Assembly rules for aggregate-species production models: simulations in support of management strategy evaluation

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ABSTRACT: Ecosystem-based fisheries management (EBFM) emphasizes sustainability at multiple levels of organization beyond single target species. Therefore, biological reference points (BRPs) for aggregated groups are required, which optimize yields while preventing overexploitation of individual species. We evaluate the tradeoffs between yield and biodiversity objectives for a wide range of aggregation strategies using multispecies surplus production models and comparing 2 simulated fish communities. We simulated population trajectories with an operating model detailing predation and competitive interactions for all individual species within each community, and with additional stochastic environmental variability for one community. Species trajectories were then aggregated by functional feeding guild, taxonomy, habitat association, size class, and at the entire community level. We estimated production parameters and BRPs (e.g. maximum sustainable yield, MSY) using a simple assessment model applied to each aggregated time series, then we applied the MSY fishing rates to each simulated community as alternative fishing strategies and compared equilibrium biomass and yield under each strategy. We were able to define multi-species reference points to meet both yield and biodiversity objectives across full system, taxonomic, habitat, feeding, and size-based aggregations. Species complexes were best able to meet both objectives when species with broadly similar productivity, environmental sensitivity and species interactions were aggregated into the complex. The impacts of simulated environmental variability on BRPs were substantial for certain species and aggregates, so including the combined impacts of environmental variation and species interactions in precautionary reference points appears critical to EBFM.

KEY WORDS: Ecosystem-based fishery management · Multiple objectives · Surplus production models · Biological reference points · Predation · Competition · Species complexes

INTRODUCTION

Understanding the determinants of productivity of marine systems is critical to devising effective and sustainable management practices. The concept of biological production has long served as a cornerstone in the development of the theory of resource management (Watt 1968). An early focus on this issue

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in fisheries research distinguished it from other approaches in population biology in the emerging field of ecosystem-based fisheries management (EBFM: Wagner 1969). In their classic monograph on the dynamics of exploited fish populations, Beverton & Holt (1957) provided an elegant treatment of the harvesting problem with an emphasis on production of individual species at the cohort and population levels. However, Beverton & Holt (1957) clearly recognized the broader dimensions of the problem, noting that, 'This is a generalization of what is perhaps the central problem in fisheries research: the investigation not merely of the reactions of particular populations to fishing, but also of the interactions between them and the response of each marine community to man's activity' (p. 24).

Traditionally, fish stock status and management advice has been stock-specific, often assuming that the demographic rates (e.g. natural mortality) or functions (e.g. stock-recruitment) of stocks are fixed or stationary. Ecologically, this ignores the influence of interspecific interactions on stock dynamics noted by Beverton & Holt (1957). These interactions may result in compensatory dynamics among stocks that lead to assemblage dynamics that are more stable than those of the constituent species, i.e. a portfolio effect (e.g. Duplisea & Blanchard 2005). A corollary of this effect is generally lower maximum sustainable yields at the aggregate level compared to the summed yields over all species in an aggregation (Brown et al. 1976, Walters et al. 2005). It also means that realized rates of population change following management actions may not follow simple single-stock dynamics theory (e.g. Walters & Kitchell 2001, Walters et al. 2008). From a management perspective, single-stock focus disregards technical interactions in fisheries, where 2 or more stocks are captured jointly, possibly leading to greater risk of overharvesting less productive stocks or differential recovery rates following harvesting restrictions (e.g. Paulik et al. 1967, Vinther et al. 2004, Murawski 2010). It also does not take full advantage of the potentially greater simplicity of stock-aggregate management and possible greater interannual predictability of the total amount of catch in mixed-stock fisheries (e.g. Hightower 1990).

A more explicit treatment of multi-species interactions is therefore one of several motivators behind the adoption of EBFM. Amongst other things, implementation of EBFM requires a better understanding of the consequences of stock-aggregate management in achieving the manifold objectives for management. Two such common objectives are the max-

imization of sustainable fishery yields and the maintenance of biodiversity, i.e. the prevention of collapse or extinction (Worm et al. 2009). A key goal of the present study was to use simulation modelling of hypothetical fish communities to explore how the estimation of biological reference points (BRPs) at different levels of species aggregation affect the simultaneous achievement of these 2 goals.

The development of models in support of marine ecosystem-based management can be arrayed along a continuum of complexity involving tradeoffs in realism, mechanistic detail, and parameter and/or model uncertainty (Link 2002). Models of low to intermediate complexity can often outperform more complicated forms in forecast skill (Costanza & Sklar 1985, Walters 1986, Fulton et al. 2003, Hannah et al. 2010). At the ecosystem level, surplus production models have been shown to provide an effective approach to addressing data limitations (Graham 1935, T. Smith 1994) and to manage model complexity and parameter uncertainty in multispecies models (Sugihara et al. 1984). These models can also accommodate simple forms of environmental and climate forcing through changes in the intrinsic growth rate (e.g. Rose 2004) or the carrying capacity parameters (e.g. Jacobson et al. 2005). These models have fostered an improved understanding of overall ecosystem production in northeast Pacific and northeast Atlantic fish stocks (Mueter & Megrey 2006, Sparholt & Cook 2010), and provided the first demonstration that aggregate system sustainable yield is smaller than the sum of estimated single-species maximum sustainable yields (Brown et al. 1976). Collectively these prior works suggest that an aggregated approach is not only feasible, but in many instances provides improved scientific advice for EBFM, especially via direct exploration of tradeoffs.

Here, we explore the potential strengths and weaknesses of simple aggregate-species production models in support of marine EBFM. We note that management considerations based on simple extensions of traditional single-species production models provide one avenue for recasting the harvesting problem in a context that is familiar to fishery managers while accommodating a broader multispecies perspective, particularly for those stocks that are caught together in multispecies fisheries, interact highly, or have similar production characteristics. However, the risk of not accounting for differences in life history characteristics of individual species and structural elements leading to complex dynamics must be fully evaluated. Our focus is on meeting dual objectives of maximizing yield subject to the constraint of maintaining ecosystem structure (taken

here to be indexed by biodiversity in a multispecies fish community; sensu Worm et al. 2009). We take a simulation approach akin to a simple management strategy evaluation (MSE; A. Smith 1994, Sainsbury et al. 2000), where a more complex operating model is used to represent the true state of a system, and then simpler assessment models are applied to data generated by the operating model. Therefore, the performance of our simple production-based assessment models may be evaluated against the 'truth' from the operating model. In particular, we evaluate both theoretically obtainable and assessment estimated BRPs, as well as the proportion of aggregate maximum sustainable yield (MSY) that can be achieved without stock collapse for the interacting species managed under an aggregate-species framework. Additionally, we evaluate the effects of environmental stochasticity on BRPs and the implications on the species and aggregate groups.

METHODS

Modelling framework

We begin with a system of equations for an exploited community drawing from the work of Schaefer (1954), Lotka (1925), and Volterra (1926) as the operating model representing 'truth' for our MSE:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = \left[r_i + \sum_{j=1}^{n} \alpha_{ij} B_j \right] B_i - F_i B_i \tag{1}$$

where B_i is the biomass of species i, B_j is the biomass of interacting species j, r_i is the intrinsic rate of increase, α_{ij} is the effect of species j on species i, and F_i is the fishing mortality rate. We implemented the operating model using the multispecies production modeling simulator MS-PROD (Gamble & Link 2009). In MS-PROD, overall net species interactions (α_{ij}) are derived from separate specifications of competition and predation interaction terms for each species pair, as described in Gamble & Link (2009). Further, the sign of the interaction term reflects the type of interaction (e.g. negative for competitive interactions; positive for effect of prey species on predator, negative for predator effect on prey). In this simple model we included only negative effects of competition and predation.

Isolating the intraspecific and interspecific interaction terms for a particular species i, the operating model can be written:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = (r_i - \alpha_{ii} B_i) B_i + \sum_{i \neq j} \alpha_{ij} B_j B_i - F_i B_i \tag{2}$$

where α_{ii} is the effect of species i on itself. The equilibrium point for species i is given by:

$$B_i^* = \frac{1}{\alpha_{ii}} \left[r_i - F_i + \sum_{i \neq j} \alpha_{ij} B_j \right] \tag{3}$$

and for the species to persist, the following condition must hold:

$$r_i > F_i + \sum_{i \neq j} \alpha_{ij} B_j \tag{4}$$

These species-specific dynamics with multiple interaction terms form the basis of our more complex operating model.

To simulate the potential effects of environmental variability, we extended the operating model for a particular species (Eq. 2) to include stochasticity in the intrinsic growth rate:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = (r_i^s - \alpha_{ii} B_i) B_i + \sum_{i \neq j} \alpha_{ij} B_j B_i - F_i B_i \tag{5}$$

where r_i^s is the growth rate for species i as taken from a normal distribution. The value for r_i^s is given by:

$$r_i^s \sim N(\bar{r}, \sigma^2) \tag{6}$$

where N is the normal distribution of r_i with the mean $\bar{r}$ and standard deviation σ^2.

We next consider the corresponding dynamics of an aggregate group formed by summing the biomass levels of individual species, which forms the basis of our simple assessment model:

$$\frac{\mathrm{d}B_T}{\mathrm{d}t} = (r_T - \alpha_T B_T) B_T - F_T B_T \tag{7}$$

where the subscript T indicates the total for the aggregate group and r_T and α_T are logistic growth and self-interaction parameters for the group. To keep our assessment approach as simple as possible, we assume that there are no interaction terms between aggregate groups within the ecosystem; therefore α_T represents the net effect of the aggregate upon itself. The aggregate group is therefore modelled analogously to an independent single species with logistic growth, although the dynamics comprising the aggregate group are more complex. The equilibrium point for the aggregate group is therefore given by:

$$B_T^* = \frac{r_T - F_T}{\alpha_T} \tag{8}$$

For the aggregate as a whole to persist, the intrinsic rate of increase of the group (r_T) must exceed F_T.

Aggregations

Our interest centers on the effects of species interactions and environmental fluctuations on fishing mortality reference points derived from the aggregate production models, and also whether these reference points will result in stock collapse of individual species within the aggregate. For species interactions, a critical issue is whether:

$$r_T > r_i + \sum_{i \neq 1} \alpha_{ij} B_j \qquad (9)$$

Our ultimate goal is to determine whether simple aggregation rules might be applied across ecosystems to simplify fishery management. Therefore, we evaluate the extent to which predation, competition, and environmental stochasticity affect yield (MSY) and biodiversity (species richness) using many different aggregate reference points. We examined 5 approaches to assembling aggregate species complexes with groups defined according to (1) taxonomic affinity, (2) habitat preference (pelagic vs. demersal), (3) feeding functional group, (4) size class (based on average adult length), and (5) combining over all species. These might be considered reasonable candidate groupings for management in different situations. For example, habitat preference and size class could be appropriate for mixed-species fisheries (i.e. similar availability). Taxonomic affinity combines species with similar life histories (at least in some circumstances), and therefore similar productivities. Feeding functional groups combine species with a similar prey base. Combining all species into an aggregate could be appropriate in data-poor situations and where system-wide reference points are desirable. In the spirit of MSE, for each of these approaches we present operating model 'true' results and 'assessment' results for 2 simulated ecosystems.

Simulated systems

To test the performance of different criteria for aggregation, we created 2 virtual multispecies systems using MS-PROD (Gamble & Link 2009). The 2 systems were broadly based on Georges Bank in the Atlantic Ocean, and the Gulf of Alaska in the Pacific Ocean to represent distinctive fish communities, climate impacts, and exploitation histories within northern hemisphere ecosystems. Further, the 2 systems were parameterized to emphasize competitive interactions (Georges Bank) versus predation interactions (Gulf of Alaska), although both systems had both

types of interactions. We used parameters provided by Gamble & Link (2009) that were intended to be broadly representative of 10 dominant species present on Georges Bank for part or all of an annual cycle (Table S1 in the supplement at www.int-res.com/articles/suppl/m459p275_supp.pdf). A similar set of 10 dominant species was selected for Gulf of Alaska with parameters derived from Gaichas et al. (2010) and Aydin et al. (2007) (Table S2 in the supplement). We emphasize that these simulated ecosystems and our simulated assessments are used to examine general properties of production for interacting species, and are not intended to represent the actual multispecies dynamics or stock assessments used in federal waters off the USA, which are far more complex.

Operating model analyses

We applied a series of F rates increasing from 0 to 1.0 in 0.025 increments to all species in the system for 50 yr each and used the biomass and yield in Year 50 (the year by which equilibrium had been reached in all simulations) to develop 'true' equilibrium yield curves and trace biomass trajectories for each aggregation in the simulated Georges Bank and Gulf of Alaska. To simplify interpretation of fishing versus species interaction effects in these simulations and to facilitate comparison between ecosystems, we did not attempt to account for differences in catchability between species, bycatch, or other more realistic fishing conditions; these refinements could easily be included in applications for particular systems. These simulations were performed with competitive and predatory species interactions, and the resulting MSYs were estimated. We then calculated the proportion of MSY attainable with no species collapses for each aggregation. We used 2 collapse definitions: species below 10% or 25% of unfished biomass. The latter definition roughly coincides with the legal definition of 'overfished' in the USA (Federal Register 2008).

Stochastic results were compared with deterministic results for Georges Bank. We simulated the effects of environmental stochasticity by setting the coefficient of variation of r_i (Eq. 5) for each species to 0.25. The base growth rate (which was set to the deterministic model's growth rate) for each species was modified in each year (Eq. 6). We then applied the same series of F values (from 0 to 1.0 in increments of 0.025) to all species, using 1000 runs for each F increment (40 000 runs total), to develop yield curves with stochastic 'envelopes' representing environmental variability, and to calculate ranges of MSYs with means.

Assessment model analyses

We evaluated the ability to estimate biological reference points based on time series of aggregate biomass levels simulated by the model. Our operating model first simulated the unfished trajectories of the individual interacting species comprising the group using Eq. (1) and then we summed the biomass of each species to generate the aggregate group trajectory. This created the 'data' to which an aggregate production and biomass 'assessment' model could be fit. Solving the logistic growth equation (Eq. 7), with $F = 0$, the predicted aggregate biomass at time t equals:

$$B_t = \frac{r_T/\alpha_T}{1 + \gamma e^{-r_T t}} \tag{10}$$

where

$$\gamma = \frac{r_T - \alpha_T B_0}{\alpha_T B_0} \tag{11}$$

and B_0 is the input initial biomass for the assessed group. Thus, based on the time series of B_T with no fishing, the parameters r_T and α_T were estimated by nonlinear least squares through a regression of B_T on t using the nls function in R (R Development Core Team 2008). This simulated assessment approach is admittedly simpler than most real-world production model-based assessments which fit to time series of catch and biomass (as unfished biomass is rarely available). Our goal was to examine the combined effects of aggregation and of ignoring species interactions and environmental fluctuations on assessment-estimated parameters and BRPs. Therefore, we chose a simpler assessment method to distinguish the effects of interest from additional effects introduced by simulating catch and biomass time series (with error) and fitting production models in the conventional manner, although this is a clear next step.

Biological reference points for the aggregate group can be readily determined. MSY is:

$$\text{MSY}_T = \frac{r_T^2}{4\alpha_T} \tag{12}$$

and the fishing mortality rate at MSY is:

$$F_{\text{MSY}} = \frac{r_T}{2} \tag{13}$$

Parameters and resulting BRPs were estimated by the assessment model for individual species and aggregations from deterministic simulations for both the Gulf of Alaska and Georges Bank, and from a random sample of 5 stochastic realizations for Georges Bank. Then, we simulated fishing in the (deterministic) operating model with the assessment-estimated F_{MSY} values for each species and complex to compare the realized equilibrium biomass and yield of each species across aggregation strategies. Finally, we compared the operating model-derived 'true' BRPs with both the assessment-estimated BRPs and the realized equilibrium biomass and yields.

RESULTS

Operating model ('true') results

The wide variation in life history characteristics of the species considered in these simulations leads to sharply divergent production characteristics and levels of vulnerability to multispecies harvesting in Georges Bank and Gulf of Alaska (Fig. 1). In both sim-
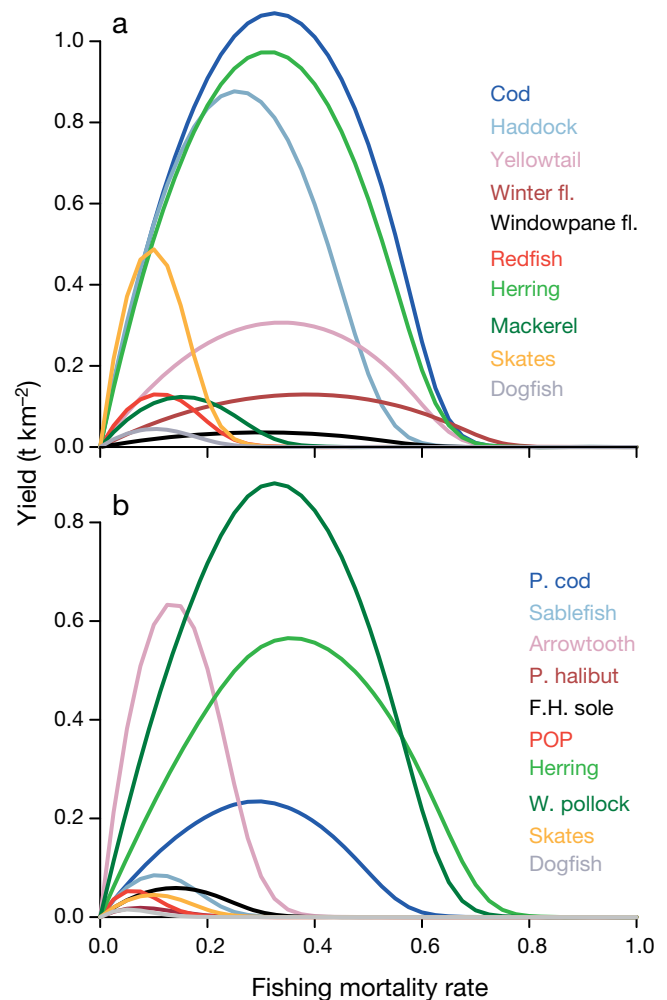

Fig. 1. Yield curves for simulated 10-species interacting fish communities: (a) Georges Bank and (b) Gulf of Alaska; comparable species have similar colors. fl.: flounder; P.: Pacific; F.H.: flathead; W.: walleye

ulated systems, the low productivity of the elasmo-branch species (skates and dogfish) with their characteristically delayed maturation, low fecundity, and relatively slow growth rates leads to a low F_{MSY} around 0.1 (Table 1). Similarly, both Georges Bank redfish and Gulf of Alaska Pacific ocean perch (POP) (both long-lived, slow growing Scorpaenids) have generally low F_{MSY} and resilience to exploitation. Conversely, cod and herring had the highest production rates in both systems, along with haddock in Georges Bank and walleye pollock in the Gulf of Alaska, resulting in relatively high F_{MSY} at 0.3 or above. However, production of flatfish differed between systems; Georges Bank species (yellowtail, winter, and windowpane flounder) had productivity similar to cod and herring, while Gulf of Alaska species (arrowtooth flounder, halibut, and flathead sole)

had productivity more similar to elasmobranchs and scorpaenids. The relatively low production to biomass ratios for both Georges Bank Atlantic mackerel and Gulf of Alaska sablefish result in low to intermediate F_{MSY}. With these contrasts as a basis, we next compare aggregate properties of the simulated systems.

Our simulated systems are 'cartoons' of the actual systems, but parameters were based on data from each ecosystem such that broad productivity comparisons are possible. Overall, the simulated Georges Bank system has higher MSYs than the simulated Gulf of Alaska system on a per unit area basis, with a full system MSY of 3.40 t km^{-2} compared with 1.96 t km^{-2}, respectively (Table 1). Results from both systems support previous findings that the sum of single species yield exceeds total system yield (with single species sums of 4.174 and 2.586 t km^{-2}, respectively).

Table 1. 'True' F_{MSY} (F, fishing mortality rate; MSY, maximum sustainable yield) and MSY with species interactions, for each species and aggregation of the various 10-species simulation models. fl.: flounder; zoopivore: consumes shrimp and other small crustacean prey; P.: Pacific

Aggregation	Species ID no(s).	F_{MSY}	MSY (t km^{-2})	Aggregation	Species ID no(s).	F_{MSY}	MSY (t km^{-2})
Georges Bank				**Gulf of Alaska**			
Species grouping				Species grouping			
Cod	1	0.325	1.069	P. cod	11	0.3	0.234
Haddock	2	0.25	0.877	Sablefish	12	0.1	0.085
Yellowtail fl.	3	0.35	0.306	Arrowtooth fl.	13	0.125	0.633
Winter fl.	4	0.375	0.129	P. halibut	14	0.075	0.019
Windowpane fl.	5	0.3	0.036	Flathead sole	15	0.15	0.059
Redfish	6	0.1	0.129	P. ocean perch	16	0.05	0.052
Herring	7	0.325	0.973	Herring	17	0.35	0.565
Mackerel	8	0.15	0.124	Walleye pollock	18	0.325	0.879
Skates	9	0.1	0.487	Skates	19	0.1	0.045
Dogfish	10	0.1	0.044	Dogfish	20	0.05	0.015
Full system	1–10	0.275	3.398	Full system	11–20	0.2	1.955
Taxonomic affinity				Taxonomic affinity			
Groundfish	1, 2, 6	0.275	1.924	Groundfish	11, 12, 16	0.15	0.254
Flatfish	3–5	0.35	0.470	Flatfish	13–15	0.125	0.705
Forage[a]	7, 8	0.275	1.015	Forage[a]	17, 18	0.325	1.440
Elasmobranchs	9, 10	0.1	0.532	Elasmobranchs	19, 20	0.075	0.056
Habitat				Habitat			
Pelagics[a]	7, 8	0.275	1.015	Pelagics[a]	17, 18	0.325	1.440
Demersals	1–6, 9, 10	0.275	2.383	Demersals	11–16, 19, 20	0.125	1.006
Feeding functional group				Feeding functional group			
Piscivores	1	0.325	1.069	Piscivores	11, 13, 14	0.15	0.809
Benthivores	2–5, 9	0.15	1.395	Benthivores	15, 19	0.125	0.101
Zoopivores	6, 10	0.1	0.174	Zoopivores	12, 20	0.1	0.093
Planktivores	7, 8	0.275	1.015	Planktivores	16–18	0.325	1.440
Average adult body length				Average adult body length			
Large	1, 2, 9, 10	0.275	1.925	Large	11, 12, 14, 19, 20	0.125	0.291
Medium	3–5	0.35	0.470	Medium	13, 15, 16, 18	0.175	1.299
Small	6–8	0.25	1.028	Small	17	0.35	0.565

[a]These categories (Forage and Pelagics) contained the same species aggregations for their respective locations

Much of the difference in full-system MSYs is driven by the relatively high MSYs for Georges Bank cod, haddock, and herring, which equal or exceed the highest Gulf of Alaska MSY for walleye pollock. Among taxonomic aggregates, Georges Bank groundfish (cod, haddock, and redfish) had much higher F_{MSY} and MSY than Gulf of Alaska groundfish (cod, sablefish, and POP). In the simulations, flatfish could be fished at a higher F_{MSY} but to a lower MSY on Georges Bank relative to the Gulf of Alaska. Despite similarities in productivity and F_{MSY} between systems, elasmobranch MSY is an order of magnitude greater on Georges Bank.

Habitat, size, and feeding guild aggregations show clear contrasts in system structure and productivity through the reference points for each simulation, suggesting that fishing similar species complexes may have contrasting results across ecosystems. Whereas pelagics (herring in both systems and Georges Bank mackerel or Gulf of Alaska walleye pollock) have roughly similar F_{MSY} and MSY between systems, demersal (groundfish + elasmobranchs) aggregate F_{MSY} and MSY on Georges Bank is double that of the Gulf of Alaska (Table 1). Size-based aggregations produced mixed results across systems: MSY is highest for Georges Bank large (cod, skates, haddock, and dogfish) and small (herring, mackerel, and redfish) size groups, but highest for the medium (arrowtooth, walleye pollock, POP, flathead sole) Gulf of Alaska size group. In both systems, planktivores (herring in both systems, Georges Bank mackerel, or Gulf of Alaska walleye pollock and POP) have similar F_{MSY} and MSYs. However, planktivores have the highest MSY in the Gulf of Alaska, while they rank third behind benthivores (skates, haddock, and flatfish) and piscivores (cod) on Georges Bank. The MSY of the Gulf of Alaska benthivore group (skates and flathead sole) is an order of magnitude lower than that for Georges Bank; the low Gulf of Alaska skate MSY drives the large contrast between the 2 systems.

The full system maximum sustained yields are produced at levels of fishing mortality F that have different impacts on individual species and species aggregates. The Georges Bank full system multispecies MSY (MMSY) occurs at $F = 0.275$ (Table 1), but at this level of fishing, 40% of the stocks are classified as collapsed (less than 10% of their maximum biomass level; Fig. 2). Similarly, the Gulf of Alaska MMSY is found at $F = 0.20$, where 40% of stocks are collapsed. Based on the contrasting structure and productivity described above, each aggregation of the 2 systems has different properties with respect to the propor-
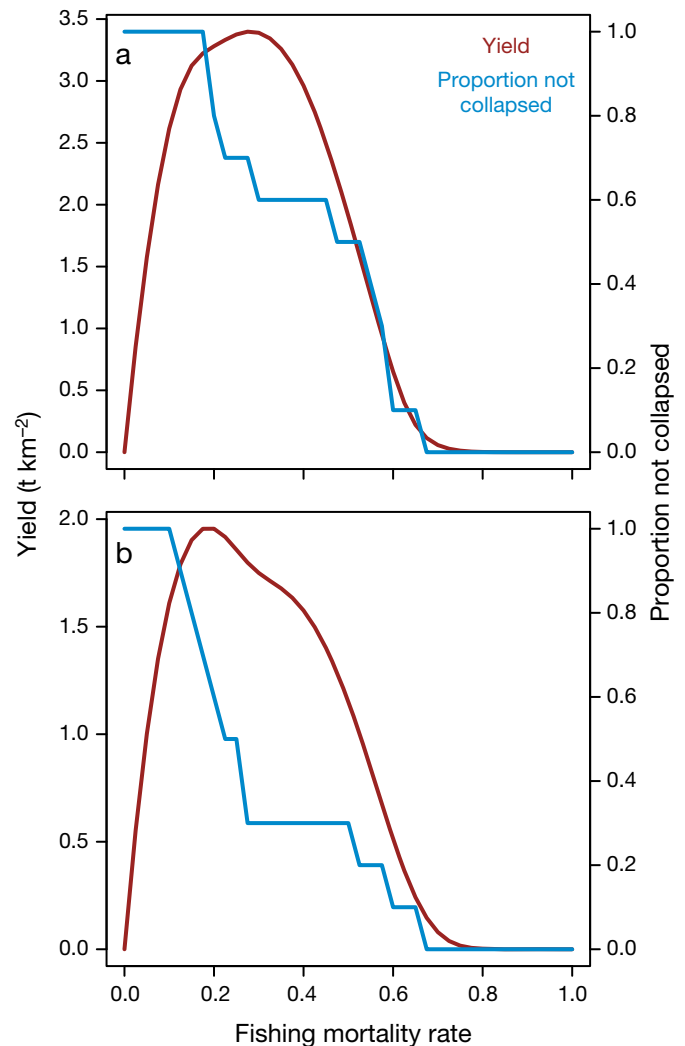

Fig. 2. Full 10-species system aggregate yield and collapse curves (where collapse is defined as biomass <10% of unfished biomass) for (a) Georges Bank and (b) Gulf of Alaska

tion of collapsed species over a range of fishing mortality rates (Fig. 3). For example, the elasmobranch complex looks very similar between the 2 systems with respect to BRPs, and collapses occur above F_{MSY}. The flatfish complexes between the 2 systems have contrasting F_{MSY} rates, but none of the species in either system is collapsed at the MSY for the complex. The pelagic complexes have similar F_{MSY} and MSY reference points between systems, but the collapse of one component happens at F_{MSY} on Georges Bank, and at F rates well above pelagic F_{MSY} in the Gulf of Alaska.

In operating model simulations, the collapse curve combined with the yield curve can be used to define a multi-objective optimal F rate for each complex. If the fishing mortality rate on Georges Bank system as
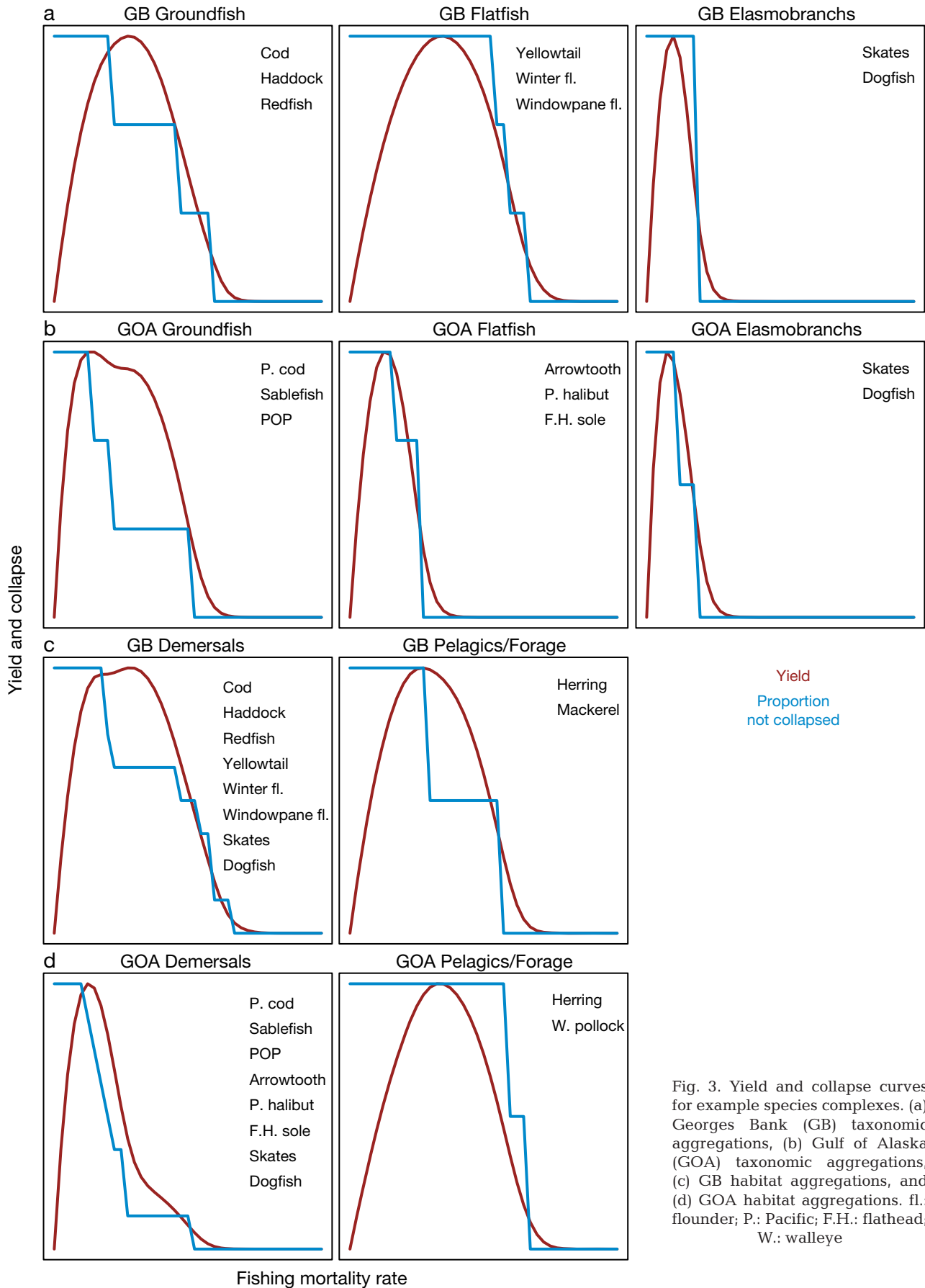
Fig. 3. Yield and collapse curves for example species complexes. (a) Georges Bank (GB) taxonomic aggregations, (b) Gulf of Alaska (GOA) taxonomic aggregations, (c) GB habitat aggregations, and (d) GOA habitat aggregations. fl.: flounder; P.: Pacific; F.H.: flathead; W.: walleye
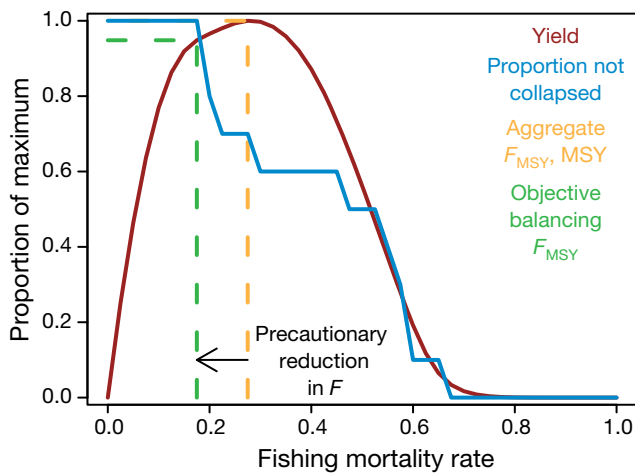
Fig. 4. In multispecies complexes, fishing mortality rate F can be reduced from aggregate F_{MSY} (MSY, maximum sustainable yield) to prevent collapses. For the full 10-species Georges Bank model, nearly 95% of MSY can be achieved with no species dropping below 10% of unfished biomass

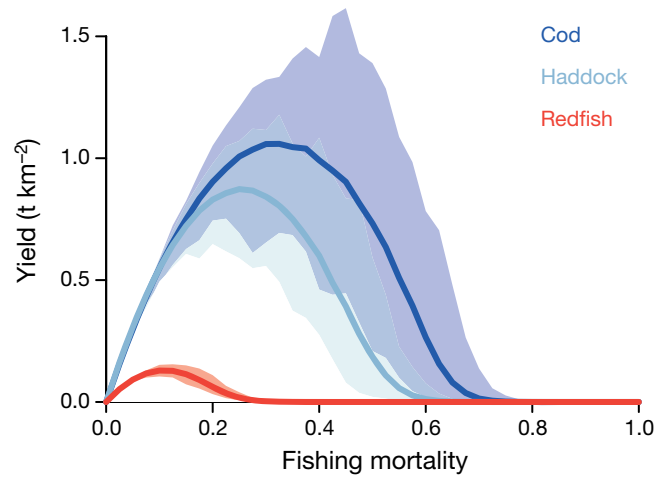

Fig. 5. Average yield curves (lines) with ranges (shading) from 1000 stochastic runs for the Georges Bank groundfish complex

a whole is reduced to 0.15, 95% of the MMSY is obtained (Fig. 4). At this fishing mortality rate, none of the stocks would be classified as collapsed using the 10% definition. Accordingly, reducing fishing mortality from the limit reference point to a precautionary exploitation rate results in little loss of yield (and a probable increase in profits since less effort is expended to obtain nearly the same catch). The proportion of MMSY theoretically obtainable without collapse is generally high (above 80%) for all Georges Bank and Gulf of Alaska aggregates (Table 2). The exception is Gulf of Alaska plankti-

vores, which combines 2 of the most productive species (herring and walleye pollock) with one of the least productive species (POP), such that only 56% of aggregate MMSY can be taken without collapse. In a comparison of biodiversity objectives where collapse is defined as biomass <10% of unfished, or as <25% of unfished, the proportion of MMSY remained relatively high for all aggregates except Gulf of Alaska planktivores. However, reductions from MMSY were larger in the Gulf of Alaska simulations where collapse was defined as <25% of unfished biomass. The only aggregate that achieved 100% of MMSY across systems and biodiversity objectives was the elasmobranch complex, which combined species with nearly identical life history traits.

The addition of stochasticity (which we used to simulate non-autocorrelated environmental variability) predictably did little to alter the average reference points in the operating model, but produced asymmetric envelopes around yield curves (Fig. 5), and differentially affected species in the simulated Georges Bank (Table 3). The shapes of the yield curve envelopes show maximal uncertainty in yield after fishing mortality rates exceed the average F_{MSY}, with less uncertainty in yield below average F_{MSY}. While the range of F_{MSY} for redfish, skates, and dogfish in 40 000 stochastic runs reflected exactly the range of variability simulated in intrinsic growth rates (25%), the range of F_{MSY}

Table 2. Percent of maximum sustainable yield (% MSY) achievable without species collapse for each aggregated species complex, where collapse is defined as <10% of unfished biomass or <25% of unfished biomass

| | Georges Bank (% MSY) | | Gulf of Alaska (% MSY) | |
	Biomass <10%	Biomass <25%	Biomass <10%	Biomass <25%
Full system	95	86	82	69
Groundfish	94	83	100	88
Flatfish	100	100	100	94
Elasmobranchs	100	100	100	100
Pelagics/Forage	100	98	100	100
Demersals	98	92	96	85
Piscivores	100	100	100	91
Benthivores	100	98	100	100
Zoopivores	100	100	100	97
Planktivores	100	98	56	38
Large	98	93	96	85
Medium	100	100	94	71
Small	99	91	100	100

Table 3. Summary of stochastic results (1000 simulations) for Georges Bank simulation (F, fishing mortality rate; MSY, maximum sustainable yield). fl.: flounder

Species	Mean		Min.–max. range	
	F_{MSY}	MSY	F_{MSY} (%)	MSY (%)
Cod	0.325	44.63	69	82
Haddock	0.25	36.81	50	61
Yellowtail fl.	0.35	12.87	64	70
Winter fl.	0.4	5.39	31	79
Windowpane fl.	0.3	1.50	58	73
Redfish	0.1	5.44	25	39
Herring	0.3	40.64	42	65
Mackerel	0.15	5.20	33	52
Skates	0.1	20.56	25	35
Dogfish	0.1	1.86	25	42

rates was amplified to 50% or more for haddock, windowpane, yellowtail, and cod, with the remainder intermediate. MSY estimates were more affected by stochasticity; skates and dogfish had the lowest range of MSY estimates in 1000 stochastic runs (35 and 42%), while cod and winter flounder had the highest MSY ranges (82 and 79%).

Table 4. 'Assessment' F_{MSY} (F, fishing mortality rate; MSY, maximum sustainable yield) for each species and aggregation (see Table 1 for assignment of each species to the various model aggregations). fl.: flounder; P.: Pacific; F.H.: flathead; W.: walleye; POP: Pacific ocean perch. –: assessment model estimation failed; values of a = 0.2 and b = 0.15 were applied in the simulation (see 'Assessment results')

Species	Species	System	Taxonomic	Habitat	Feeding	Size
Georges Bank						
Cod	0.300	0.096	0.155	0.102	0.300	0.091
Haddock	0.061	0.096	0.155	0.102	0.072	0.091
Yellowtail fl.	0.300	0.096	0.285	0.102	0.072	0.285
Winter fl.	0.354	0.096	0.285	0.102	0.072	0.285
Windowpane fl.	0.399	0.096	0.285	0.102	0.072	0.285
Redfish	0.112	0.096	0.155	0.102	0.103	0.138
Herring	0.366	0.096	0.470	0.470	0.470	0.138
Mackerel	0.076	0.096	0.470	0.470	0.470	0.138
Skates	0.099	0.096	0.089	0.102	0.072	0.091
Dogfish	0.024	0.096	0.089	0.102	0.103	0.091
Gulf of Alaska						
P. cod	0.197	0.104	0.060	0.058	0.100	0.064
Sablefish	0.103	0.104	0.060	0.058	0.084	0.064
Arrowtooth	0.159	0.104	0.025	0.058	0.100	0.167
P. halibut	–[a]	0.104	0.025	0.058	0.100	0.064
F. H. sole	–[a]	0.104	0.025	0.058	–[b]	0.167
POP	0.058	0.104	0.060	0.058	0.200	0.167
Herring	0.292	0.104	0.287	0.287	0.200	0.292
W. pollock	0.291	0.104	0.287	0.287	0.200	0.167
Skates	0.099	0.104	0.073	0.058	–[b]	0.064
Dogfish	0.049	0.104	0.073	0.058	0.084	0.064

Assessment results

Our simple 'assessment' estimated logistic growth parameters for each species and aggregate complex using the F = 0 runs from the Georges Bank and the Gulf of Alaska simulations (Table 4; see also Figs. S1 & S2 in the supplement at www.int-res.com/articles/suppl/m459p275_supp.pdf). Parameters were estimable for all Georges Bank species and aggregates, but even with 'perfect' data we were unable to estimate parameters for Gulf of Alaska halibut, flathead sole, and benthivores (which include flathead sole). This is likely due to the shapes of these trajectories (Fig. S2), which arise from the combination of input parameters for these species. Since these parameters were based on data from the system and were incorporated into the operating model without difficulty, we chose not to revise them for these simulations. In the absence of assessment-estimated F_{MSY} rates, we applied fishing mortality rates of 0.2 for halibut and flathead sole in the single-species F_{MSY} simulation, and of 0.15 for benthivores in the feeding guild F_{MSY} simulation. These proxy F_{MSY} rates for both flatfish were derived from the estimated current harvest rate of 0.2 for halibut (Hare 2010), and the benthivores F_{MSY} rate is an average of 0.2 and the estimated skate F_{MSY} is ~0.1. Only the realized equilibrium biomasses and yields (Figs. S3 & S4 in the Supplement) depend on these assumptions.

The BRPs estimated in assessments for both the Gulf of Alaska and Georges Bank were generally lower than the operating model-derived 'true' values of F_{MSY} and MSY presented above (Figs. 6 & 7), with some exceptions. In the Gulf of Alaska, arrowtooth flounder had an assessment-estimated F_{MSY} rate greater than true rate, while POP and sablefish had only slightly higher estimated F_{MSY}. Similarly, Georges Bank windowpane flounder, herring, and the pelagics/planktivores complexes had assessment-estimated F_{MSY} rates greater than true rates, with redfish slightly higher. In both systems, elasmobranchs showed good agreement between estimated and true BRPs. Where the remaining estimates are close to the true values for F_{MSY}, this may simply reflect a difference be-
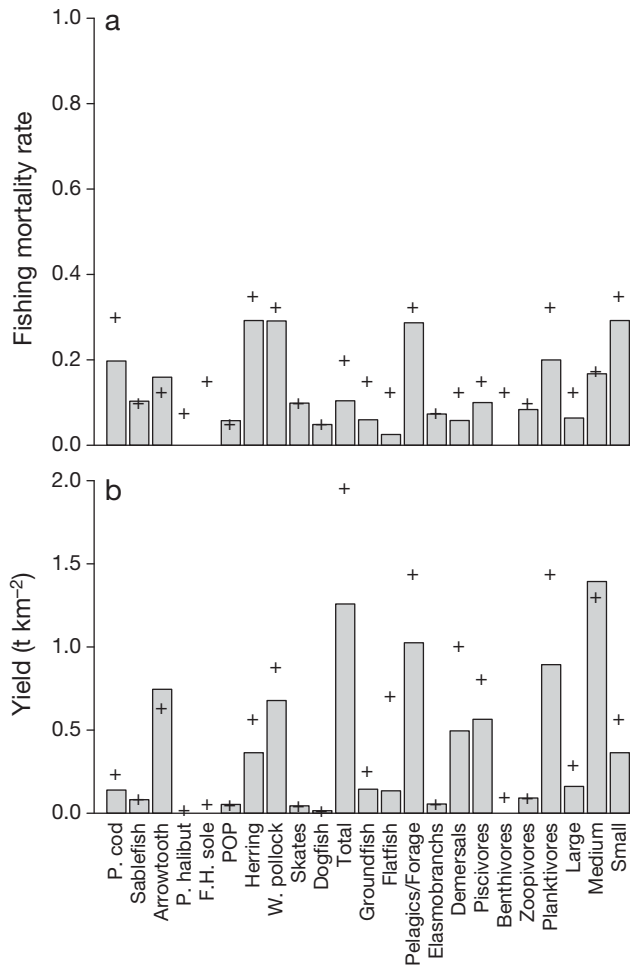
Fig. 6. Estimated (a) fishing mortality rate at maximum sustainable yield (MSY), and (b) MSY from deterministic assessments (bars) for the Gulf of Alaska, with 'true' biological reference points (BRPs) from the simulation model (+). Estimation failed for flathead (F.H.) sole, halibut, and benthivores. P.: Pacific; W.: walleye
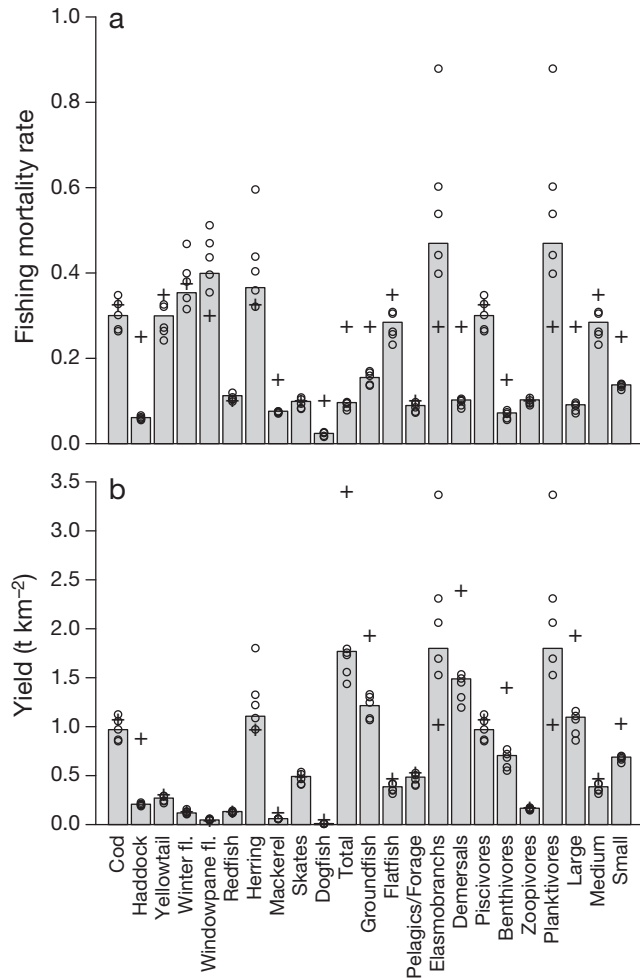
Fig. 7. Assessment-estimated (a) F_{MSY}, and (b) MSY from deterministic (bars) and 5 randomly selected stochastic (open circles) simulations for Georges Bank, with 'true' BRPs from the operating model (+)

tween the fishing mortality increments we selected for the true simulations and the estimated values from the assessment. However, this could also reflect a bias in the estimation procedure, which then gets magnified for MSY estimates. Assessment estimates of B_{MSY} were nearly always indistinguishable from true estimates (not shown), suggesting that the carrying capacity parameter was well estimated by our simple assessment.

Environmental variability implemented as stochasticity in the intrinsic growth rate in the simulated Georges Bank ecosystem led to a wider range of 'assessment' results and amplified contrasts with the 'true' results (Fig. 7). The contrasts in stochastic assessment-estimated and true F_{MSY} rates are most pronounced for herring among the single species, where true F_{MSY} was 0.325 but assessment-estimated

F_{MSY} ranged from 0.3 to 0.6. Assessments performed for the aggregated groups, including herring (forage, pelagics, and planktivores), were generally biased towards higher values by environmental variation, with ranges of aggregate F_{MSY} from 0.4 to 0.9, compared with 'true' F_{MSY} of 0.275 and the deterministic assessment F_{MSY} of 0.470 (Tables 1, 3, 4, Fig. 7). Assessments from stochastic realizations were close to both the deterministic assessment and the true F_{MSY} rates for redfish, skates, and the elasmobranch and zoopivores (shrimp and other crustacean-eating) complexes. Stochastic and deterministic assessments agreed with each other, but differed from the true F_{MSY} for haddock, mackerel, dogfish, and many aggregates, including the full system, groundfish, demersals, benthivores, large, and small.

Equilibrium biomass and yield resulting from simulated fishing under alternative assessment-estimated

F_{MSYs} showed that some aggregation strategies resulted in extinctions. Georges Bank mackerel went extinct under the under the taxonomic, habitat, and feeding guild aggregate F_{MSY} strategies, and Gulf of Alaska POP went extinct under the feeding guild strategy. Gulf of Alaska POP also essentially collapsed under the size-based F_{MSY} strategy. Among species without collapses, the most contrast in biomass and yield between strategies was for Georges Bank cod, yellowtail flounder, and herring, and for Gulf of Alaska arrowtooth flounder, pollock, and herring. Equilibrium yields for skates and dogfish in both systems were very similar across aggregation strategies due to low contrast between F_{MSY} values (Table 4). We note that our application of 0.2 as the Gulf of Alaska halibut single species F_{MSY} resulted in very low halibut biomass and catch under the single species strategy (see Figs. S3 & S4 in the Supplement for all results.)

Fig. 8. Comparison of assessment-predicted MSY (bars), true MSY (+), and realized equilibrium yield (X) from 50 yr of fishing at assessment estimated F_{MSY} in (a) Georges Bank and (b) Gulf of Alaska. fl.: flounder; P.: Pacific; F.H.: flathead; W.: walleye

Comparisons between 'assessment'-predicted MSY, 'true' MSY, and realized equilibrium yield demonstrate the effects of applying the fishing strategies simultaneously in the simulated systems (Fig. 8). The realized equilibrium yields are close to the assessment-predicted MSY for most individual species, and generally below or equal to the true MSY, but differences are larger for aggregated species complexes in both the simulated Georges Bank and Gulf of Alaska. In many cases across systems, realized equilibrium yields were higher than assessment-predicted MSYs, especially where true MSY was underestimated by the assessment. The realized equilibrium yields agreed particularly well with true MSY in cases where the assessment-estimated MSY greatly exceeded the true MSY (Georges Bank pelagics/planktivores, and to a lesser extent herring, and Gulf of Alaska arrowtooth and medium size complex). No realized equilibrium yields were higher than true MSYs for any species or aggregate.

DISCUSSION

Based on our results, we draw 4 main conclusions that are summarized here and discussed in detail below. First, we were able to define multi-species reference points to meet both yield and biodiversity objectives across full system, taxonomic, habitat, feeding, and size-based aggregations. Second, species complexes were best able to meet both objectives when species with broadly similar productivity, environmental sensitivity and species interactions were aggregated into the complex. Third, the impacts of simulated environmental variability on biological reference points were substantial for certain species and aggregates, so including the combined impacts of environment and species interaction in precautionary reference points appears critical. Finally, our simple assessment method estimated BRPs reasonably well for many species and aggregates without explicitly including species interactions but showed some bias even with the high-quality simulated 'data' we used.

Multi-objective BRPs from simple models

Our simulations demonstrate that we can define multi-objective multispecies reference points by combining a minimum biomass threshold level with aggregate species yield, as suggested in Worm et al. (2009). We used this as a measure of performance for

various aggregation strategies where the best aggregates minimized the reduction in MSY to preserve biodiversity. However, most of the aggregation strategies we examined worked well in this simple case, with minimal tradeoffs between yield and biodiversity objectives across systems. One explanation for these minimal tradeoffs may be that the 'true' BRPs we estimated here already included the effects of species interactions in our operating model. Gamble & Link (2009) found that considering species interactions in these models generally resulted in lower MSYs relative to models with species interactions 'turned off'. Larger tradeoffs between yield and biodiversity might therefore be observed in comparisons of BRPs estimated without consideration of species interactions.

The differences in performance between systems may reflect the set of more productive stocks in Georges Bank relative to the Gulf of Alaska combined with our parameterizations emphasizing competition on Georges Bank versus predation in the Gulf of Alaska. We note that while these differences between ecosystems help us understand differences in responses to fishing aggregates, they do not necessarily reflect actual differences between the systems. However, the results from just these 2 simulated systems suggest that strong predation interactions combined with lower overall productivity may amplify tradeoffs between yield and biodiversity, especially at the full system level. Management of this tradeoff at the ecosystem scale has been examined for Antarctic systems, where fisheries for krill are managed both for yield and to preserve forage for predators (May et al. 1979, Constable 2001). Our operating model did not include bottom-up effects of prey on predators, but adding this interaction may either allow for compensation which lessens this tradeoff (i.e. fishing reduces predators, releases prey and may then benefit fished predators; see Walters et al. 2005), or lead to more complex dynamics with unpredictable effects. Fuller consideration of this interaction seems warranted (Tyrrell et al. 2011), and could be simulated using larger datasets of species productivity (e.g. Walters et al. 2008, Eero & MacKenzie 2011).

Aggregation: developing species complex assembly rules

The species complexes best able to balance yield and biodiversity objectives are those that combine species with similar productivity rates, environmental sensitivity and species interactions. Conversely, the poorest performing complex combined species with high contrast in productivity rates (Gulf of Alaska planktivores). This accounts in part for the good performance of many taxonomic aggregations, as closely-related taxa often share life history characteristics (Winemiller & Rose 1992) and maximum rates of population growth (Myers et al. 1999). The influence of life-history on productivity is not a surprising result, but our simulations show how both species interactions and environmental stochasticity combine to further enhance or compromise the effects of fishing on individual species and aggregations. For example, elasmobranchs combined dogfish with skates in both systems, and MSY was always obtainable from this complex without population collapses across both simulated systems, despite differences in the biomass distribution between systems. Assessments also performed well for this complex, if not always for each species in it, and even the introduction of environmental stochasticity did not greatly affect BRP estimates. Therefore, the productivity of these species, combined with broadly similar species interactions and response to environmental variability, made elasmobranchs a very good complex for management in our simulations. However, caution is warranted even within the elasmobranchs. The mixture of life history traits between smaller and larger skate species has led to apparent population stability for the aggregated 'skate' group in many areas where fisheries occur, and this, combined with the common practice of managing skate species within aggregate complexes, has masked the decline of individual skate species in European fisheries (Dulvy et al. 2000). Similarly, in the Atlantic off New England, substantial shifts in species dominance have occurred within the skate complex over time (Sosebee 2006).

Other aggregates showing mixed performance exhibit the effects of system characteristics, life history and species interactions, indicating that assembly rules and assessments for aggregates still need fine-tuning within specific ecosystems. Habitat groupings showed mixed results when considering operating model ideals versus assessment realities. For example, demersals, with 8 species in each system having a wide range of productivity, interactions, and exploitation susceptibilities, worked surprisingly well in terms of both balancing management goals and assessment performance. The pelagic aggregations in both systems worked well in balancing management goals in the operating model results. However, assessment results for the Georges Bank pelagic habitat aggregate consistently overestimated productivity for this complex (an effect that was magnified in stochas-

tic realizations of the assessment), resulting in the extinction of mackerel. The underlying differences in productivity and initial biomass in this simulation between Georges Bank mackerel and herring led to aggregate biomass trajectories which were apparently difficult to fit, contributing to poor performance in the pelagic habitat aggregation, as well as the planktivore feeding-guild aggregation which also combined herring and mackerel. While this result may reflect the poor performance of our simple assessment model as much as the performance of the pelagic habitat aggregate, real management applications will require examination of interactions between potential assessment methods and proposed aggregate groups within an extended MSE framework to optimize assessment-estimated BRPs.

Feeding mode and size groupings also generally worked well for theoretically balancing management objectives in the operating model results, with one clear exception. By adding the very low productivity POP to the simulated Gulf of Alaska pelagic habitat group to form the planktivore feeding group, a substantial loss of performance was noted. This suggests that unlike taxonomic groupings, aggregates by feeding mode may be less likely to have similar productivity. Further refinements to the feeding categories might be useful in addressing this problem.

Our fairly optimistic outcomes may reflect the fact that we had a maximum of 10 species in a complex. In practice, species complexes may contain more than 10 species, many of which are data poor. For example, in the Gulf of Alaska Fishery Management Plan (FMP) there are 12 species complexes identified, with over 10 species in the non-target complexes other skates (11), other slope rockfish (17), and sculpins (39; NPFMC 2011). In the New England and Mid-Atlantic regions, there are 9 and 7 FMPs, respectively, with several managed as various stock complexes, including 7 skate species in a complex, 5 hake stocks in a small-mesh plan, 4 small pelagic in a plan, and 19 groundfish in a multispecies plan. These plans contain 27 and 13 managed species, respectively, excluding any state-managed, non-target or protected species. These are mainly taxonomic aggregates, so the species within them should be broadly comparable in terms of productivity. Perhaps future simulations exploring the effect of the number of interacting species in a community could provide further insight, although the cumulative effect of species interactions on BRPs may not increase with complex size if not all interact strongly (sensu Gamble & Link 2009). However, based on our results we suspect that the tradeoff between yield and biodiversity could increase as complexes include more species, magnifying potential differences in productivity, species interactions, and sensitivity to environmental variability.

Our results support the recent definition of appropriate management aggregates for US fisheries, where 'stock complex' is defined as 'a group of stocks in an FMP that are sufficiently similar in geographic distribution, life history, and vulnerability to the fishery that the impacts of management actions on the stocks in the complex is similar (Federal Register 2008). For example, the 'other species' complex in the Gulf of Alaska which contained all species of skates, sharks, sculpins, squids, and octopuses (Reuter et al. 2010) was recently split into taxonomic complexes to better manage these species with widely divergent productivity. Based on our results, we suspect there will be additional benefits of this action in improving yield and protecting biodiversity because elasmobranchs, sculpins, and cephalopods also have very different sensitivities to environmental change and roles as predators, prey, and competitors.

Environmental impacts

Our simple form of simulated environmental forcing showed considerably varied effects across species and aggregates, in some cases dwarfing the effects of species interactions. In particular, assessments conducted on individual stochastic runs resulted in widely divergent BRPs for several Georges Bank species and aggregates, such that including the combined impacts of environment and species interaction in precautionary reference points appears critical. Environmental variability also exaggerated the assessment bias which overestimated some BRPs for pelagics (see discussion above of aggregate performance). However, the asymmetry in the stochastic envelopes around yield curves suggests that low fishing mortality rates in general can buffer against environmental uncertainties, whereas high fishing mortality rates exacerbate environmental uncertainty. In surplus production models, this can be explained by the fact that the intrinsic rate of growth r, and therefore also its variability, increasingly influence the rate of population change for a stock the further that stock is from its carrying capacity. In nature, both fishing alone (Hsieh et al. 2006) and fishing combined with environmental fluctuations (Shelton & Mangel 2011) have been shown theoretically to increase the variability in exploited fish stock bio-

mass. Changes in demographic rates were found to be the most likely explanation for the effect of fishing alone (Anderson et al. 2008), and environmentally-driven biomass variability increased further as fishing neared F_{MSY} (Shelton & Mangel 2011), both consistent with our simulation results. The magnifying effect of fishing on variation caused by environmental variability and downstream impacts on BRPs could be further investigated with refinements to our operating and assessment models. In particular, the effects of more complex and realistic forms of environmental variability (e.g. temporal autocorrelation, regime shifts) may have more dramatic effects on productivity and resulting BRPs. These studies combined with ours show that without at least considering environmental or ecological effects, single species or aggregate BRPs run the risk of misinforming the status of stocks, with stocks potentially being unknowingly overfished.

Simple assessment performance

The simple stock assessment method we employed generally underestimated the 'true' F_{MSY} rate based on the intrinsic growth rate, but estimated carrying capacity well for most groups. Although the assessments did not explicitly attempt to account for species interactions, the $F = 0$ species trajectories included these effects. It is encouraging that these aggregate models, fit in ignorance of species interactions, tended to underestimate rather than overestimate F_{MSY} for deterministic assessments; however, we do not suggest that this will always be the case (see for example the discussion of the Georges Bank pelagic habitat group above). Further, aggregated models can show resilience not present in full models of all interactions including weak diet links (Pinnegar et al. 2005); this optimism may not always be appropriate to the underlying dynamics. In particular, our stochastic results discussed above demonstrate how an assessment under environmental variability may greatly overestimate biological reference points for certain species and aggregates. Therefore, it remains important to test the results of multiple assessments simultaneously within the larger system to evaluate system-wide effects, whether the assessments are for single species (Walters et al. 2005) or for aggregates.

We note also that the simulated 'data' we had to fit our assessment model was vastly better than what may exist in reality for data-poor stocks, yet it was still unable to estimate all parameters and showed slight bias. Surplus production models are most often

fit to time series of catch and biomass (as in Bundy et al. 2012, Lucey et al. 2012, and Holsman et al. 2012, all in this Theme Section), in contrast to our method. We simulated time series of species biomass with no fishing such that populations recovered to carrying capacity, and then we fit logistic models to these curves to focus on aggregation effects. Clearly, this situation is rare in practice. Before implementing management based on aggregate groups in a particular ecosystem, further simulation testing with more realistic 'data' and assessments is recommended.

Management applications

Managing a few well-designed species complexes may be much simpler than tracking the status of many (even hundreds of) individual species, especially if fisheries are managed on short temporal scales. For practical applications which may further simplify fishery management, at least one additional aggregation type should be considered: fishery-specific aggregations. Many species are caught together in fishing gear that is not equally effective at catching all species it encounters; this type of information could be included in future analyses. Fishery-specific BRPs could then be developed that account for the reality of mixed-species fisheries as well as the ensemble of productivities and interactions in the catch. In addition, for a particular ecosystem, simulations should include environmental variability reflecting the *in situ* observations to give more specific advice on appropriate reference points and management aggregations.

In ecosystems with fewer data resources, our approach could be modified to provide more general advice on aggregating species to balance yield and biodiversity. For example, predictions of the simulation models could be made more general by parameterizing hypothetical fish communities and their interactions using allometric-trophic-network principles (Berlow et al. 2009). Reasonable trophic network structures can be simulated based on macroecological patterns relating species' body sizes, abundances, and trophic positions (e.g. Cohen et al. 2003, Jonsson et al. 2005, Hall et al. 2006, Romanuk et al. 2011), with species interactions strengths based on metabolic theory (e.g. Yodzis & Innes 1992) and empirical consumer-resource, body-size relationships (e.g. Brose et al. 2006). Added to this would be different species productivities, constrained by empirical patterns relating life histories to body size (e.g. Winemiller & Rose 1992, Patrick et al. 2010).

CONCLUSIONS

Our simulations suggest that it is possible to achieve multiple EBFM objectives by managing aggregate species groups. The general strategy of aggregating species into complexes based on taxonomy, habitat, foraging, size or other rules can work well for balancing the objectives of yield and biodiversity under certain conditions. Most importantly, species of similar productivity, interactions, and sensitivity to environmental perturbations should be aggregated to optimize both management objectives. In this simple example, all aggregation types performed reasonably well, with taxonomic aggregates performing better than other aggregates across both simulated ecosystems. Our very simple assessments generally underestimated the 'true' MSY when we didn't explicitly account for species interactions. Realized equilibrium yields based on these assessments generally fell at assessed MSY or at the operating model 'true' MSY if the assessment overestimated MSY relative to truth.

However, caution is warranted with applying aggregate BRPs, as also shown by our results and as noted by many previous authors (e.g. Ricker 1975, Larkin 1976, Mace 2001). Poor aggregations sacrifice biodiversity for yield, leading to severely depleted (or extinct) stocks within the aggregate, as well as more subtle effects such as loss of genetic diversity (e.g. Smith et al. 1991). In particular, expecting similar performance of aggregation types across ecosystems without some basic knowledge of the species life history, interaction strengths, and environmental sensitivity is a poor strategy. For example, the planktivores group displayed either poor theoretical or assessment performance in each of our simulated systems. Therefore, we recommend careful attention to the basics in assembling species complexes: combine similar productivity, followed by consideration of potential environmental sensitivity and strength of species interactions. Then, in managing species complexes, our results show that modest reductions from aggregate F_{MSY} have the dual benefits of maintaining biodiversity and buffering against environmental uncertainty.

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