = \alpha_j + \beta_j x_{i,j} \tag{A.1.2}$$

where $\alpha$ is the intercept, $\beta$ is the slope, and $x$ was a species-dependent regressor (Table A2). Annual PPI was used to scale $M$ for input to CSA, analogously to PPI based on time-invariant PFO (Eq. (3)).

Trends in $PPI_A$ and PPI both indicated generally higher predation pressure after the mid-1990s, but trends diverged after 2009 with $PPI_A$ declining steadily and PPI remaining relatively high (Fig. A2). The decline in $PPI_A$ was due primarily to a drop in Pandalid $PFO_{ij}$ for redfish and spiny dogfish diets (Table A1), but many species had declining Pandalid $PFO_{ij}$ during this period, paralleling a decline in northern shrimp abundance (Fig. 5).

The CSA model using $PPI_A$-scaled $M$ fit more poorly than the constant $M$ or PPI-scaled M models (NLL = −92.6 vs. −112.9 and −121.6, respectively). Despite this, retrospective patterns were reduced by 37% in the $PPI_A$ model compared to the constant $M = 0.5\ \mathrm{year}^{-1}$ model.

With only two predators dominating in recent years, $PPI_A$ was sensitive to inter-annual variation in both PFOs and biomass indices. This could be either a strength or a weakness, depending upon how much of the variation is random error and how much reflects true predation pressure. Using the long term average PFO dampens some of the fluctuation, and provides a more general indicator of the potential importance of each predator. The $PPI_A$ approach merits further investigation in the Gulf of Maine given the substantial increases in food habits sampling that began in 1999, but in the current study did not improve on the simpler approach of estimating PPI using time-invariant PFO.

## Appendix B.

This Appendix provides documentation for the CSA modeling approach.

5.1 Population dynamics

Abundance of exploitable individuals in each year $N_y$ is:

$$N_y = P_y + R_y \tag{A.2.1}$$

where $R_y$ is the number of new recruits ('recruits') to the exploitable population in year $y$ and $P_y$ is the abundance of fully recruited individuals ('post-recruits'). Post-recruits are related to total abundance in the previous year:

$$P_y = N_{y-1} e^{-Z_{y-1}} \tag{A.2.2}$$

where $Z_y = F_y + M_y$ is the instantaneous annual rate for total mortality, and $F_y$ and $M_y$ are instantaneous annual rates for fishing and natural mortality. Stock biomass is calculated as:

$$B_y = N_y b_y \tag{A.2.3}$$

where $b_y$ is a mean weight per individual in the population based on survey data.

Post-recruits in the first year, recruitments and fishing mortality rates are parameters that can be estimated in the model. Natural mortality rates and mean weights are fixed and may change over time. In our application, $M$ varied over time in accordance with the PPI or was constant (Fig. 4).

5.2 Observations

Predicted catch in number is calculated:

$$C_y = \frac{F_y}{Z_y} N_y \left(1 - e^{-Z_y}\right) \tag{A.2.4}$$

Catch weight is:

$$\hat{W}_y = C_y \hat{w}_y \tag{A.2.5}$$

where $\hat{w}_y$ is the mean weight of individuals in the catch estimated from port sampling and "$\hat{}$" denotes an estimate from goodness of of fit calculations.

Survey data can be entered either as indices of recruits and post-recruits ('split' surveys') or as 'aggregate' indices (recruits plus post-recruits). Multiple surveys of either type can be used in the same model run. In our application, the summer shrimp survey was split into recruits and post-recruits and the fall indices were used in aggregate.

Post-recruit indices were estimated as:

$$\hat{p}_y = q_p P_y \tag{A.2.6}$$

where $q_p$ is a catchability coefficient.

Recruit indices were predicted as:

$$\hat{r}_y = \nu_p q_p R_y \tag{A.2.7}$$

where $\nu_p$ is a relative catchability parameter for recruits relative to post-recruits. Relative catchability is specified by the user while catchability for post-recruits $q_p$ is a parameter estimated in the model.

**Table B1**
Initial and adjusted CVs used to weight survey series in the northern shrimp CSA models. Catch CV was not adjusted.

| Component | Initial CV | Adjusted CV |
|---|---|---|
| Shrimp survey recruits | 0.15 | 0.34 |
| Shrimp survey post-recruits | 0.15 | 0.55 |
| Fall survey abundance (1984–2008) | 0.26 | 0.53 |
| Fall survey abundance (2009–2012) | 0.36 | 0.37 |
| Catch | 0.05 | |

Aggregate survey indices are predicted as:

$$\hat{u}_y = Q\left(gR_y + P_f\right) \tag{A.2.8}$$

where $g$ and $Q$ are selectivity and catchability parameters that can be estimated in the model.

5.3 Parameter estimation

Parameters are estimated to minimize the negative log likelihood (NLL) of the data. The NLL used to measure goodness of fit to the catch data assumed that measurement errors were log normal:

$$\mathcal{L} = \sum_y \left\{ \ln(h) + 0.5\left[\frac{\ln(C_y) - \ln(\hat{C}_y)}{h}\right]^2 \right\} \tag{A.2.9}$$

where $h$ is a log scale standard deviation based on an assumed CV supplied by the user (CV = 0.05 in this application):

$$h = \sqrt{\ln\left(\mathrm{CV}^2 + 1\right)} \tag{A.2.10}$$

The negative log likelihood for goodness of fit to a survey index also assumed log normal errors but the standard deviation may vary from year to year and among surveys. Using an aggregate survey as an example:

$$\mathcal{L} = \sum_y \left\{ \ln h + 0.5\left[\frac{\ln(u_y) - \ln(\hat{u}_y)}{h_y}\right]^2 \right\} \tag{A.2.11}$$

The annual variances were calculated from observed CVs for each survey and were tuned as a group by adjusting the assumed CVs over the course of several runs until the implied CV based on residuals approximately matched the assumed value (Table B1):

$$\mathrm{CV}_{\mathrm{implied}} = \sqrt{e^{h^2} - 1} \tag{A.2.12}$$

where $h^2$ is the variance of the log scale residuals.

The total negative log likelihood used to estimate parameters was:

$$\mathcal{L}_{total} = \sum_j \omega_j \mathcal{L}_j \tag{A.2.13}$$

where the $\omega_j$ are user-specified weights for each type of data in the model. The user-specified weights were set to one in our application.

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