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Measuring the balance between fisheries catch and fish production

Joseph D. Zottoli[1,*], **Jeremy S. Collie**[1], **Michael J. Fogarty**[2]

[1]Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA
[2]Northeast Fisheries Science Center, Woods Hole, MA 02543, USA

ABSTRACT: Balanced harvesting has been proposed as a fisheries management strategy to mitigate the impacts of fisheries removal on ecosystem structure. One definition of balanced harvest is that all species should be harvested in proportion to their annual production. However, most marine ecosystems lack comprehensive production estimates necessary to empirically measure the degree of balance. We developed and tested 2 new methods for estimating fish biomass production at the species level with limited data requirements. Application of our techniques to 4 ecological production units in the northwest Atlantic (Mid-Atlantic Bight, Georges Bank, Gulf of Maine, and western Scotian Shelf) from 1991–2013 provided a direct estimate of 1.9 million t yr^{-1} of total fish production. The degree of balance between catch and production distributions at the species level, assessed using the proportional similarity index, ranged from 0.34 to 0.83 on a scale from near 0 to 1. Increased balance was positively associated with yield in the Gulf of Maine (Spearman's, $p = 0.04$). Increased balance was negatively associated with an ecosystem impact indicator in the Gulf of Maine (Spearman's, $p = 0.03$) and Mid-Atlantic Bight (Spearman's, $p = 0.02$). These case studies provide some evidence of benefit to humans and reduced ecosystem harm from more balanced harvest. More importantly, we provide a unique empirical metric of balanced harvest at the species level, and develop potential indicators and methods for ecosystem-based fisheries management.

KEY WORDS: Fish production · Balanced harvest · Ecosystem-based fisheries management · EBFM · Ecological production unit · Northwest Atlantic

1. INTRODUCTION

In contrast to traditional management, whereby single-species yields are considered individually, a number of ecosystem-based harvest strategies have been proposed with the intent to reduce the negative ecosystem impacts associated with fishing and to increase total yield. These approaches include harvesting equal proportions of everything above a certain size (Larkin 1977); in proportion to each species' rate of natural predation (Fowler 1999); all harvestable species from all trophic levels in equal proportions to their production (Bundy et al. 2005); and in proportion to the productivity of all species, stocks, sexes, and sizes to the furthest extent feasible (Zhou et al. 2010, 2019).

The latter 2 approaches listed above illustrate differing definitions of what has become known as balanced exploitation or balanced harvest, which has garnered recent attention and controversy. A number of modeling studies advocate the utility of balanced harvest (Jacobsen et al. 2014, Law et al. 2016, Zhou & Smith 2017, Nilsen et al. 2020), while others raise concerns of feasibility, economic tradeoffs, and ecological impacts (Froese et al. 2016, Pauly et al. 2016). Much of the controversy has focused on balanced harvest across the size spectrum, which we do not address here. Instead, we investigate the degree of

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*Corresponding author: jzottoli@uri.edu

balance among species. Most studies of balanced harvesting have relied on multispecies or ecosystem models with idealized fishing fleets. Balanced harvesting is generally expected to increase total yield by targeting more species in the community, provided that all species are harvested at sustainable rates (ICES 2014).

Empirical data for assessment of balanced harvest is limited to a few freshwater case studies (Kolding & van Zwieten 2014), largely due to the requirement of comprehensive production (or productivity, depending on how balanced harvest is defined) estimates and other uncommonly collected metrics. For this study, we consider production, defined by Clarke (1946), and paraphrased by Waters & Crawford (1973, p. 286), as the 'amount of tissue elaborated per unit time per unit area, regardless of its fate'. Bundy et al. (2005) did empirically assess the balance of the eastern Scotian Shelf with their index method but limited their assessment to balance at the trophic level and relied on static productivity estimates from an Ecopath model. It is apparent that reliable, dynamic, species-specific production estimates are essential for implementing balanced harvest at the species level, with subsequent partitions required for implementation at the level of size and sex.

Although productivity has been an important determinant of catch limits in single-species management (Ricker 1975), acquiring estimates for all species in an ecosystem, both harvested and unexploited, is daunting. Ecosystem energetics modeling has produced estimates of total fish production in ecosystems for decades, beginning with simple models based on total primary production and trophic transfer efficiencies (Ryther 1969). These models advanced with computing power into modern end-to-end models that calculate fish production indirectly by balancing energy budgets with combinations of top-down and bottom-up processes and various assumptions (Fulton 2010). However, direct estimates of production for all species in a community are rare due to the extensive information required to estimate production of individual species. Time-varying production estimates are currently restricted to the widely accepted but data-intensive increment-summation technique or application of production to biomass (P:B) ratios to biomass estimates (Cusson & Bourget 2005, Dolbeth et al. 2005). These approaches are limited by data availability and accuracy of P:B ratios, respectively, which prevent wide-scale application across whole ecosystems.

Surplus-production models require minimal data inputs, enabling ecosystem-wide application. Estimates of surplus production can be obtained with just a fisheries-dependent or -independent index of abundance and an index of removals or effort. However, surplus production is fundamentally different from production because it excludes biomass that dies naturally between sampling events (Fig. 1). Estimation and addition of this dead biomass to surplus production should produce estimates of production for any species, given accurate estimates of biomass and mortality.

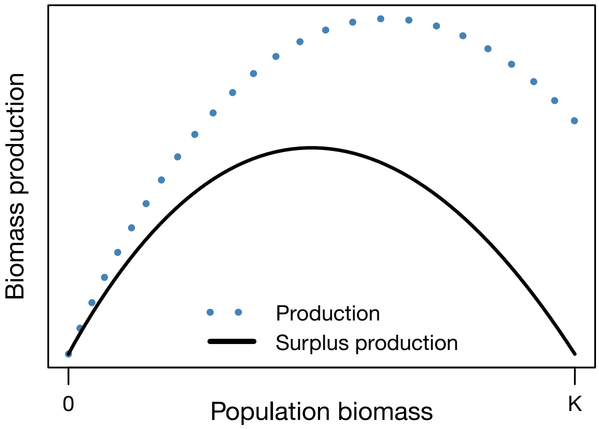

Fig. 1. Hypothetical annual production and annual surplus production as functions of population biomass from 0 to the carrying capacity (K). The difference between curves is due to biomass that dies naturally between sampling events (represented by the right-hand side of Eq. 5)

We demonstrate the effectiveness of incorporating dead biomass to produce estimates of production using 2 new techniques with comparisons to real data and age-structured simulations. We apply these techniques to dominant fish and invertebrate populations in 4 ecological production units (EPUs) to produce direct whole-ecosystem estimates of fish production. Comparison of the proportions of catch and production across EPUs with indices adapted from ecological literature provides a rare empirical assessment for one balanced harvest approach. Specifically, we relate balanced harvest, defined as harvesting all species in equal proportions to their production, to total catch and an ecosystem impact indicator in order to assess potential benefits for yield and ecosystem health, respectively.

2. METHODS

2.1. Study area and data

Our study area comprised 4 EPUs, as designated by the Northeast Fishery Science Center (NEFSC), located on the continental shelf along the northeastern

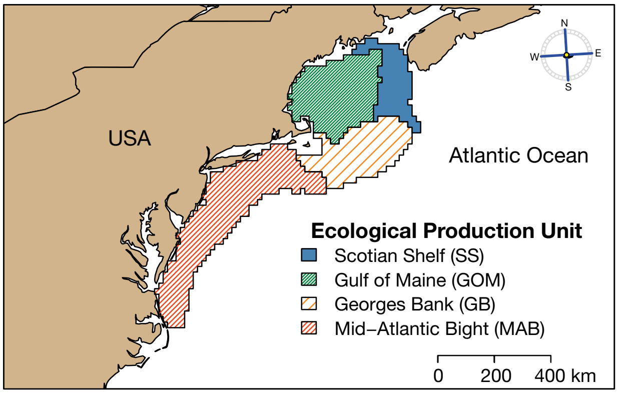

Fig. 2. Boundaries of the 4 study regions (ecological production units; Ecosystem Assessment Program 2012)

USA (Fig. 2). The EPUs included the 115 965 km^2 Mid-Atlantic Bight (MAB), 50 708 km^2 Georges Bank (GB), 60 737 km^2 Gulf of Maine (GOM), and 26 998 km^2 Scotian Shelf (SS). Biomass data for each EPU were primarily obtained from the NEFSC autumn bottom trawl survey. Survey biomass data were adjusted for catchability with a set of coefficients, estimated by NEFSC (Link et al. 2008). Autumn survey data were supplemented with or replaced by the NEFSC spring bottom trawl survey, clam survey, and scallop survey or the Virginia Institute of Marine Science/Maryland Department of Natural Resources blue crab winter dredge survey for better representation of some highly variable species and benthic invertebrates (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m643p145_supp.pdf). Estimates of commercial discards from the NEFSC observer program were corrected for discard mortality and combined with commercial landings to obtain catch estimates. We selected the species that constituted the top 95% of biomass or catch in each EPU for further analysis.

2.2. Production estimation

Annual surplus production and biomass were estimated for all species in each EPU, then again for all EPUs combined by fitting stochastic surplus-production models in continuous time (SPiCT) as described by Pedersen & Berg (2017). Informative prior estimates of the catchability parameter were applied when initial estimates exceeded 1 order of magnitude (<0.1 or >10) under the assumption that the prescaled survey data were reasonably accurate. Robust fits were used when catch or biomass indices contained outliers that greatly altered model fits. A number of species were excluded due to poor model fits, often caused by poor survey representation.

To obtain production estimates from surplus-production model fits, we exploited the interrelatedness of the 2 terms. According to Hilborn & Walters (1992, p. 299) 'the term surplus production is generally used to represent the difference between production and natural mortality.' It can therefore be represented as:

$$\mathrm{SP}_t = P_t - D_t \tag{1}$$

where SP is surplus production, P is production, t is year, and D is dead biomass from natural mortality. D was estimated by applying the conditional rate of natural mortality:

$$D_t = \hat{B}(1 - \mathrm{e}^{-M}) \tag{2}$$

where M is the instantaneous rate of natural mortality and $\hat{B}$ is estimated biomass at the beginning of the year, which can be acquired from a fitted SPiCT model. Using additional fitted SPiCT parameters m (maximum sustainable yield), K (carrying capacity), and n (controls shape of production curve), we can let:

$$\gamma = \frac{n^n / (n-1)}{(n-1)} \tag{3}$$

and estimate annual surplus production with:

$$\mathrm{SP}_t = \gamma m \frac{\hat{B}_t}{K} - \gamma m \left(\frac{\hat{B}_t}{K}\right)^n \tag{4}$$

Combining Eqs. (1), (2), and (4) gives the following equation that can be used to calculate annual production, which we further refer to as the SP conversion method:

$$P_t = \gamma m \frac{\hat{B}_t}{K} - \gamma m \left(\frac{\hat{B}_t}{K}\right)^n + \hat{B}_t(1 - \mathrm{e}^{-M}) \tag{5}$$

To estimate production without using surplus-production estimates, we applied the definition of production when considering solely the fate of biomass during a time period (Holme & McIntyre 1984):

$$P = \Delta B_{t_0 \rightarrow t} + A \tag{6}$$

Eq. (6) illustrates that production is equal to the difference in biomass B between sampling events plus dead biomass lost from all sources of mortality (A), which is subdivided into natural losses (Eq. 2) and catch. This approach, subsequently referred to as the direct method, enables the use of a time series of biomass estimates such as those outputted from a SPiCT model fit or stock assessment, given that accurate catch and natural mortality data are also available and the population is closed. We used constant estimates of instantaneous natural mortality from recent stock assessments or calculated using Jensen's (1996) estimate of the second Beverton and Holt invariant applied to published von Bertalanffy growth parameters (see Table S2).

2.3. Methods comparison

To assess the accuracy of our production estimation techniques, we compared our estimates to those from the increment-summation method as described by Gillespie & Benke (1979) for 8 stocks within the study area that had the necessary age-structured information readily available.

Additional assessment of our techniques was performed with simulation studies. We developed an age-structured model that simulated the population biomass, annual catch, and an annual survey index for 2 representative species at 2 levels of stochasticity (for full set of governing equations, see Text S1 and Tables S2–S4). The large, long-lived species represented a predator species while the small, short-lived species represented a forage fish or small predator. Results from the SPiCT model fitted to the simulated catch, and survey indices were compared to the actual production values calculated with the increment-summation method.

2.4. Ecological analysis

To investigate regional and temporal patterns of fishing, a number of ecological indices were applied to the species composing the top 90 % of catch or production each year from 1989 to 2015. Production was estimated using the direct method applied to the NEFSC spring, fall, or both surveys except for GB, GOM, and SS winter skate, and MAB and SS spiny dogfish *Squalus acanthias*, which were estimated with the SP conversion method. Striped bass *Morone saxatilis*, ocean quahog, and Atlantic surfclam were calculated using the direct method applied to stock assessment biomass. The first and last 2 years in the time series were excluded due to missing data and poor SPiCT model fits at boundary years.

Preference for each species by the fishery in relation to its production was assessed with Chesson's (1978) adaption of Manly et al.'s (1972) selection index α with constant prey:

$$\alpha_i = \frac{c_i / p_i}{\sum_j (c_j / p_j)} \tag{7}$$

for which c is the proportion of species i in the catch of all species (j), and p is the proportion of total production. If ns is the number of species, a species with $\alpha = 1/ns$ is neutrally selected relative to the other species. The whole-ecosystem catch–production balance was assessed by comparing the frequency distribution of available production to the frequency distribution of catch composition for all species (j) using the proportional similarity (PS) index (Feinsinger et al. 1981):

$$\mathrm{PS} = 1 - \sum_j \left| c_j - p_j \right| \tag{8}$$

The PS index ranges up to 1, at which point an ecosystem is harvested exactly in proportion to production. This index measures how closely the proportions in the catch match those for production of the same species, recognizing that the proportions of production are unequal across species. The same PS value could be obtained at high and low fishing pressure.

The impact on the ecosystem was determined using a slightly modified version of an indicator developed by Jacobsen et al. (2017):

$$I = \frac{1}{ns} \sum_j 1 - 100^{-\left(\frac{B_{F,j}}{B_{0,j}} - 0.2\right)} \tag{9}$$

The indicator is an aggregate of the current biomass B_F of each species in relation to unfished biomass B_0 with higher penalties for species below 20 % unfished biomass. This is an aggregate measure of fishing pressure, with lower values of the indicator I representing a more disturbed ecosystem.

Associations among ecological indices were explored with Spearman's rank correlation to avoid assumptions about relationship structure and to minimize the influence of outliers.

3. RESULTS

3.1. Method comparison

Mean annual production estimates from both the SP conversion and direct methods applied to survey data were similar in magnitude to those calculated with the increment-summation method for 8 stocks with age-structured assessments. There was no consistent pattern of bias for either new technique, and both produced less or equal temporal variability relative to the increment-summation estimates. For half of the species, the SP conversion and direct methods produced similar estimates, as exhibited by GOM haddock, American plaice, summer founder, and scup (Fig. 3). This minimal discrepancy between methods resulted from relatively small and stable annual changes in biomass estimates and catch that was con-

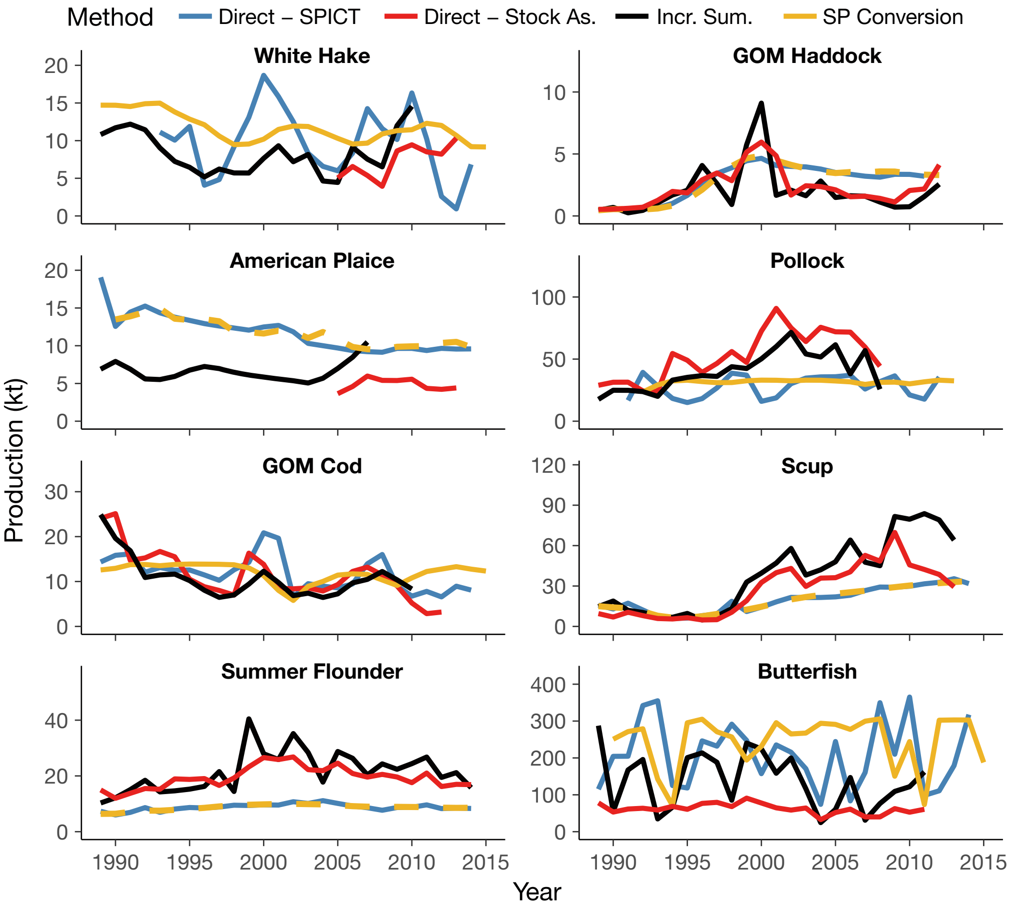

Fig. 3. Estimates of annual production for 8 stocks with age-structured assessments from 3 proposed methods (colors; SPICT: surplus-production model in continuous time ; Stock As.: stock assessment; SP: surplus production) compared to the increment-summation method (Incr. Sum., black). Estimates are shown as continuous lines for ease of comparison. GOM: Gulf of Maine

sistently near equal to surplus production.

The direct method applied to survey data slightly outperformed the SP conversion method but application of the direct method to stock assessment biomass was consistently most precise overall based on normalized root mean squared deviations (NRMSDs). For 5 of the 8 species, NRMSDs were lower for the direct method applied to survey data than for the SP conversion method, but differences were typically minimal (Table 1). Noticeably lower NRMSD resulted from application of the direct method to stock assessment biomass except for butterfish. This minimal difference for butterfish may have resulted from use of spawning stock biomass rather than total biomass when applying the direct method to stock assessment output, or from difficulties in estimating the high *M* for this species.

Production estimates from the simulation study further validated the general accuracy of our techniques in cases for which the SPiCT model accurately estimated biomass (NRMSD < 0.2). The direct method performed better than the SP conversion method

Table 1. Differences in normalized root mean squared deviation of production estimates between the increment-summation method and the surplus production (SP) conversion method, direct method applied to fall survey data, and direct method applied to stock assessment biomass. GOM: Gulf of Maine stock

Method	White hake	GOM haddock	American plaice	Pollock	GOM cod	Scup	Summer flounder	Butterfish
SP conversion	0.522	0.974	0.942	0.550	0.457	0.700	0.665	1.133
Direct (survey)	0.866	0.930	0.931	0.631	0.403	0.703	0.663	1.084
Direct (stock)	0.337	0.576	0.455	0.300	0.228	0.450	0.246	1.011

based on NRMSD in scenarios with moderate variability, but both methods performed similarly with low variability (Table 2, Fig. 4). The SP conversion method also failed and often produced negative estimates of production when biomass was estimated to exceed carrying capacity (results not shown).

The simulation results also demonstrated the importance of accurate natural mortality estimates, and highlighted the difference between production and surplus production (Fig. 4). Based on NRMSD, production estimates were more accurate when the applied mean adult natural mortality (*M*) matched the value used in the simulation (0.25 for large species or 0.325 for small species) compared to other values (0.1, 0.175, 0.25, 0.325, 0.4) in 3 out of the 4 simulated scenarios (Fig. 4A–D) for both methods. In the special case with $M = 0$ in the SP conversion method (Eq. 5), results are equivalent to surplus production. These instances produced median estimates that were 53–64 % less than actual median production, demonstrating that surplus production is not an acceptable stand-alone proxy for fish production. The magnitude of this difference was influenced by population size, and would be exacerbated with higher real *M.*

Table 2. Normalized root mean squared deviation between true production and estimates from the surplus production (SP) conversion and direct methods using accurate natural mortality estimates for 4 simulated scenarios; large and small species with low and moderate stochasticity

Method	Large, low	Large, moderate	Small, low	Small, moderate
SP conversion	0.069	0.373	0.075	0.421
Direct	0.061	0.209	0.076	0.299

In addition to varying adult natural mortality, varying juvenile mortality also determined the degree of bias (Fig. 5). The simulation used natural mortality that decreased exponentially with age. If early-juvenile natural mortality in the simulations was too low, production estimates employing the correct mean adult natural mortality were positively biased for reasons explained in Section 4.

3.2. Ecological analysis

Our estimates of production and exploitation revealed a number of latitudinal patterns. Estimated total mean annual production from 1991–2013 ranged from 215 000 t (215 kt) in the most northerly EPU (SS) to 894 kt in the most southerly EPU (MAB) (Table 3), with no clear temporal trends except for a general

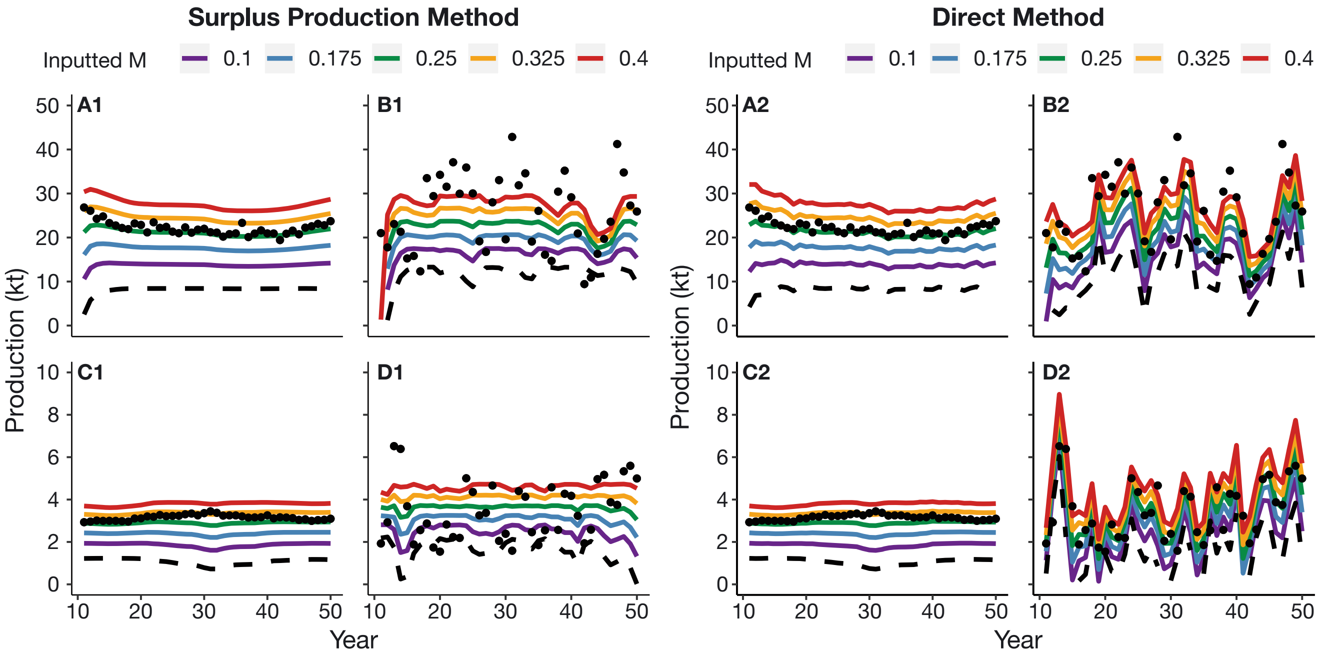

Fig. 4. Production estimates of a simulated population from different inputted natural mortality (colors) and estimation techniques. Surplus production (SP) conversion method (A1–D1) and direct method (A2–D2). Actual production from simulations of a large species (instantaneous rate of mortality, $M = 0.25$) with (A1, 2) low and (B1, 2) moderate stochasticity, and a small species ($M = 0.325$) with (C1, 2) low and (D1, 2) moderate stochasticity are shown as black points. The dashed black line represents inputted natural mortality = 0

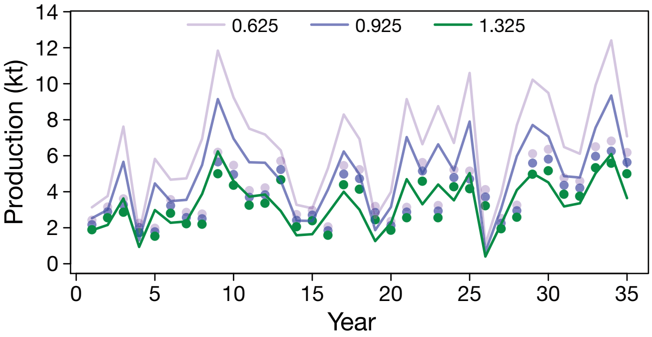

Fig. 5. Production estimates from the direct method applied to simulated populations (lines) compared to the real values (points). All parameters except for early-juvenile mortality were constant in the simulations. Purple, blue, and green indicate simulations with age 0 instantaneous mortality rates of 0.625, 0.925, and 1.325, respectively; in this simulation, we used 1.325 as the early juvenile mortality

decline of production in the MAB (Fig. 6). When scaled by area, GB was the most productive EPU, while the SS returned the highest yield. Production and catch were both dominated by fewer species in the more northerly GOM and SS EPUs (Fig. 7). Relative exploitation of production was also greater in northerly EPUs, with 15–40 % of production harvested in most years (Fig. 8).

P:B ratios calculated from production estimates and biomass from model outputs were mostly consistent with species longevity (Table 4). Productivity (P:B) ranged from 0.02 for GB ocean quahog, which live over 100 yr, to 1.86 for MAB northern shortfin squid, which is an annual species. Although most estimates were within reason, many species exhibited variable P:B ratios across EPUs and, to a lesser extent, through time (Table 4).

Species with the highest estimated biomass in each EPU were not the most productive species in 64 % of years across all EPUs. This confirms that comparisons of catch to production are more appropriate than comparisons to biomass. Species-level analysis showed that a number of species, including butterfish, Atlantic croaker, and spot, were negatively selected in relation to other species in the same EPU, while others like northern shortfin squid, sea scallops, and Acadian redfish were positively selected (Fig. 9). The selectivity of most species varied considerably over time, with some species reversing the direction of their selectivity. A few species, including spiny dogfish and little skate, were over-selected in at least 1 EPU and under-selected in another during the same years (Fig. 9).

Table 3. Total mean annual production, production per km^2 and catch per km^2 in each ecological production unit (EPU) modeled individually (MAB: Mid-Atlantic Bight; GB: Georges Bank; GOM: Gulf of Maine; SS: Scotian Shelf) and modeled together (All) from 1991–2013. The standard deviations (σ) of total production and mean proportional similarity (PS) index values are also shown

	MAB	GB	GOM	SS	Total (σ)	All
Production (kt)	894	468	325	215	1902	1878
SD (σ)	138.7	60.2	39.9	26.2	174.9	220.7
Production (t km^{-2})	7.7	9.2	5.3	8.0	7.5	7.4
Catch (t km^{-2})	2.06	2.65	2.05	3.67	2.35	2.35
Balance (PS index)	0.52	0.45	0.74	0.58	n/a	0.64

The balance between catch and production varied regionally and temporally within each EPU. PS index values were highest in the GOM and SS (Table 3). Although there were no dramatic long-term changes, there was a general decrease in balance in the last 3 to 5 yr of the study window in most EPUs (Fig. 10). These decreases were caused by disproportionate increases in Atlantic herring catch in the MAB and GB, lobster catch in the SS, and both herring and

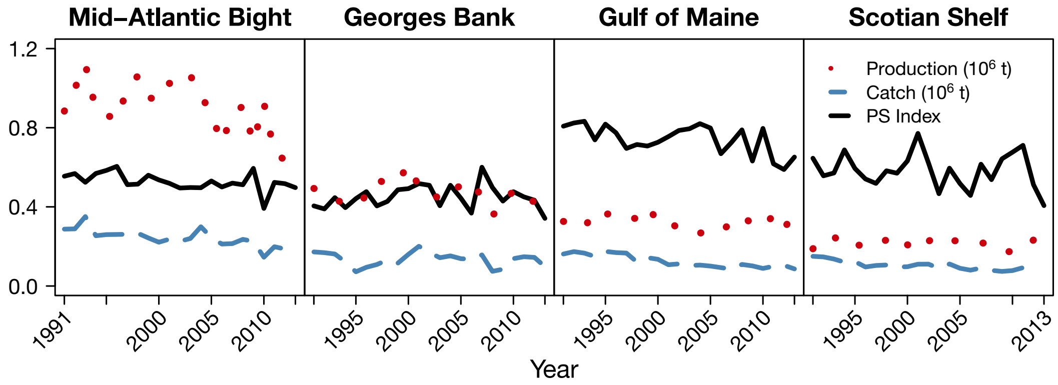

Fig. 6. Proportional similarity (PS) index (black), catch (blue dashed), and total production (red dotted) estimates in the mid-Atlantic Bight throughout the study period

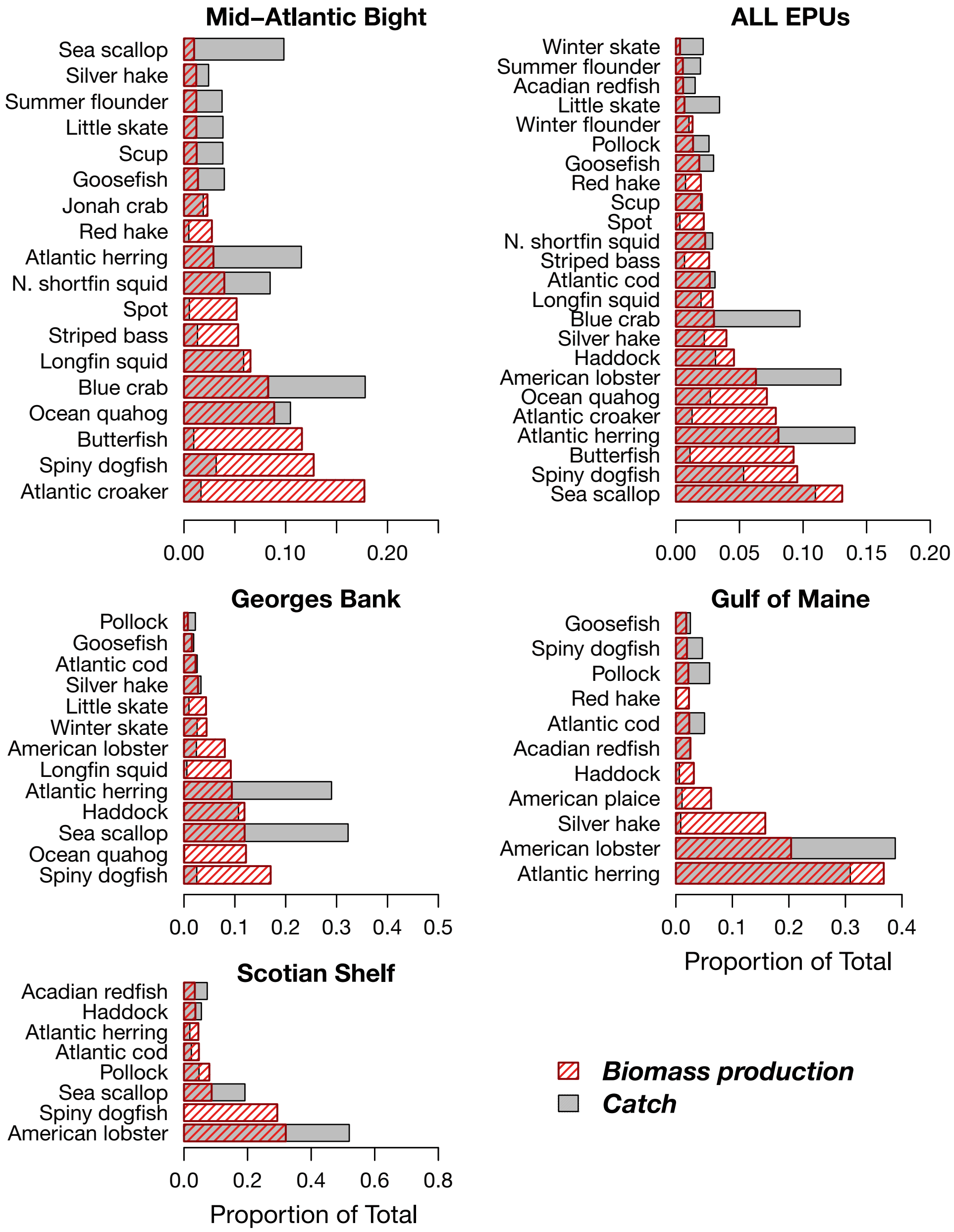

Fig. 7. Median proportions of production and catch for species comprising the top 90 % of production or top 90 % of catch from 2010–2013. Production bars (red) are overlaid on catch bars (gray). EPU: ecological production unit

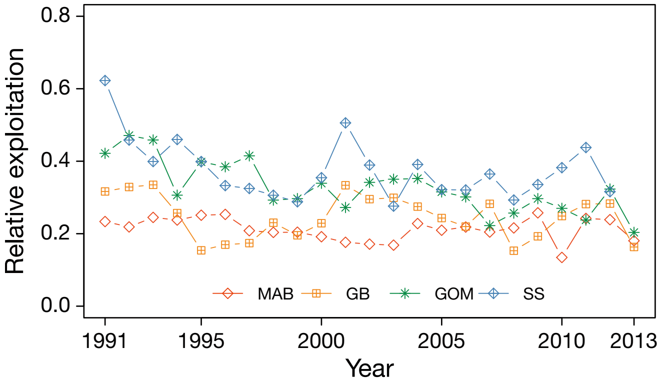

Fig. 8. Annual relative exploitation (total catch divided by total production) in each ecological production unit (MAB: Mid-Atlantic Bight; GB: Georges Bank; GOM: Gulf of Maine; SS: Scotian Shelf) during the study period

Table 4. Mean (μ) and standard deviation (σ) of annual production to biomass ratios calculated from 1991−2013 for each ecological production unit (EPU; abbreviated as in Table 3). Values are only provided for species that were part of the top 95% of survey biomass in each EPU during the period

Species	Production to biomass ratio							
	MAB		GB		GOM		SS	
	μ	σ	μ	σ	μ	σ	μ	σ
Acadian redfish *Sebastes fasciatus*					0.18	0.08	0.45	0.11
American lobster *Homarus americanus*	0.59	0.47	0.31	0.03	0.80	0.30	0.96	0.58
American plaice *Hippoglossoides platessoides*			0.89	0.24	0.24	0.14		
Atlantic cod *Gadus morhua*			0.31	0.17	0.47	0.26	0.36	0.36
Atlantic croaker *Micropogonias undulatus*	0.31	0.15						
Atlantic herring *Clupea harengus*	0.82	0.19	0.85	0.65	0.34	0.13	0.31	3.88
Atlantic surfclam *Spisula solidissima*	0.13	0.03	0.11	0.03				
Barndoor skate *Dipturus laevis*	0.34	0.54					0.29	0.11
Black sea bass *Centropristis striata*	0.96	0.82						
Blue crab *Callinectes sapidus*	1.38	0.29						
Bluefish *Pomatomus saltatrix*	0.20	0.05						
Butterfish *Peprilus triacanthus*	0.75	0.42			0.73	0.89		
Clearnose skate *Raja eglanteria*	0.31	0.21						
Goosefish *Lophius americanus*	0.96	0.35	0.47	0.23	0.47	0.02		
Haddock *Melanogrammus aeglefinus*			0.79	0.48	0.45	0.31	1.05	0.48
Jonah crab *Cancer borealis*	0.81	0.05	6.20	3.19				
Little skate *Leucoraja erinacea*	0.41	0.11	0.26	0.06				
Longfin squid *Doryteuthis pealeii*	1.69	0.40	1.02	0.08				
Northern shortfin squid *Illex illecebrosus*	1.86	1.37			0.69	0.15		
Ocean quahog *Arctica islandica*	0.03	0.00	0.02	0.01	0.03	0.00		
Pollock *Pollachius virens*			5.10	4.88	0.64	0.26	0.23	0.13
Red hake *Urophycis chuss*	1.20	0.42	0.54	0.37	0.28	0.26		
Scup *Stenotomus chrysops*	0.39	0.11						
Sea scallop *Placopecten magellanicus*	0.27	0.11	0.89	2.13			0.94	3.17
Silver hake *Merluccius bilinearis*	0.76	0.74	1.07	0.25	0.40	0.30	0.83	0.55
Smooth dogfish *Mustelus canis*	0.18	0.07						
Spiny dogfish *Squalus acanthias*	0.15	0.05	0.09	0.02			0.12	0.91
Spot *Leiostomus xanthurus*	0.64	0.23						
Summer flounder *Paralichthys dentatus*	0.55	0.20						
Thorny skate *Amblyraja radiata*					0.12	0.06	0.08	0.02
Weakfish *Cynoscion regalis*	0.32	0.18						
White hake *Urophycis tenuis*			0.69	0.52	0.36	0.02	0.28	0.09
Winter flounder *Pseudopleuronectes americanus*			0.43	0.26	0.31	0.08	0.58	0.20
Winter skate *Leucoraja ocellata*	0.24	0.34	0.22	0.17	0.34	0.31	0.11	0.17
Yellowtail flounder *Limanda ferruginea*			0.35	0.44				

lobster catch in the GOM. The SS decline in particular demonstrated the sensitivity of the PS index to large changes or errors in catch or abundance of a single species.

Ecosystem impact ranged from 0.14 on GB during the early 1990s to 0.76 in the GOM in recent years (Fig. 11). Impact generally declined during the study period in all EPUs except for the SS, which ended with impact scores higher than the mean. Significant negative associations between the PS index (balance) and ecosystem impact were observed in the GOM ($p = 0.03$) and MAB ($p = 0.02$), but there were no significant relationships in other EPUs (Table 5).

Investigation of the relationship between balance and total catch found positive associations in all EPUs, but only the GOM ($p = 0.04$) had a significant relationship (Table 5). There was also a significant positive relationship between production and catch in the MAB ($p = 0.01$) and a negative relationship between balance and production in the SS ($p = 0.001$). No other significant relationships were observed between balance, catch, and production.

4. DISCUSSION

4.1. Method comparison and limitations

Results demonstrate that the direct and SP conversion methods can produce relatively accurate esti-

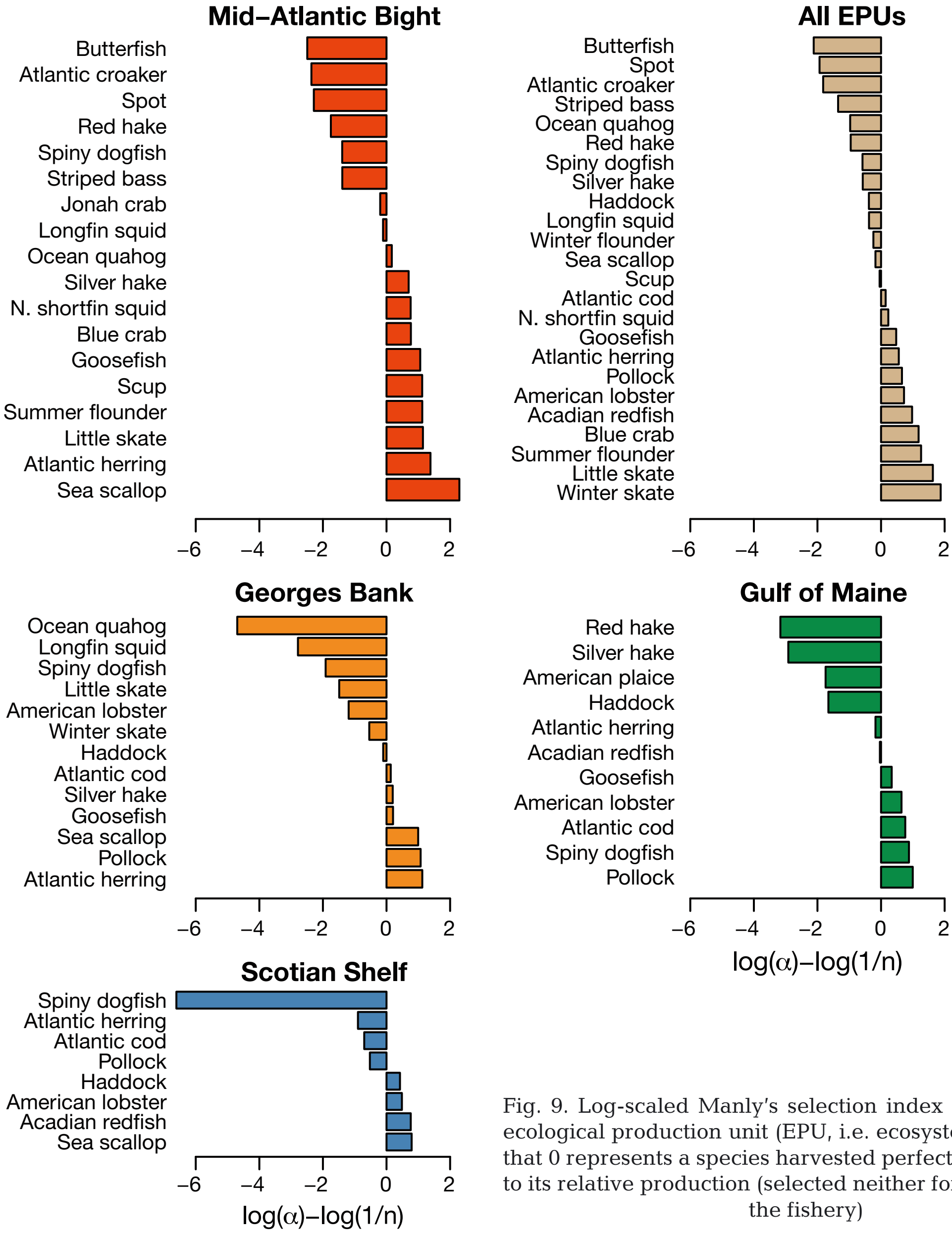

Fig. 9. Log-scaled Manly's selection index scores for each ecological production unit (EPU, i.e. ecosystem) adjusted so that 0 represents a species harvested perfectly in proportion to its relative production (selected neither for nor against by the fishery)

mates of annual production when accurate model fits are achieved, but the direct method appears superior. In addition to outperforming the SP conversion method in both simulations and comparisons to increment-summation, the direct method has fewer assumptions and greater flexibility. It can be applied to a time series of biomass and catch from a stock assessment or other source without fitting a surplus production model. This flexibility enables utilization of biomass estimates from more complex and informed models that should, in theory, produce more accurate results. The direct method also better accounts for temporal changes in productivity. Unlike the SP conversion method that is restricted to the shape of the surplus-production curve, the direct method can produce different estimates of production for the same level of biomass, depending on the change in biomass and catch. Both methods leave room for improvement.

As with stock assessment methods in general, our production estimates are most sensitive to uncertainty in catchability (q) and natural mortality (M). For the purposes of this work, both approaches for estimating production made the unlikely assumption that natural mortality is constant over time. In the case of the SP conversion method, density-dependent

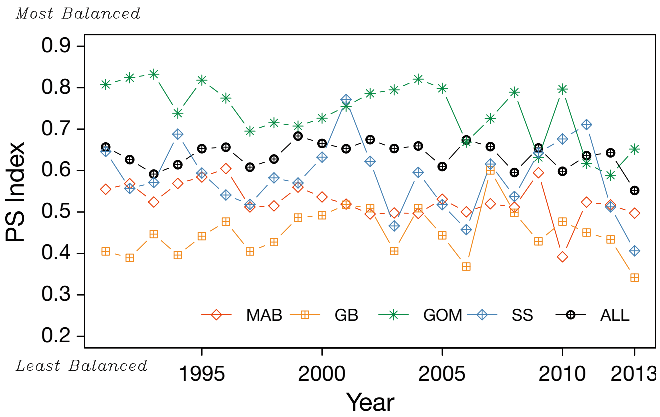

Fig. 10. Proportional similarity (PS) index as a measure of ecosystem catch–production balance for each ecological production unit (MAB: Mid-Atlantic Bight; GB: Georges Bank; GOM: Gulf of Maine; SS: Scotian Shelf) throughout the study period

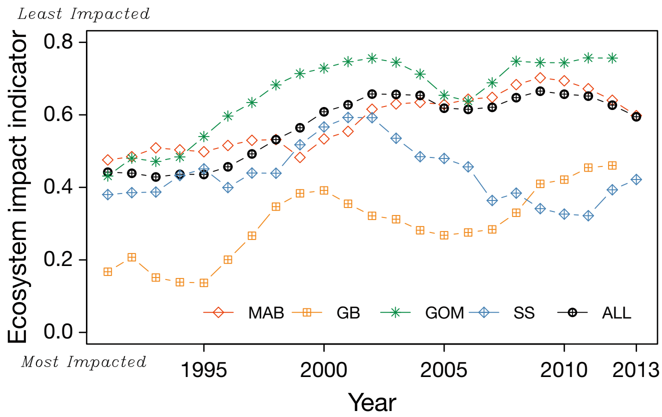

Fig. 11. Ecosystem impact indicator for each ecological production unit (MAB: Mid-Atlantic Bight; GB: Georges Bank; GOM: Gulf of Maine; SS: Scotian Shelf) throughout the study period

Table 5. Significance (p-values) of relationships between the proportional similarity index (balance), total production, total catch, and Jacobsen's ecosystem impact indicator within each ecological production unit (EPU) according to Spearman's rank correlation (MAB: Mid-Atlantic Bight; GB: Georges Bank; GOM: Gulf of Maine; SS: Scotian Shelf). All significant relationships were positive except for those between balance and ecosystem impact. *Significant, $\alpha = 0.05$.

EPU	Balance: catch	Production: catch	Balance: production	Balance: impact
MAB	0.11	0.01*	0.32	0.02*
GB	0.20	0.09	0.60	0.09
GOM	0.04*	0.11	0.23	0.03*
SS	0.09	0.59	<0.01*	0.42

natural mortality was accounted for by the surplus-production curve, but the reincorporation of dead biomass was based on constant *M*. Perhaps this *M* value could follow a relationship based on the shape of the surplus-production curve for future implementation. However, the production curve is fixed through time by default in the SPiCT model, such that temporal variability in productivity and natural mortality from regime shifts, predator–prey relationships, etc. are not accurately reflected without a time-varying curve. In the case of the direct method, density dependence is not directly considered but is indirectly exhibited through differences in the incremental change of biomass, so temporal changes in productivity are incorporated. Temporal variability in natural mortality could easily be accounted for by varying the *M* value, but, as is also the case with the SP method, producing reliable estimates of *M* is extremely difficult.

Using conditional *M* is also problematic because it can lead to overestimation of natural deaths, as noted by Ricker (1975). However, *M* estimates are generally restricted to represent harvested and observed ages, excluding younger ages with high associated mortality. We argue that inclusion of the high-mortality early-stages of the age spectrum in our analysis adequately negates the effects of using conditional *M* under the assumptions that juvenile fish have higher *M* and contribute a sufficiently large proportion of production. These assumptions are supported by the similarity between our production estimates and those from the increment-summation method using real data. They are also supported by the simulations because, as mentioned in the results section, positive bias prevailed unless juvenile mortality was sufficiently high.

These methods rely heavily on accurate estimates of biomass. Careful model fitting is imperative for valid results. The SPiCT model is quite flexible and affords modelers a number of tools to obtain sensible fits. Validating biomass trends with other sources is highly recommended, and can be aided with the use of confidence intervals for biomass estimates provided by SPiCT model fits. The estimated confidence intervals for biomass could potentially be used to incorporate uncertainty into estimates of production and the applied ecological indices.

4.2. Ecological findings

Our estimates of total production of all harvestable species appear comparable, but consistently lower, than estimates from ecosystem energetics modeling.

Au (1973) estimated with a bottom-up approach that, depending on the number of trophic steps, between 1500 and 3800 kt of fish biomass was produced annually within shelf waters of the International Commission for the Northwest Atlantic Fisheries Subareas 5 and 6. This region roughly covers our study EPUs except for the SS; excluding the SS, we estimated annual mean production of 1687 kt. However, our estimates exclude species that did not compose the top 95% of survey biomass or top 90% of catch and species that are poorly represented by trawl surveys, such as pelagic and net-avoiding species. Conversely, we included some exploitable invertebrate species, which likely negates some of the impact of excluding fish species so, by our estimation, real fish production is likely at the lower end of Au's range.

Sissenwine et al. (1984) used the relationship between consumption to biomass ratios and P:B ratios in the GB fish community to balance an energy budget and produced estimates of 2210 and 3650 kt of annual fish production for the mid-1960s and mid-1970s, respectively. These estimates far exceed our 1991–2013 mean estimate of 468 kt. The estimate of Sissenwine et al. (1984) may be elevated due to inclusion of young fish (< age 1) not represented in our study or because of overestimation of primary production. Collie et al. (2009) compiled an end-to-end energy budget that appraised GB fish production (including young fish) at a lower rate of 3.562 g carbon m^{-2} (1445 kt total assuming 1 g carbon = 8 g wet weight) using 15% less primary production. Other than the impacts of excluding species as mentioned previously, our estimates may be lower due to the effects of migration or misrepresented catch. It is possible that seasonal migrations of species reflected in the fisheries were not properly represented by the biannual survey, leading to over- or under-estimation of production. GB and the SS may be particularly vulnerable to effects of migration due to their small size, and in the case of the SS, largely politically defined boundary. This could also explain why relative exploitation in the SS was noticeably higher than in other EPUs. Low estimates of relative exploitation and production can also be caused by underestimated catch (Omori et al. 2016). We may have compounded the influence of any underreported catch by excluding recreational catch in our analysis. However, most species included in the analysis experience negligible recreational fishing pressure.

Early estimates of P:B, calculated by Grosslein et al. (1980) using the increment-summation method applied to results of virtual population analyses, provide a unique comparison to our results for some GB species. As was true with our estimates, Grosslein et al. (1980) reported time-variant P:B ratios, with geometric means for GB Atlantic cod (0.60), haddock (0.41), yellowtail flounder (0.63), silver hake (0.59), and Atlantic herring (0.29). Despite the 3 decade time difference, our P:B ratios were comparable for the first 3 species (0.31, 0.79, 0.35) but much higher for silver hake (1.07) and Atlantic herring (0.85). It is surprising that herring had the lowest P:B ratio because herring are relatively small and productivity tends to increase allometrically with body size (Banse & Mosher 1980), so it appears that Grosslein et al. (1980) underestimated herring P:B. The same argument can be made for silver hake, but the GB ratio is 29% higher than the next largest EPU estimate and falls at the high end of our range of P:B ratios, so the true ratio likely lies between 0.59 and 1.07. Dynamic stock-recruitment analyses (Tableau et al. 2019) indicate decreasing productivity of cod and yellowtail flounder and increasing silver hake productivity, which is consistent with the differences between our estimates and those of Grosslein et al. (1980).

Assuming that increased yield is beneficial to humans, our empirical evidence suggests that there are potential benefits from harvesting species in proportion to relative production. All EPUs had positive associations between total catch and balance, with the GOM exhibiting a significant relationship. Comparing across regions, total catch (scaled by area) was more related to production than to balanced harvest. The 2 EPUs with the lowest production (MAB and GOM) also had the lowest catch. GB is one of the most productive marine ecosystems in the world because of its unique geographic and physical characteristics (Cohen et al. 1982), so the high catch observed there may be driven by high productivity. According to our calculations, GB had the highest production per area by more than 1 t km^{-2}. The high catch on the SS can be explained by a combination of its productivity and balanced fishery with high relative exploitation.

Comparing across regions, the degree of balance was related to ecosystem impact. The EPU with highest balance (GOM) also had the highest ecosystem impact value. By contrast, GB had the lowest balance and lowest impact indicator, suggesting that ecosystems with more balanced fisheries are less impacted. This broad result is consistent with the minimum disturbance in trophic structure predicted by some modeling studies (Jacobsen et al. 2014, Zhou & Smith 2017). Many traditional indices used for assessing ecosystem health (e.g. species diversity) are not applicable to our EPU production estimates because selection of the dominant-species subset truncated the number of species included. Jacobsen's impact indicator is a viable representation of EPU health because it is normalized for the number of species. However, using traditional management benchmarks such as single-species carrying capacities has been cautioned against because of the large uncertainty in estimating unfished population size. If harvesting in proportion to the production of species increased ecosystem health within ecosystems, one would expect a positive relationship between the PS index and Jacobsen's ecosystem impact indicator, assuming that having more species closer to carrying capacity is representative of a healthier ecosystem. Contrary to expectations, most EPUs showed no significant trend except for the MAB and GOM, which demonstrated a negative relationship. However, measuring ecosystem health is a topic of much debate, and there is skepticism about the practicality of health indices (Suter 1993). In the case of Jacobsen's indicator, a pristine (i.e. unfished) ecosystem is healthiest, which contradicts all fisheries management objectives that require harvest.

Spatial comparisons revealed some consistent patterns in the degree of balance among the EPUs. The fish communities in the 2 northern EPUs (SS and GOM) were dominated by fewer species. These 2 EPUs had higher catch–production balance and higher relative exploitation despite relatively low production per unit area in the GOM. By contrast, the 2 southern EPUs had lower species dominance, lower balance, and lower relative exploitation rates, even though they are more productive. Our results are consistent with the observation that the relationship between biodiversity and productivity is bidirectional (Worm & Duffy 2003), such that the goals of maximizing single-species catches and biodiversity are not necessarily aligned (Steele 2006).

Despite some evidence of human benefit and ecosystem harm from balanced harvest, our study region and period may not be adequate to observe the full effects of ecosystem-based harvest approaches. In most EPUs, the variability in catch–production balance was greater than any long-term trends. Intentional ecosystem-based fisheries management (EBFM), rather than coincidental patterns with minimal temporal discrepancies in balance, will be required to overcome any lasting effects of the long history of heavy exploitation of the northwest Atlantic and contributions of process and observation error. Multiyear periods of high catch–production balance are likely required to overcome processes like variability in recruitment, oscillatory predator–prey interactions, competition, etc. Additionally, our indices assess partitioning of catch and production in this study, but exclude the magnitude of total fishing pressure. Unsustainable total removals from the ecosystem could easily negate any benefits of ideal harvest patterns, and appropriate community-level harvest rates must be carefully determined for implementation of EBFM.

In summary, we demonstrated that the direct method for estimating fish production is an effective approach for providing production estimates for individual species based on simulations and comparison to other works using real data. Application of ecological indices to catch and production estimates provides a simple framework for empirically assessing the degree of balance between catch and production at the species level. A case study in the northwest Atlantic provided evidence that increased catch–production balance was associated with increased catch. The relationship between balance and ecosystem health/impact appeared negative, but other metrics for measuring ecosystem health and intentional implementation of balanced harvest may be necessary for observation of ecological benefits to be possible.

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