



Viewpoint article

The importance of including predation in fish population models: Implications for biological reference points

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ABSTRACT

A suite of applications utilizing various fisheries models have demonstrated that natural mortality due to predation is: (1) temporally and ontogenetically variable and (2) especially for forage species, generally higher than assumed in traditional single species stock assessments. Here we demonstrate that biological reference points generated by explicitly incorporating predation mortality into population dynamic models are generally more conservative (e.g., recommend higher standing biomass) than those produced using traditional assessment methods. Because biological reference points are the benchmark against which fisheries management decisions are made, they should reflect the ecological realities faced by each species to the fullest extent possible. We suggest much broader consideration of the more conservative biological reference points produced by explicitly incorporating predation mortality as a component of natural mortality to population models. This approach could implement a powerful yet tractable facet of ecosystem based fisheries management and is especially important for those stocks where predation mortality is known or suspected to be important.

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1. Introduction

Continued anthropogenic impacts have led to calls for a more holistic approach to marine resource management (Larkin, 1996; Micheli, 1999; Garcia et al., 2003; Browman and Stergiou, 2004). Several recent high profile papers have indicated globally serious situations for many marine species, in effect calling for more ecological factors to be considered (e.g., Jackson et al., 2001; Pauly et al., 2002; Myers and Worm, 2003; Pikitch et al., 2004; Worm et al., 2009). Admittedly these observations have not been without their critics and caveats (e.g., Hilborn, 2006). Regardless, there remains a recognized need to examine marine resource management from a more holistic, ecosystem-based perspective (Constable, 2001; Walters et al., 2005; Link, 2010). Central to this ecosystem-based perspective is accounting for all factors that can influence a fisheries stock, including ecological interactions.

There have been calls for fisheries managers to account for species interactions in fish population assessments for at least several decades (e.g., May et al., 1979) yet incorporating basic ecological processes (such as predation) into fisheries stock assess-

ments is still uncommon (Link, 2002; Townsend et al., 2008). Implementing a precautionary, ecosystem-based approach to fisheries management (EBFM) is becoming increasingly advisable for the sustainable harvest of marine capture fisheries (Botsford et al., 1997; Pauly et al., 2002; Garcia et al., 2003; Jennings, 2004). The accumulation of novel approaches to account for ecological interactions in fisheries models (e.g., Hollowed et al., 2000; Whipple et al., 2000; Hvingel and Kingsley, 2006), which have recently begun to be extensively reviewed (Plaganyi, 2007; Townsend et al., 2008), verify that the tools to do so are extant.

Forage species are a particularly germane instance where such ecological interactions should be given due consideration. Such species usually occupy middle trophic levels, serve as a mechanism of converting lower trophic level energy or biomass into forms suitable for upper trophic level consumption, are common prey for a wide range of such upper trophic level species, and can be an important source of standing biomass in an ecosystem. As such, forage species—which are often subject to both predation pressure and to commercial harvesting—are a logical starting point for demonstrating the efficacy of incorporating predation into fisheries population dynamics models. Various authors have found that when consumption of a particular forage species is calculated, the predation mortality values that had been assumed as a part of the total natural mortality in traditional stock assessments were underestimates (e.g., ICES, 1997; Hollowed et al., 2000; NEFSC, 2006) and, unsurprisingly, that predation mortality is temporally and ontogenetically variable (e.g., Gislason and Helgason, 1985; Mohn and

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Bowen, 1996; Tsou and Collie, 2001b). For forage species in particular, careful examination of traditional assumptions regarding predation mortality is needed because the abundance of their major predators (e.g., demersal fish, marine mammals, etc.) could reasonably be expected to increase in the next several years as stocks are rebuilt to meet legal requirements (e.g., Overholtz et al., 2008).

Biological reference points (BRPs) are values assigned to a fishery stock that indicate its status (e.g., biomass, fishing mortality, etc.) and are then used to make fisheries management decisions and actions. BRPs are often compared to signposts with target reference points depicting desirable conditions and limit reference points indicating conditions that should be avoided. There are many types of BRPs (e.g., Restrepo et al., 1998; Restrepo, 1999). Some of the most common limit BRPs are production based and are designed to prevent recruitment overfishing. Examples of these types of reference points are maximum sustainable yield (MSY), and the biomass and fishing rate, B_{MSY} and F_{MSY} respectively, at MSY. Yield per recruit based BRPs are intended to avoid growth overfishing (fishing a stock so heavily that individuals fail to reach their full growth potential). Some examples of these types of reference points are: F_{MAX} (the fishing mortality rate that will produce the maximum yield per recruit) and $F_{0.1}$ (the fishing mortality rate at which a small increase in fishing effort will bring only an additional 10% of the yield per recruit that would occur in an unfished population with the same increase in effort). MSY and its related or proxy reference points can be difficult to pinpoint due to a lack of contrast in survey or landings data and the dynamic nature of fisheries populations (e.g., Mace, 2001), so the International Council for the Exploration of the Seas (ICES) had adopted a precautionary approach to management. These precautionary reference points for biomass, B_{pa} , and fishing mortality, F_{pa} , are respectively higher than and lower than the limit reference points B_{lim} and F_{lim} (ICES, 1998). Yet despite all the caveats among particular BRPs, they remain widespread in their use for fisheries management.

One way to facilitate implementation of EBFM is to calculate BRPs that reflect and account for important ecological interactions. Biological reference points are expected to differ between single and multispecies contexts (ICES, 2001; Walters et al., 2005; Brodziak et al., 2008) and predation mortality in particular can exert a strong influence on BRPs (ICES, 1997). Additionally, the sensitivity of a wide variety of BRPs to trophic interactions has been explored (Collie and Gislason, 2001); thus an appraisal of the effects of incorporating predation or multispecies interactions to BRPs seems warranted to further support EBFM as an operational concept. Our objectives in this manuscript were to: (1) demonstrate the need to consider predation mortality for some stocks by examining example (i.e., not exhaustive, but certainly illustrative) instances where doing so has been significant, (2) elucidate the consequences of failing to do so, particularly for forage species, and (3) note that the tools and approaches to do so are extant as informed by the well studied/high data availability situations discussed herein and that these approaches could be applied to similar but less studied/lower data availability situations.

Here we examine the results of multiple modeling approaches that explicitly incorporated predation mortality for one or more forage species (Table 1). Predation mortality, M_2 , is a component of natural mortality, M . Other sources of natural mortality (M_1) are due to factors such as disease, senescence and injury. Thus, total natural mortality is a combination of M_1 and M_2 :

$$M = M_1 + M_2$$

which in turn is only one facet of total mortality Z , which also includes fishing mortality F :

$$Z = F + M$$

Some of the approaches used thus far for explicit consideration of predation mortality include: production models such as biomass dynamic (e.g., Overholtz et al., 2008; Moustahfid et al., 2009b) and “minimally realistic models” (Punt and Butterworth, 1995), single species age structured models (e.g., Livingston and Methot, 1998; Hollowed et al., 2000; Moustahfid et al., 2009a), multispecies VPA (MSVPA) (e.g., Gislason and Helgason, 1985; Livingston and Jurado-Molina, 2000; Tsou and Collie, 2001a; Tyrrell et al., 2008; Garrison et al., 2010), stochastic multispecies model (SMS; Koster et al., 2009), an area, age and length structured model MULTSPEC (Bogstad et al., 1997), multispecies statistical catch-at-age (e.g., Jurado-Molina et al., 2005), and a flexible, multispecies, spatially explicit statistical model, GADGET (Globally applicable Area-Disaggregated General Ecosystem Toolbox; Begley and Howell, 2004). Again, these examples are meant to be illustrative, not exhaustive. A subset of these investigations compared BRPs calculated using traditional single species methods with those derived with explicit consideration of predation mortality or from aggregated biomass approaches. For these applications, we compare the ratio between BRPs produced by each approach.

2. Observations on BRPs with and without predation

2.1. Interaction between fishing and predation mortality

As noted above, traditional approaches to stock assessment that underestimate the magnitude and dynamic nature of natural mortality for forage species lead to biomass and yield projections that are too optimistic and therefore, not precautionary. There are many geographically diverse examples of a species being subject to substantial predation pressure in addition to being commercially exploited (e.g., capelin, *Mallotus villosus*, in the Barents Sea (Hjermann et al., 2004), walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska and the Bering Sea (Jurado-Molina and Livingston, 2002) and herring, *Clupea harengus*, in the Northeast US (Overholtz and Link, 2007)). Heavy fishing pressure on species such as these that occupy mid-to-lower trophic levels could lead to competition between humans and other predators for the same relatively low valued fish (e.g., Overholtz et al., 2000; Hjermann et al., 2004). The consequence of this situation could be forgone biomass of higher trophic level species (Gamble and Link, 2009) - which are usually more economically valuable - due to the exploitation of lower trophic levels species.

The relative magnitude of fishing vs. natural mortality, in addition to the timing of peak predation mortality relative to fishing mortality, can also affect productivity estimates of a stock. For example, at low fishing mortality levels, predation mortalities that are only 50% of the fishing mortality value will lead to substantially inaccurate BRPs if predation mortality is not explicitly incorporated into the stock assessment model (ICES, 1997). If landings and consumptive removals are approximately equal, this is even more the case, with predator consumption typically influencing younger age classes of prey species and the resultant changes to BRP estimates (NEFSC, 2007; Overholtz et al., 2008). Similarly, if timing of high commercial exploitation and predatory removals are out of sync and dynamic over the year, traditional single species models that assume constant natural mortality rates will overestimate the stock's recovery potential (e.g., Moustahfid et al., 2009b).

2.2. Traditional assumptions about predation mortality should be carefully examined

Estimates of natural mortality range widely between species and with different modeling approaches (Fig. 1). Nevertheless, from the examples in Fig. 1 (and others, see below) a geographi-

Table 1

Examples of population models that have explicitly accounted for predation mortality and the salient observations derived from doing so. Superscript letters reference natural mortality estimates from different models presented in Fig. 1.

| Authors | Predator species | Prey species | Ecosystem | Model type | Observations from including predation |
|---|---|--|---------------------------------|-----------------------------|---|
| Gislason and Helgason (1985) | 10 fish species | e.g., herring, sandeel, sprat, mackerel | North Sea | MSPVA | Amount of biomass killed via predation is 1.6 times greater than the amount taken by fisheries |
| Punt and Butterworth (1995) | Fur seals, Cape hake, other predatory fish | Cape hake, deep water hake | South African west coast | Minimal realistic model | The effect of seal culls could be small or even detrimental to the hake fishery because of increased predation of one hake species on a congeneric resulting in diminished hake biomass overall |
| ^a Bogstad et al. (1997) | Cod, harp seal, minke whale | Capelin, herring, cod | Barents Sea | MULTSPEC | Increases in marine mammal populations will affect herring, capelin and cod |
| ^g Livingston and Methot (1998) | Walleye pollock, cod, northern fur seals | Walleye pollock | Eastern Bering Sea | SS age structured | Cannibalism by walleye pollock strongly affects recruitment of this species to the fishery. |
| Hollowed et al. (2000) | Arrowtooth flounder, halibut and Stellar sea lion | Walleye pollock | Gulf of Alaska, USA | SS age structured | Models that failed to account for uncertainty in natural mortality underestimated stock biomass by 20% |
| ^g Livingston and Jurado-Molina (2000) | 5 fish and 1 seal species | e.g., Walleye pollock, cod, herring | Eastern Bering Sea, USA | MSVPA | Predation and cannibalism important influences on walleye pollock, especially age 0 |
| Constable (2001), Constable et al. (2000) | Patagonia toothfish | Krill | Antarctic | Generalized yield | Precautionary catch limits for Patagonia toothfish were revised to take into account other predators' demands for krill |
| ^c Tsou and Collie (2001b) | 6 demersal fish | Silver hake, herring, mackerel, sand lance | Georges Bank, USA | MSVPA | For all important prey except mackerel, predation mortality was high compared to residual natural mortality |
| ^h Garrison and Link (2004), NEFSC (2006) | Striped bass, weakfish, bluefish | Menhaden | Eastern US coast | MSVPA-X | Predation mortality increased with increased predator populations and has a notable impact on the menhaden |
| Jurado-Molina et al. (2005) | Walleye pollock, cod | Walleye pollock | Eastern Bering Sea | MS statistical catch-at-age | For older age classes, the statistical model, MSVPA and SSVPA all provide similar population estimates |
| ^f NEFSC (2007) | 18 predator species | Northern shrimp | NE US Continental Shelf | Biomass dynamic | Consumptive removals of shrimp were higher than the amount of exploitable biomass estimated from the biomass dynamic model |
| Harvey et al. (2008) | Pacific hake | 3 rockfish species | U.S. Pacific coast | 2 species age structured | Estimated time to rebuild was substantially increased by incorporating predation and spatio-temporal overlap (bycatch) |
| ^d Overholtz et al. (2008) | 29 species inc. fish, mamm, seabirds | Herring | Georges Bank/Gulf of Maine, USA | Biomass dynamic | Predation mortality rate of herring is related to both its abundance and that of its predators. |
| ^b Tyrrell et al. (2008) | 11 demersal fish species | Herring, mackerel | NE US Continental Shelf | MSVPA-X | Predation mortality on youngest age classes of herring and mackerel substantially higher than values used in traditional single species assessments |
| Koster et al. (2009) | Cod | Juvenile cod, herring, sprat | Eastern Baltic Sea | Age-length SMS | BRP's need to be revised to account for environmental regime shifts and the effects of incorporating cannibalism varies with different assumptions re: environment and recruitment interactions |
| ^e Moustahfid et al. (2009a) | 13 demersal fish species | Mackerel | NE US Continental Shelf | SS age structured | Magnitude and uncertainty of mackerel's SSB and recruitment underestimated when predation is not explicitly modeled |

MSVPA: multispecies virtual population analysis, MULTSPEC: an area, age and length structured multispecies simulation model, SS age structured: single species age structured, MSVPA-X: expanded multispecies virtual population analysis, MS statistical catch at age: multispecies statistical catch at age, Age-length SMS: age-length-structured multispecies model.

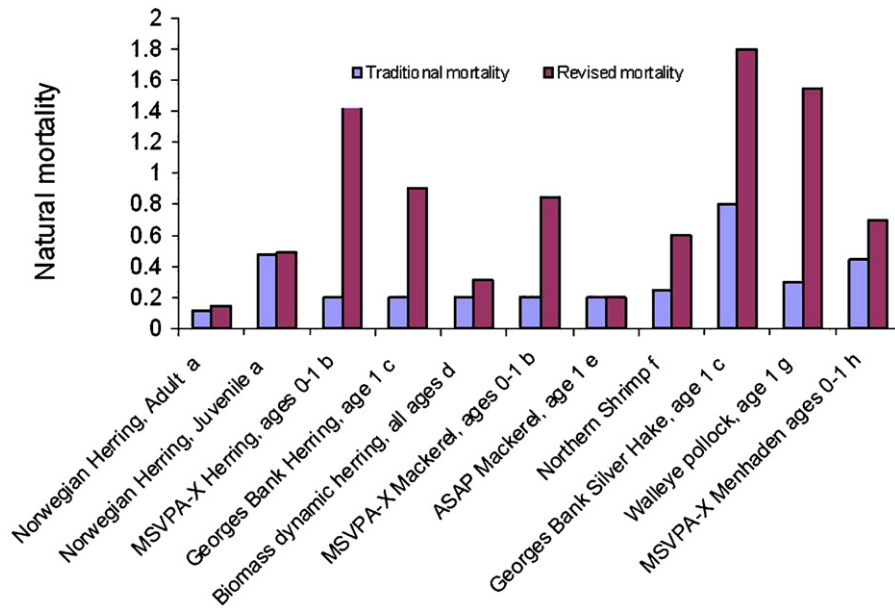


Fig. 1. Comparison of natural mortality rates from traditional stock assessments and models that calculate consumption to more precisely formulate predation mortality (i.e. revised). Source citations for each species that correspond to their superscript for Table 1 are provided.

cally diverse cross-section of forage species' natural mortality rates shows that they can be quite high and in most cases strongly exceed the rates traditionally assumed for these species. For instance, a recent review of the estimated consumptive removals of northern shrimp, *Pandalus borealis*, indicated that a natural mortality rate of 0.6 is more likely than the current value of 0.25 (NEFSC, 2007; Link and Idoine, 2009). When the revised 0.6 value was used to calculate abundance and biomass, an increase of 4–5 times was observed for both biomass and abundance of this species, aligning more closely in magnitude to estimates derived from predatory consumption.

For the majority of the species in Fig. 1, predation mortality forms the bulk of the natural mortality rate. For example, Tsou and Collie (2001a) reported the average annual predation mortality rate over a fourteen year period for age 1 silver hake, *Merluccius bilinearis*, was 1.6. One of the consequences of this chronic underestimation of predation mortality in traditional stock assessments is that the strength of the relationship between prey species population dynamics with that of their predators is underrated.

The importance of incorporating temporally and ontogenetically variable predation mortality has been recognized, especially in the ICES arena, for many years. For instance, although traditional single species methods are still used to calculate BRPs, stock assessments for Baltic herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) incorporate species interactions such as predation mortality and cannibalism from multispecies models (e.g., ICES, 2008). Similarly for the North Sea, higher natural mortality rates from MSVPA are imported to single species assessments (ICES, 2007). The same has begun in assessments of Atlantic menhaden (*Brevoortia tyrannus*; Garrison and Link, 2004; NEFSC, 2006).

2.3. Effect of accounting for predation on abundance and fishery yield

The revised estimates of natural mortality produced by accounting for predation mortality will also lead to alterations in abundance and fishery yield estimates. For most forage species, the changes in abundance are likely to be particularly dramatic, especially for the youngest age classes. For example, Livingston and Jurado-Molina

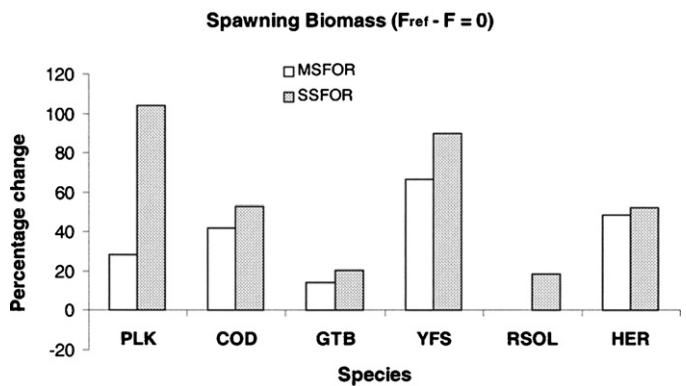


Fig. 2. Percent change in spawning biomass from multispecies and single species forecast models under F_{ref} (average fishing mortality in recent years) vs. a no-fishing scenario. Figure re-printed with permission from Allen Press, North American Journal of Fisheries Management as adapted from Jurado-Molina and Livingston (2002). SSFOR: single species forecasting model, MSFOR: multispecies forecasting model, PLK: walleye pollock, COD: Pacific cod, GTB: Greenland turbot, YFS: yellowfin sole, RSOL: rock sole, HER: Pacific herring.

(2000) found an order of magnitude increase in abundance of age 0 walleye pollock in the Eastern Bering Sea as estimated by MSVPA vs. single species VPA. Similarly, estimates of age 0 menhaden between MSVPA and single species methods differed by approximately 10 billion fish because of the inclusion of predation in the multispecies model (Garrison and Link, 2004). For simulations examining the effect of zero fishing pressure in the eastern Bering Sea ecosystem, MSFOR (multispecies forecast model) produced much smaller increases in spawning biomass than SSFOR (single species forecast model) for 5 of 6 fisheries species (Jurado-Molina and Livingston, 2002, Fig. 2). This is due to multispecies models incorporating the changes in predation mortality that affect commercial species as their predator's populations increase under a no fishing scenario while single species models either ignore or treat this interaction as static. For rock sole, *Lepidopsetta bilineata*, the MSFOR results did not predict an increase in spawning biomass because it was input as a prey item and therefore, increased populations of its predators resulted in higher consumption of rock sole and thus low-

Table 2

Comparison of MSY (maximum sustainable yield) based biological reference points (B_{MSY} : biomass at maximum sustainable yield, SSB_{MSY} : spawning stock biomass at maximum sustainable yield) produced by explicitly incorporating predation (= revised; numerator) and traditional (= fishery; denominator) methods.

| Prey species, author | Predators | Revised B_{MSY} or SSB_{MSY} / Traditional B_{MSY} or SSB_{MSY} | Revised MSY/ Traditional MSY |
|--|--|--|---------------------------------|
| Atlantic herring, Overholtz et al. (2008) | 29 species inc. fish, mar mamm, seabirds | 1.62 | 2.39 |
| Atlantic herring, Tyrrell et al. (2008) | 11 demersal fish species | 1.38 | 1.25 |
| Atlantic mackerel, Moustahfid et al. (2009a) | 13 demersal fish species | 2.71 | 1.83 |
| Atlantic mackerel, Tyrrell et al. (2008) | 11 demersal fish species | 1.11 | 1.57 |
| Longfin squid, Moustahfid et al. (2009b) | 15 demersal fish species | 4.21 | 3.36 |

ered its projected spawning biomass estimates. Similar results have also been observed for several species simulated for the southeast Australian fisheries ecosystem (Fulton et al., 2007).

Yield projections for individual species can both increase and decrease when ecological interactions are taken into account, depending on the dynamics between the focal species and whether alternate prey are available. Under the assumption that gray seal, *Halichoerus grypus*, predation on Atlantic cod was additive to other predation mortality, Mohn and Bowen (1996) showed >50% reductions in yield for cod during a time of increased seal abundance. Similarly, in the Northeast US, yields of prey species such as herring will likely decline as their predator stocks recover from decades of overfishing (Overholtz et al., 2008).

For predators with limited foraging areas and little alternate prey, precautionary approaches to calculating fisheries yields are of critical importance. Everson and de la Mare (1996) incorporated the requirements of land based predators (seals, penguins, petrels and other birds) on Antarctic krill, *Euphausia superba*, around South Georgia Island. They suggested a 75% reduction in the precautionary catch limit to allow for acceptable impacts of the krill fishery for these predators with limited foraging ranges.

2.4. Biological reference points are different with ecological considerations

Biological reference points derived with multispecies models differ from their traditional single-species counterparts in that they generally result in more precautionary management advice (Hall, 1999; ICES, 2008). In addition to the studies described in some detail below, many other studies support the finding that BRPs change when predation is explicitly modeled (e.g., ICES, 1997; Collie and DeLong, 1999; Hvingel and Kingsley, 2006). Table 2 summarizes a suite of studies that explicitly compared BRPs from traditional stock assessment model parameterization vs. a situation where consumption on the focal species was calculated and the resulting revised predation mortalities and biomasses were used for BRP estimation.

An important example of changed BRPs from including predation comes from the Baltic Sea ecosystem, where Gislason (1999) reported complex relationships between reference limits for cod and herring and sprat, but with a straightforward overriding conclusion – BRPs of stocks that interact should not be considered in isolation. Similarly, under the adverse recruitment conditions of recent decades, Koster et al. (2009) found that incorporating cannibalism for Eastern Baltic cod lowered the estimated fishing mortality rate that was required to reach B_{pa} . Collie and Gislason (2001) concluded that fishing mortality reference points for prey such as sprat should be conditioned on changes in predator abundance and Jurado-Molina and Livingston (2002) found that their three prey species were also sensitive to the harvest levels of their predators. For Barents Sea capelin Gjøsaeter et al. (2002) advocated stochastic reference points should be developed to account for variable predation by cod and marine mammals. Accurate calculation of reference limits, especially for forage species, requires consid-

eration of the dynamic biomass levels of both predator and prey populations.

Another example of changed BRPs is the northwest Atlantic herring fishery. Overholtz et al. (2008) used a delay difference model to calculate surplus production of age 2+ herring with predatory removals by demersal fishes, marine mammals, large pelagic fishes and seabirds. The B_{MSY} derived from the model with predation explicitly incorporated was higher than the fishery only B_{MSY} by a factor of 1.6. Moustahfid et al. (2009b) incorporated predatory removals of longfin inshore squid, *Loligo pealeii*, using a surplus production model in a similar manner as Overholtz et al. (2008) and found that B_{MUP} (a proxy for B_{MSY} , maximum usable production) increased by more than a factor of three when predation was explicitly accounted for. Similarly, MSY almost doubled and SSB_{MSY} increased by almost three times when predation by 13 demersal fish species was explicitly incorporated into an age-structured assessment model for Atlantic mackerel (*Scomber scombrus*, Moustahfid et al., 2009a). In an MSVPA of 14 predator stocks and 2 age structured prey species (Atlantic herring and Atlantic mackerel) of the Northeast US Continental shelf ecosystem, Tyrrell et al. (2008) found that herring's MSY and B_{MSY} increased in a multispecies vs. single species context, but not to as strongly as reported by Overholtz et al. (2008). For mackerel, the MSVPA biomass estimates also resulted in BRPs that were more conservative than the reference points produced by traditional single-species methods (Tyrrell et al., 2008). Different types of modeling approaches (e.g., age structured vs. non-age structured) and different suites of predators and input parameters have resulted in variable point estimates of BRPs (e.g., Overholtz et al., 2008 vs. Tyrrell et al., 2008). Despite variation in the absolute value of BRPs with and without predation incorporated, B_{MSY} or SSB_{MSY} increased by >10% for all situations where these types of comparisons were made (Table 2). For other reference points such as F_{crash} and $F_{0.1}$ (both based off of stock-recruitment relationships, with $F_{0.1}$ being the fishing mortality rate at 10% of the maximal yield per recruit rate, and F_{crash} being the fishing rate which will produce a long-term spawning biomass per recruit (S/R) equal to the inverse of the instantaneous rate of variation of R with the biomass, at the initial point ($S=0, R=0$)), a similar finding of more conservative reference points being calculated has been reported by other authors. For example, both $F_{0.1}$ and F_{crash} were lower in a multispecies context for MSVPAs of the Barents Sea and the North Sea (ICES, 1997).

As the majority of the aforementioned studies show, inferences from a variety of models for various fisheries species indicate that BRPs for forage species are different and generally point to more conservative harvest rates when ecological considerations are accounted for. To broaden the applicability to EBFM, BRPs can also be calculated for a suite of species in addition to individual values for each species. Mueter and Megrey (2006) aggregated fisheries species into a surplus production model to calculate an ecosystem-level MSY (termed multi-species maximum surplus production) for the Gulf of Alaska and Bering Sea commercially exploited groundfish species. They found that in both ecosystems, this ecosystem-level MSY was smaller than the component sum of single species MSYs (Table 3) and furthermore, that incorporation

Table 3
Comparison of MSY based biological reference points produced by summing single species reference points vs. ecosystem estimated reference points from surplus production models.

| Ecosystem, author | Focal species | Ecosystem B_{MSY}/sum of SSB_{MSY} | Ecosystem MSY/sum of $SS\ MSYs$ |
|---|---|--|---|
| Northeast US Continental Shelf, NEFSC (2008) | 19 groundfish stocks, 2007 assessment | 0.89 | 0.96 |
| Northeast US Continental Shelf, NEFSC (2008) | 19 groundfish stocks, previous assessment | 0.53 | 0.63 |
| Gulf of Alaska, Mueter and Megrey (2006) | 12 groundfish species | NA | 0.61 |
| Bering Sea/Aleutian Islands, Mueter and Megrey (2006) | 11 groundfish species | NA | 0.72 |

of environmental variability led to further depressed maximum multi-species surplus production estimates. The authors interpreted these results as indicating that more conservative reference points are the appropriate management targets. Similarly, for the Georges Bank fish community, Collie and DeLong (1999) found that multi-species yield was lower than single species yields when the same combination of harvest rates were used for each calculation. They attribute this result to predators consuming some of the “surplus production”. A similar exercise was undertaken for the Northeast US Continental shelf ecosystem with calculations for all 19 commercially exploited groundfish stocks (NEFSC, 2008). For groundfish, both the most recent and previous assessments indicated that aggregate MSY was lower than the sum of single species MSYs and aggregate B_{MSY} was also lower than the sum of analogous single-species components. However, for the most recent assessment, the difference between the aggregate and summed single species reference points had narrowed, indicating that the current management reference targets were more reasonable (NEFSC, 2008). Overall, most research suggests that current single-species management targets may not be conservative enough to support maximum system-wide production.

2.5. Reevaluating the argument of “increasing uncertainty” by adding in predation mortality

There are several forms of uncertainty in the assessment process (Peterman, 2004; Link et al., 2010) and they all can be important when evaluating the status of fish stocks. We challenge the assertion that precision or estimation uncertainty (i.e., statistical estimation) outweighs other sources of uncertainty such as magnitudinal, process or accuracy uncertainty (i.e., closer to correct order of magnitude of estimates by inclusion of additional factors). These other sources of uncertainty are often downplayed because of concerns regarding adding extra information to these models (Peterman, 2004). The concerns of the precision types of uncertainty largely center about estimation error, particularly of predatory consumption and consumptive removals from food habits data because those data and associated calculations are used to estimate predation mortality. Yet we note that even without requisite food habits data and the ability to model consumption directly, there are other approaches to generically include predation mortality in assessments (see below). For example, M need not be a fixed parameter; in terms of process error, having a time invariant natural mortality for stocks can lead to erroneous projections and estimates, as seen in the shrimp example above (NEFSC, 2007; Link and Idoine, 2009). This process error is magnified when an assessment is using an age or stage-based model, as noted in numerous examples in the previous section as compared to using an age invariant natural mortality (Tables 1 and 2). The simple point we make is that including ecological interactions may in fact increase estimation uncertainty, but may also decrease process uncertainty. Often the two are tradeoffs between better precision in parameter estimates and more accurate magnitudes of those same parameter estimates.

By excluding predation, model results will certainly reflect improved precision uncertainties. But as we have shown, doing so can affect accuracy of the estimates by several orders of magnitude. In such instances we suggest relaxation of variance/confidence interval precision criteria to incorporate predation and to better minimize process, magnitude and accuracy uncertainties.

We recognize that even if predation is suspected to be important and should be considered, not all ecosystems or regions have the extant data to estimate a long time series of consumption (e.g., Overholtz et al., 2008), to validate various functional forms of predation (Moustahfid et al., 2010), or to estimate predation mortality directly and thus address the process uncertainty concern. However, we note even in instances where there are no food habits data, there are models and general principles very much extant (e.g., ICES, 1997; Collie and DeLong, 1999; *sensu* Moustahfid et al., 2010) that can relate predator and prey abundance to inform predation parameters used in calculating predation and revised BRPs. Usually, at least in most fisheries contexts, there are some set of surveys that can estimate the abundances or biomasses of both predators and prey in a given ecosystem, which can then be statistically linked (e.g., GLMs relating abundance to % BW consumed or to other consumption values; *sensu* Overholtz et al., 2008) or linked via process modeling (e.g., various functional response forms; *sensu* Moustahfid et al., 2010). Certainly using such an indirect approach may initially only provide contextual information in stock assessments, perhaps only informing suggested revisions to M or Z (e.g., the *Pandalus* example above; NEFSC, 2007; Link and Idoine, 2009). And certainly the sensitivities to the parameters and functional forms will need to be examined and presented in full sensitivity or risk analysis contexts (Punt and Butterworth, 1995; Peterman, 2004; Kinzey and Punt, 2009). Clearly not all instances will resolve concerns over uncertainty to the point of being useful, and certainly such approaches will need to be evaluated with and compared to best practices and results from similar situations in comparable ecosystems. And certainly these indirect approaches should be considered with all the appropriate caveats. Yet what we have noted here is at least one way to initially scope out the possible effects of predation on stocks when doing so is germane and where highly resolved data may not be available. This highlights that there are theoretical and empirical approaches readily available to begin to elucidate the magnitude of these ecological interactions in instances where there is a real or perceived limited set of data.

2.6. Effect of rebuilding or recovery of marine predators

In the US as in many other areas around the world, fisheries managers are attempting to rebuild severely depleted stocks. As the abundance of high trophic level demersal fish increases, the importance of their predation on forage stocks will likewise be enhanced. For instance, the abundance of marine mammals along the US east coast has generally increased over the past two decades (Waring et al., 2002) and these escalating marine mammal populations are expected to have a negative influence on the abundance of forage

stocks (Bogstad et al., 1997; Overholtz and Link, 2007). This is also the case for seals in Atlantic Canada (Bowen et al., 2008, 2009), such that concerns over seal predation on fish stocks have led to calls for seal culls to allow various fish species to escape from a “predator pit” that may be regulating the abundance of these stocks. In the North Sea, herring are recovering from overfishing in the late 1960s and their consumption of sandeel, *Ammodytes marinus*, larvae may have led to food shortages for breeding seabirds (ICES, 2007). Rebuilding predator populations, whether they are fisheries species; or protected, endangered or threatened marine mammals; or other consumers such as seabirds, will affect the abundance of their prey (e.g., Punt and Butterworth, 1995; Constable, 2001; ICES, 2008). Failing to account for these types of predatory interactions in estimating the stock recovery trajectory of prey species will lead to poor management advice such as overly optimistic recovery times (ICES, 1997; Bjørnsson and Sigurdsson, 2003; Moustahfid et al., 2009b). As an example, Harvey et al. (2008) found that by incorporating predation by Pacific hake, *Merluccius productus*, on widow rockfish, *Sebastes entomelas*, there were significant increases in the median time to rebuild widow rockfish populations.

3. Conclusions

We assert that the need to consider species interactions in fisheries management has been reasonably documented here and elsewhere (e.g., Hollowed et al., 2000; Jurado-Molina and Livingston, 2002). We recognize that the influence of predation mortality for estimating abundance is more important for some fish species than others. But we trust that the exemplary case studies we have shown highlight the importance of considering predation for at least some marine fish species. The methods to incorporate predation mortality into quantitative determinations of BRPs exist across a wide range of applications. The concerns over increasing precision uncertainty by including predatory considerations are largely offset by improvements such inclusions provide to process and accuracy uncertainties. None of what we point out is singularly novel, but what we have collectively documented is how important including M_2 can be, especially for forage species.

An ecosystem based approach to fisheries management calls for, among other things, a “best practice” approach for BRP calculations. Population dynamics models that explicitly include predation mortality indicate that BRPs that treat overall natural mortality as low and constant through time result in management advice that is overly optimistic. We show that a wide variety of modeling approaches have produced BRPs that are more conservative when predation mortality is explicitly incorporated in prey abundance calculations. For a strongly interacting predator prey complex (e.g., cod, herring and sprat in the Baltic) simultaneously achieving MSY as determined by single-species methods has been deemed impossible (ICES, 2008; *sensu* NEFSC, 2008; *sensu* Worm et al., 2009). Explicitly adopting the more conservative reference points will not insure sustainability of the fisheries for forage species in and of itself. Nevertheless, we recommend that these revised reference points be presented as part of the package of management informing advice because they represent an easily implemented component of EBFM, account for more factors that can affect a stock, and represent a precautionary approach. More so, we conclude by noting that the need to do them is apparent, the tools to do so are extant, and the consequences of continuing to ignore these considerations could be problematic.

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