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Comparative analysis of marine fisheries production

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INTRODUCTION

What drives marine fisheries production?

Sarah K. Gaichas[1,*], Alida Bundy[2], Thomas J. Miller[3], Erlend Moksness[4], Konstantinos I. Stergiou[5]

[1]National Atmospheric and Oceanic Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, Massachusetts 02543, USA
[2]Department of Fisheries and Oceans, Bedford Institute of Oceanography, Halifax, Nova Scotia, Canada, B2Y 14A2
[3]Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, Maryland 20688, USA
[4]Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway
[5]Department of Biology, Aristotle University or Thessaloniki, Thessaloniki 54 124, Greece

ABSTRACT: This paper introduces the MEPS Theme Section (TS) 'Comparative Analysis of Marine Fisheries Production'. The unifying theme of the studies in the TS is the relative influence of a 'triad of drivers' — fishing, trophodynamic, and environmental — on fisheries production. The studies were developed during 2 international workshops held in 2010 and 2011, which assembled a database of fisheries, trophodynamic, and environmental time series from 13 northern hemisphere marine ecosystems, and applied a common production-modeling approach to this data. The studies encompass empirical examinations of the datasets, production models fitted to the data at multiple levels of organization from single species to full ecosystems, and simulation studies examining the impacts of climate effects and alternative management strategies on fisheries production. The body of work presented in the TS demonstrates that using both production modeling and the comparative approach together makes rapid progress towards ecosystem-based fishery management, whether the aim is a better understanding of the ecosystem or the provision of operational management advice.

KEY WORDS: Marine fisheries · Production models · Comparative approach · Ecosystem based fishery management

Ecosystem drivers of marine fisheries production

Marine fisheries, which provide an important source of protein for human consumption worldwide (Garcia & Rosenberg 2010), take place within the larger context of marine ecosystems. The sustainability of fisheries resources is inextricably linked with the sustainability of ecosystem processes (Sherman 1994, Pikitch et al. 2004, Link 2010). Therefore, understanding the linkages between ecosystem processes and fisheries production is critical to the effective management of marine fisheries resources. The unifying theme for the MEPS Theme Section (TS) 'Comparative analysis of marine fisheries production' is that ecosystem processes can be organized into a 'triad of drivers': (1) exploitative, (2) biophysical, and (3) trophodynamic, supporting fisheries production (See Fig. 1 in Link et al. 2012, this TS). What, however, is the extent to which each of these drivers control fisheries production across marine ecosystems? To address this question in the TS, we adopted a comparative approach using a standardized production-modeling framework.

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*Email: sarah.gaichas@noaa.gov

Production modeling for a comparative approach

Many multispecies or ecosystem models have been developed over the last few decades, and several reviews are available (e.g. Plagányi 2007, Townsend et al. 2008). They range from extended single species models to multispecies minimum realistic models, and from food web models to whole ecosystem models with age and spatial structure. All models have strengths and weaknesses: simplicity may entail missing key processes, whereas complexity requires more data, time and resources. For a comparative exercise such as this, production models (also called biomass-dynamics models) were selected because of their simple data requirements and the flexibility to apply them at different scales of space, time and species aggregation.

Production models have a long history of use in ecology and fisheries science (Graham 1935, Schaefer 1954, Pella & Tomlinson 1969, Ricker 1975, Hilborn & Walters 1992). Although many current single species stock assessments used to advise fisheries managers employ more complex age-structured population dynamics models, the simple production model can provide important information for ecosystem-based fisheries management (EBFM; see e.g. Browman & Stergiou 2004, 2005, Link 2010). Production models require only the basic data inputs of catch and biomass, and so are applicable for incidentally caught, relatively data-poor non-target species as well as data-rich commercial target species. Production models can be applied at multiple levels of organization, from single species to functional groups to ecosystems, simply by summing the appropriate biomass and catch time series. Importantly, biological reference points (BRPs) currently used for fisheries management, such as maximum sustainable yield (MSY), can be derived directly from production models. Therefore, production models are capable of providing BRPs for non-target species, for functional groups, and for whole ecosystems; BRPs that are not estimable from the age-structured single species stock assessment models applied to commercial target species.

The simplicity of the production-modeling approach, combined with the general availability of necessary input data, forms an ideal framework for comparative analysis of marine ecosystems. The comparative approach to ecosystem analysis is an effective way to examine the underlying drivers of ecosystem structure and productivity, given that direct marine ecosystem-scale experimentation is usually impractical, and replicate experimentation near impossible (Murawski et al. 2010). Previous work on marine ecosystems of the northeast Pacific, northwest Atlantic and northeast Atlantic demonstrates the power of the comparative approach for revealing common trends as well as structural differences critical to both ecosystem understanding and management (Drinkwater et al. 2009, Gaichas et al. 2009, Link et al. 2009, Megrey et al. 2009a,b, Mueter et al. 2009). In this MEPS TS, we extend this work, using the standardized production-modeling framework, which allows for direct comparisons of BRPs and other model-derived quantities of interest across ecosystems.

Workshops

Two international workshops focusing on annual surplus production-modeling were held in May of 2010 and 2011 in Woods Hole, Massachusetts, USA (Link et al. 2010). These workshops, jointly funded by the US Comparative Analysis of Marine Ecosystem Organization (CAMEO), the Norwegian Research Council (NRC), and the Fishery and Oceans Canada Ecosystem Research Initiative (ERI), extended previous comparative work, including many of the same ecosystems (Megrey et al. 2009c), but with focus on the common surplus production-modeling framework. Our late colleague and friend Bernard Megrey was instrumental in developing the production-modeling approach for these workshops, in fostering the international collaboration, and in enthusiastically promoting the comparative approach to marine ecosystem analysis. We dedicate the TS to him (Moksness et al. 2012).

At the May 2010 workshop, biomass and catch time series data were compiled for 13 Northern Hemisphere ecosystems ranging from the northeast Pacific to the northwest and northeast Atlantic (See Fig. 2 in Link et al. 2012; see also Fu et al. 2012, their Table 1, and Bundy et al. 2012, their Tables 1 & A1). In addition, time series for environmental covariates (e.g. sea surface temperature, the North Atlantic Oscillation), and trophodynamic covariates (e.g. primary production, predator biomass, diet matrices) were assembled for each ecosystem (Bundy et al. 2012, their Tables 2 & A2, Fu et al. 2012, their Table 2). The standardized database built for this project during the first workshop provided the foundation for the comparative analyses presented in this TS. The database, with over 70 000 records and including 466 biological and 162 environmental time series across the 13 ecosystems, is itself a significant contribution to EBFM. At the workshop, experts from each ecosystem identified key environmental covariates and mechanisms for testing, and also assigned species to appropriate aggregate groups (e.g. pelagic vs. benthic feeder, large vs. small size category) for cross-system comparisons. Standardization and quality control of the database was completed simultaneously with initial production model development between workshops.

During the May 2011 workshop, several working groups applied the production models to the data from all of the ecosystems: working groups focused on comparing ecosystems by evaluating empirical data, single species production models, full ecosystem production models, and production models applied at intermediate aggregation levels for habitat, size, feeding functional group, and taxonomic categories. Comparisons were primarily across ecosystems, but also among modeling approaches, aggregation methods, driver types (i.e. fishing, biophysical, trophodynamic) and driver scales (i.e. basin, local).

Results

The comparative modeling and empirical work conducted by workshop attendees and presented in this TS identify emergent trends and common patterns governing fishery productivity in northern hemisphere temperate marine ecosystems. Two papers examine the rich time series data assembled in the database empirically (Fu et al. 2012, Pranovi et al. 2012). Using multivariate approaches, Fu et al. (2012) compared temporal variability in ecosystem indicators derived from biomass or catch data across the ecosystems, finding that catch-based indicators showed consistent trends primarily within ocean basins. Structural equation modeling related the triad of drivers to both biomass- and catch-based ecosystem indicators, revealing that biophysical drivers tended to influence biomass-based indicators, exploitative drivers influenced catch-based indicators, and that trophodynamic drivers had some influence across both biomass- and catch-based indicators (Fu et al. 2012). A potential new ecosystem indicator is presented by Pranovi et al. (2012) who examine cumulative biomass curves by trophic level and their changes through time in all of the ecosystems. Changes in the inflection point and slope of the curves may be used as indicators of community status, with some ecosystems showing trophic stability over time, and others substantial structural changes (Pranovi et al. 2012).

Three studies presented in this TS fit production models to the data from as many of the 13 ecosystems as possible, at various levels of aggregation (Bundy et al. 2012, Holsman et al. 2012, Lucey et al. 2012). All compared a production-modeling approach (i.e. a simple linear regression and/or a dynamic model) with a null model of constant surplus production. Holsman et al. (2012) applied models at the single species level of organization, comparing both cod and herring production across ecosystems. Lucey et al. (2012) applied models at intermediate levels of organization, including habitat-based groups (i.e. demersal and pelagic), size-based groups (i.e. small, medium, and large average adult size), and trophic functional groups (i.e. planktivores, zoopivores — shrimp-feeders, piscivores, and benthivores). Bundy et al. (2012) applied models at the full system level. In nearly all cases, a production-modeling approach provided better fits to the data than the null model across all levels of aggregation. A striking result of all 3 studies was the general similarity of estimated BRPs across ecosystems at each level of organization, a result highlighted in a synthesis paper (Link et al. 2012). Two of these studies also explored whether including system-specific environmental covariates would improve model fits; their results support the hypothesis that environmental covariates affect fisheries production at both the single species and full ecosystem levels (Bundy et al. 2012, Holsman et al. 2012).

Four other contributions focus on fisheries production and management implications, either in particular regions or at a larger scale. Two papers use simulation modeling to address the influence of the triad of drivers on BRPs in 1 or 2 representative ecosystems (Gaichas et al. 2012, Gamble & Link 2012), and 1 study compares the results of fitted production models at the system and single species level within a single ecosystem, the Gulf of Maine (Fogarty et al. 2012). Finally, a synthesis paper examines the implications for EBFM across all of the studies (Link et al. 2012). Simulation modeling was conducted using MS-PROD, a multispecies production model incorporating both competitive and predatory species interactions (Gamble & Link 2009). Gaichas et al. (2012) used MS-PROD, parameterized for two 10-species communities based on Georges Bank and the Gulf of Alaska, as an operating model within a management strategy evaluation (MSE) framework to determine how best to structure aggregate species complexes to achieve the dual objectives of maximizing yield and maintaining biodiversity. Gamble & Link (2012) parameterized MS-PROD for the wider northeast US continental shelf ecosystem, to examine the potential effects of climate change on BRPs. Moving from simulation to model fitting for operational management advice, Fogarty et al. (2012) used the Gulf of Maine ecosystem as a case study comparing the results of a system-level aggregate production model with a set of single species production models, as well as the results of single species stock assessments. That study, as well as the overall synthesis, reiterates that the sum of single species BRPs exceeds any aggregate BRP for the ecosystem (Fogarty et al. 2012, Link et al. 2012), an important overall finding for EBFM.

In summary, the body of work presented in this TS demonstrates that using both production modeling and the comparative approach together makes valuable and rapid progress towards EBFM, whether the aim is a better understanding of the ecosystem, or the provision of operational management advice. The breadth and depth of analyses presented here (which were achieved within a 2-yr timeframe) highlight the utility of relatively simple models combined with long-term time series maintained by the participating international institutions. This body of work also highlights the benefits of collaborative projects where the total profit to be gained is much greater than the sum of the parts (contrasting with findings reported here that multispecies MSY is generally less than the sum of single species MSYs). We expect that this approach will be useful in other areas of the world, especially where data may be limiting but EBFM is equally as important.

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Contribution to the Theme Section 'Comparative analysis of marine fisheries production'

Bernard Megrey: pioneer of Comparative Marine Ecosystem analyses

Erlend Moksness[1], Jason Link[2,*], Ken Drinkwater[3], Sarah Gaichas[4]

[1]Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway
[2]National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, Massachusetts 02543, USA
[3]Institute of Marine Research, Box 1870 Nordnes, 5817 Bergen, Norway
[4]National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, Washington 98115, USA

ABSTRACT: The MEPS Theme Section on 'Comparative Analysis of Marine Fisheries Production' is dedicated to Dr. Bernard Megrey. Dr. Megrey was well known for comparative studies of ecosystems, but his contributions to science were far broader. His pioneering of comparative marine ecosystem studies began long before they achieved a high profile in the field. He played a leading role in a number of international projects comparing marine ecosystems in northern hemisphere countries, and championed the use of simple but robust models for this purpose. He was central in organizing a successful trilateral workshop that modeled stock production in the USA, Canada and Norway. This was followed up by the Surplus Production Modelling Workshop in Woods Hole in 2011, which encompassed a broader range of modeling approaches, as well as additional countries and their associated marine ecosystems. The resulting manuscripts are presented in this Theme Section. Dr. Megrey's flair for bringing together scientists with diverse perspectives led to a cohesiveness among such disparate scientists, resulting in the successful completion of this and related workshops and ultimately the works in this Theme Section.

KEY WORDS: Comparative studies · Fisheries production · Modeling · Memorial

The MEPS Theme Section on 'Comparative Analysis of Marine Fisheries Production' is dedicated to the memory of Dr. Bernard Megrey, whose untimely death in October 2010 significantly set back fisheries science in general, and in particular, the art and science of marine ecosystem comparisons. In addition to comparative ecosystem studies, Bern contributed significantly to wide-ranging areas of fisheries science, including ecosystem modeling, population dynamics, and stock assessments. Much of this article is derived from recent tributes from Ecosystem Studies of Subarctic Seas (ESSAS), the North Pacific Marine Science Organization (PICES) and the Alaska Fisheries Science Center (AFSC), but we also emphasize his pivotal role behind much of the work in this Theme Section.

Bern began his career with the NOAA National Marine Fisheries Service at the AFSC in Seattle, where he developed the first stock assessment for the walleye pollock fishery, which was emerging in the Gulf of Alaska at the time. His work enabled timely forecasts of abundance and biomass to be made to the North Pacific Fishery Management Council. It required innovative analyses of the very short time series that were then available. He subsequently took on the task of integrating assessment data from fishery and research vessels into a more complete assessment that could be used to forecast stock size and composition. Bern was then assigned to the Fisheries Oceanography Coordinated Investigations (FOCI) program where he developed recruitment prediction models. His Gulf of Alaska recruitment

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[*]Corresponding author. Email: jason.link@noaa.gov

prediction model for walleye pollock is one of the few that incorporate both environmental and biological data and that is based on an underlying mechanistic model. Additionally, he helped to implement a series of individual-based models at the AFSC and in other venues, some of which are still in use today.

As a co-chairman of the MODEL Task Team of the PICES/GLOBEC Climate Change and Carrying Capacity (CCCC) Program, Bern was instrumental in the development of the PICES-NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) model. With his leadership, the NEMURO model became an open source public model used by researchers worldwide. His scientific insights were essential for the development of NEMURO, but it was his guidance of the NEMURO 'Mafia', that led to its success in providing a better understanding of marine ecosystems (Kishi et al. 2007). More recently, he was engaged in several national and international efforts to develop integrated end-to-end fisheries ecosystem models.

Bern worked tirelessly for several international organizations, most notably AFS (American Fisheries Society), ICES, GLOBEC (Global Ocean Ecosystem Dynamics) (via ESSAS) and PICES. He served terms as President of the AFS International Fisheries and Computer User sections. The AFS recognized Bern's lifetime achievement in 2009 with the Oscar Elton Sette Award for sustained excellence in marine fishery biology through research, teaching, and/or administration. Posthumously, Bern was given a Wooster Award in 2011 by PICES for his career of sustained excellence in research, teaching, and administration of North Pacific marine science.

Bern was a member of the editorial board of the ICES Journal of Marine Science from 2001 to 2007 and was a member of the ICES Working Group on Data and Information Management. He suggested new Theme Sessions for the Annual Science Conference and regularly presented cutting-edge science there. He was an inaugural member of ESSAS and became the driving force as co-chair of the ESSAS Working Group on Modeling Ecosystem Responses. There, he played a leading role in the development of the End-to-End model based on the NEMURO modeling system. Bern was on the ESSAS Scientific Steering Committee (SSC) and was an enthusiastic supporter of the ESSAS goal of using the comparative approach to gain scientific insights.

Bern also chaired the Technical Committee on Data Exchange (TCODE), led the Marine Ecosystem Model Inter-comparison Project and was a member of the Science Board of PICES. PICES recently recognized his achievements with the 2009 PICES Ocean Monitoring Service Award (jointly awarded to S.A. Macklin) for his work in coordinating, organizing and combining the member countries' meta-databases for the North Pacific. Bern worked hard to promote cooperation between ESSAS, AFS, PICES and ICES, particularly in bridging the divide between Pacific and Atlantic perspectives of how the oceans and fisheries functioned among those groups. Just prior to his death, Bern served as the lead liaison for fisheries issues in the US Mississippi Canyon 252 Command Center in Washington, DC, in response to the oil well blow-out in the Gulf of Mexico.

Bern pioneered marine fishery ecosystem comparative works before these became high profile (Murawski et al. 2010), often by simply contrasting common datasets and simpler models (e.g. Hunt & Megrey 2005, Megrey et al. 2005). Always a big fan of large, international group projects, he was heavily involved in the studies comparing marine ecosystems of Norway and the United States (MENU, endorsed by ESSAS). He helped to organize a MENU Workshop held in Bergen in 2007, led the push to get ICES to sponsor a theme session on 'Comparative marine ecosystem structure and function: descriptors and characteristics' to help highlight the MENU work, co-chaired this session in 2007 in Helsinki, Finland, and was the lead editor of the resulting special volume in Progress in Oceanography (Megrey et al. 2009a, 2009b). Continuing from this work, he helped to organize a trinational workshop on stock production modeling involving the USA, Canada and Norway in Woods Hole in 2010 (Link et al. 2010). The workshop resulted in over 15 presentations at global meetings as varied as AFS, ICES, PICES, ESSAS or IMBER. In this context, he championed the use of simple but robust models to compare ecosystems (e.g. Richards & Megrey 1994, Megrey et al. 2005, Mueter & Megrey 2006). A follow-up workshop was held in Woods Hole in 2011, the Surplus Production Modelling Workshop, expanded to include additional countries and their associated marine ecosystems, as well as a broader range of modeling approaches. The resultant manuscripts from that workshop are presented in this Theme Section.

Bern's global network of colleagues, which he readily shared with others, was of great benefit to the entire marine fisheries ecology community. Of particular note was Bern's concern for young scientists getting established in the field. Remembering his days as a struggling student, he very much appreciated the value of travel grants for students to test the waters in various international forums. He provided significant personal donations to support such efforts, and his family established a memorial fund to support the travel and participation of students in joint ICES/PICES activities such as the Early Career Scientists Conferences). He readily encouraged junior scientists; for many he was their first established collaborator, and he always treated them as respected equals, irrespective of his high standing and decades of experience — an attitude that will be much missed and that warrants emulating. Bern had a reputation for 'getting it done', and his scientific productivity — as measured not only in his numerous publications, but in his many other endeavours as well — was exemplary.

Bern had many friends and colleagues in the scientific world, but his first love was his family. He leaves behind his wife, Ronnette, sons Christopher and Nicholas, daughter Sarah, mother Anna Marie Megrey, brothers Joseph Megrey, Robert Megrey and David Megrey, and sister, Catherine Megrey. Friends and family around the world will miss Bernard's gentle spirit, his smile, and his contagious laughter.

Bern was excellent at bringing together people from disparate backgrounds. It is highly unlikely that the degree of cohesiveness among scientists from so many different perspectives would have been as strong as it was, thus facilitating such productive workshops and international collaborations, without people trusting that Bern was doing the right thing and involving the right people. That comfort and ease of interaction facilitated numerous follow up workshops and ongoing collaborations.

Bern had the analytical gravitas to speak authoritatively. Without being authoritative or pedantic, his depth and breadth of knowledge were very reassuring to the many very different people he collaborated with. Our decision to use production models, often subject to much debate in fisheries science (Mohn 1980, Ludwig & Walters 1985, 1989, NRC 1998, Punt 2003, Mangel 2006), was bolstered by the positive aspects that Bern readily noted and so well articulated (cf. Mueter & Megrey 2006, Link et al. 2010). The potential to compare useful, readily available information, across multiple ecosystems, across multiple drivers, and across multiple levels of biological hierarchy, to both help better understand the fundamentals of how marine ecosystems functioned and in ways that could be of practical use for living marine resource management, was decisive for Bern. He will be sorely missed, but the foundations he laid, and upon which we build with these models and comparisons, will ensure that his influence continues.

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Contribution to the Theme Section 'Comparative analysis of marine fisheries production'

Relative importance of fisheries, trophodynamic and environmental drivers in a series of marine ecosystems

Caihong Fu[1,*], Sarah Gaichas[2], Jason S. Link[3], Alida Bundy[4], Jennifer L. Boldt[1], Adam M. Cook[4], Robert Gamble[3], Kjell Rong Utne[5], Hui Liu[3], Kevin D. Friedland[6]

[1]Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia V9T 6N7, Canada
[2]NOAA, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, Washington 98115, USA
[3]NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, Massachusetts 02543, USA
[4]Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada
[5]Institute of Marine Research, Nordnesgt 33, 5085 Bergen, Norway
[6]NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, Narragansett, Rhode Island 02882, USA

ABSTRACT: Marine ecosystems are influenced by drivers that operate and interact over multiple scales, resulting in nonlinear or abrupt responses to perturbation. Because of the inherent complexity of marine ecosystems, progress towards an understanding of factors that affect fisheries production will be most efficient if researchers adopt a comparative approach across ecosystems using suites of indicators. The goals of this study were to explore a suite of biomass- and catch-based ecosystem response indicators for 9 northern hemisphere ecosystems relative to indices that capture the influence of fisheries, trophodynamic and environmental drivers, and to compare the relative influence of the triad of drivers. Partial least squares regression was used to explore relationships between the ecosystem response indicators and predictor drivers and to estimate the relative importance of each of the triad of drivers. Across ecosystems we have identified a few common observations: (1) environmental drivers, particularly temperature-related independent variables, are most likely related to total system biomass and biomass of specific biological groups (e.g. gadoid or clupeid fishes); (2) trophodynamic drivers are most relevant to the mean trophic level of community and the demersal-to-pelagic biomass ratio; and (3) fisheries drivers tend to be related to the catch-based indicators, such as fishing-in-balance and percent of primary production required to support fisheries. Overall, each of the triad of drivers was important for all ecosystems; however, the relative importance of each driver and the indicators they most affected varied among ecosystems, suggesting that an examination of a suite of indicators and drivers is required. A key finding is that fishing is categorically an important driver, but to explain biomass trends it is very important to consider environmental drivers as well.

KEY WORDS: Marine ecosystems · Ecosystem indicators · Partial least squares regression · Multiple drivers

INTRODUCTION

Living marine resources, particularly those targeted by fisheries, are affected by a triad of drivers: anthropogenic (fisheries), trophodynamic and environmental processes. The interactions of these multiple drivers are complex and are often manifested in nonlinear responses of ecosystems to perturbation (e.g. Hare & Mantua 2000, Scheffer & Carpenter 2003, Steele 2004). These responses put greater demands on management systems for living marine resources, creating a need for more holistic approaches that

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*Email: caihong.fu@dfo-mpo.gc.ca

incorporate multiple species in the ecosystem models and account for multiple drivers. The evaluation of new management systems must also move beyond single-species oriented evaluation based solely on performance of commercial fisheries to become more comprehensive. In an ecosystem context, measures of 'success' of management strategies beyond the human dimension of benefits and trade-offs should be included to evaluate the ability to maintain ecosystem stability and resistance to perturbation, and to maintain ecosystem structure and functioning and sustainability of resource potential (Shin et al. 2010b). These types of measures, known as ecosystem indicators, have received increasing attention in recent years (e.g. Cury & Christensen 2005, Shin & Shannon 2010, Shin et al. 2010a,b).

Ecosystem indicators are generally accepted as tools for evaluating ecosystem status and trends (e.g. Shin & Shannon 2010, Shin et al. 2010a,b), identifying key ecosystem processes (e.g. Ojaveer & Eero 2011), serving as signals that something is happening beyond what is actually measured (NRC 2000), and assessing the impacts of human activities and climate forcing (e.g. Coll et al. 2010, Link et al. 2010b, Ojaveer & Eero 2011). Hundreds of potential ecosystem indicators exist, including environmental, species-based, size-based, trophodynamic and integrated indicators (Cury & Christensen 2005). For example, indicators available for the Northeast US Continental shelf ecosystem include 26 biotic state indicators, 25 indicators of climate and physical environmental change and 18 indicators of human-driven pressure on the ecosystem (Ecosystem Assessment Program 2009). Similarly, information on 59 physical, biological and ecological status and trend indicators and 14 ecosystem-based management indicators are available for US marine ecosystems off Alaska (Zador 2011). For a particular study, a suite of indicators needs to be selected to reflect human activities, ecosystem components and ecosystem attributes (e.g. Jennings 2005, Piet et al. 2008). In this study, we select a suite of indicators to compare ecosystem responses to a triad of external drivers across 9 northern hemisphere ecosystems. The suite of indicators is derived from standard fisheries-independent survey data and fisheries-dependent catch data (e.g. Pauly & Christensen 1995, Christensen 2000, Cury & Christensen 2005, Shin et al. 2010a,b). The triad of drivers considered encompasses fisheries exploitation, trophodynamic interactions and local- and basin-scale environmental factors.

Our objective is to infer cause–effect relationships by examining linkages between the suite of indictors and the triad of drivers. Multiple regression analysis is often applied in this type of investigation (Carrascal et al. 2009), which works well as long as the predictor variables are fairly few and uncorrelated. For instance, Blanchard et al. (2005) used multiple linear regression to relate ecosystem indicators to fishing and temperature drivers. However, the traditional regression approach poses problems when it comes to handling multivariate predictor variables that are correlated and have redundancies. To overcome this problem, researchers often preselect a few predictor variables that are independent based on expert knowledge; however, this process can unknowingly screen out potentially important predictor variables. Another limitation of the traditional regression approach is that it does not allow multiple response variables to be considered at the same time. Just as body condition can be measured in several ways, and health should be assessed as a combination of the several measurements, marine ecosystem condition and health should be investigated using a combination of indicators that reflect different aspects of the ecosystem structure and functioning (Link 2005, 2010). A more inclusive practice is to use multivariate reduction methods such as principal component analysis to derive independent principal components, which are then used in subsequent multiple regression analyses (Wold et al. 2001). However, the derived principal components maximize the covariation among the predictor variables independent of the variation in the response variables and thus they are not likely to be the good predictors for the response variables.

In this study, the ecosystem indicators and the triad of drivers were explored as response and predictor variables, respectively, using partial least squares (PLS) regression, an ideal statistical tool for inferring probable cause–effect interactions between response and predictor variables that overcomes the limitations of the traditional regression approach stated above. Although the application of PLS regression in ecological studies has been uncommon (Carrascal et al. 2009), there is great potential for the use of PLS regression given its properties, and there are a few recent applications of this approach in the field of marine fishery science (e.g. Wells et al. 2008, Friedland et al. 2012). Because marine ecosystems are inherently complex, adopting a comparative approach will expedite the understanding of factors that affect fisheries production (Link et al. 2010a); in particular, comparisons of ecosystem indicators across different ecosystems advance the understanding of ecosystem structure, functioning and state

(Coll et al. 2010, Shannon et al. 2010, Shin et al. 2010b). Such indicator-based comparisons allow contrasts in the structure and functioning of the ecosystems related to their intrinsic features and exploitation history to be developed (Coll et al. 2006). Through multivariate and comparative analysis, we aim to explore the effects of common drivers on ecosystem indicators at the basin scale, compare the relative influence within the triad of drivers among ecosystems and explore the connections between fishing and environmental variability.

MATERIALS AND METHODS

Ecosystems and data sets

The 9 northern hemisphere ecosystems we explored are the eastern Bering Sea, Gulf of Alaska and Hecate Strait in the Pacific Ocean, and the Barents/Norwegian Seas, southern Gulf of St. Lawrence, eastern Scotian Shelf, western Scotian Shelf, Gulf of Maine and Georges Bank in the Atlantic Ocean (see Fig. 2 in Link et al. 2012, this Theme Section). These ecosystems have varied species composition, fishery exploitation histories and environmental influences. A summary of key characteristics of these ecosystems is listed in the supplement (www.int-res.com/articles/suppl/m459p169_supp.pdf). In order to calculate indicators, annual survey biomass and catch time series for the period from 1984 to 2006 were compiled for the 9 ecosystems. The number of species that provided time series data in each ecosystem is given in Table 1. Each species within an ecosystem was then assigned to a specific ecological group based on habitat (demersal and pelagic), feeding guild (planktivore, zoopivore (shrimp and/or euphausiid eater), benthivore, piscivore and omnivore), or taxonomic grouping (clupeid, elasmobranch, pleuronectid, gadoid, *Sebastes*, invertebrates, forage fish and mammals). The trophic level for each species was also obtained either from Ecopath models, if available, or from Fishbase (Froese & Pauly 2011). The trophodynamic and environmental drivers for each system used as predictors in the PLS regression were selected by regional experts who were asked to identify those regional and basin-scale variables that are generally considered to be important drivers of productivity in a given ecosystem (Bundy et al. 2012, Table S2 in their supplement). Available biotic and abiotic time series data compiled for each system included abundance indices of zooplankton and important top-level predators, water temperature, stratification, large-scale climate indices and freshwater discharge (Table 1). All the biomass, catch and trophodynamic and environmental drivers were compiled into a common database for use in this and other comparative studies of fishery production (Link et al. 2010a).

Ecosystem response indicators

Many ecosystem indicators have been proposed to describe ecosystem status and detect fishing effects on ecosystems (e.g. Fulton et al. 2005, Jennings 2005, Link 2005). Here we have focused on a few common ecological indicators derived from survey biomass and catch data, following to some extent the approach of the IndiSeas Project (Shin et al. 2010a). Annual data points from these time series were used as response variables in PLS regression.

We explored 2 common biomass-based indicators: total biomass (B) to indicate ecosystem status, and proportion of predatory fish (%pred$B$) to measure functional diversity of fish in the community and reflect the potential effects of fishing on the functioning of marine food webs (Shin et al. 2010a). In addition, the demersal-to-pelagic fish biomass ratio (D/P) was calculated as an indicator of the processes leading to demersal or pelagic energy pathways (Coll et al. 2010). Biomasses of clupeids (B_{clupeid}) and gadoids (B_{gadoid}) were used as 2 indicators reflecting temporal dynamics of these 2 fish groups, which are represented in all of the ecosystems we compared. We also calculated the mean trophic level of the community (mTLco) based on trophic levels (TL) of all species with available biomass time series, weighted by annual species-specific biomass, to reflect the structure of the community.

For catch-based time series indicators, exploitation rate (denoted as F') was calculated as the ratio of total catch to total biomass in each year aggregated over the same set of species. In addition, we used 3 other commonly used catch-based quantities as response indicators: the mean trophic level of the catch (mTLc), primary production required to sustain fisheries (Pauly & Christensen 1995) and the fishing-in-balance index (Christensen 2000). The mean trophic level of the catch is calculated as the weighted average trophic level of all species included in the catch data, thereby reflecting the fishing strategy in terms of its species selection (Christensen & Walters 2004). The primary production required (PPR) indicator is an estimate of the amount of primary production required to support fishery catch. PPR expresses the full ecosystem ‘cost’ of fisheries and is given by:

Table 1. Number of species in biomass and catch data and trophodynamic and environmental drivers available in 9 ecosystems

No. species		Trophodynamic and environment drivers						
In biomass	In catch	1	2	3	4	5	6	7
Eastern Bering Sea								
58	14	Bcope: abundance index of copepods	sSST: summer average surface water temperature	ice: ice cover index	ONI: oceanic Niño index	NPI: North Pacific index	ALPI: Aleutian low pressure index	PDO: Pacific Decadal Oscillation
Gulf of Alaska								
42	22	sSST: summer average surface water temperature	discharge: April freshwater discharge	ONI: oceanic Niño index	NPI: North Pacific index	ALPI: Aleutian low pressure index	PDO: Pacific Decadal Oscillation	
Hecate Strait								
30	25	Bafl: biomass index of arrowtooth flounder *Atheresthes stomias*	wSST: winter average surface water temperature	wSSH: winter sea surface height	ONI: oceanic Niño index	NPI: North Pacific index	ALPI: Aleutian low pressure index	PDO: Pacific Decadal Oscillation
Barents/Norwegian seas								
8	11	Bzoo: abundance index of zooplankton	Bseal: biomass index of harp seal *Phoca groenlandica*	BS_SST: annual average surface water temperature in Barents Sea	NS_SST: annual average surface water temperature in Norwegian Sea	ice: ice cover index	NAO: North Atlantic Oscillation index	
Southern Gulf of St. Lawrence								
36	29	Bszoo: abundance index of small zooplankton	Blzoo: abundance index of large zooplankton	Bseal: biomass index of grey seal *Halichoerus grypus*	SST: annual average surface water temperature	90mT: fall average water temperature at 60–120 m		
Eastern Scotian Shelf								
42	74	Bseal: biomass index of grey seal	SST: annual average surface water temperature	sBT: summer average water temperature at bottom	50mT: annual average water temperature at 50 m	100mT: annual average water temperature at 100 m	strat: index of stratification	
Western Scotian Shelf								
33	29	SST: annual average surface water temperature	sBT: summer average water temperature at bottom	50mT: annual average water temperature at 50 m	100mT: annual average water temperature at 100 m	strat: index of stratification	BoFstrat: index of stratification, Bay of Fundy	
Gulf of Maine								
27	25	Bzoo: abundance index of zooplankton	SST: average annual surface temperature	NAO: North Atlantic Oscillation	AMO: Atlantic Multidecadal Oscillation			
Georges Bank								
28	26	Bzoo: abundance index of zooplankton	SST: average annual surface temperature	NAO: North Atlantic Oscillation	AMO: Atlantic Multidecadal Oscillation			

$$\mathrm{PPR} = \frac{1}{9} \cdot \sum_i [Y_i(\mathrm{TE})^{\mathrm{TL}_i - 1}]$$

where Y_i is the catch of a given species (or group) i, TL_i is the trophic level of the species i and factor 1/9 is the average conversion coefficient from wet weight to grams of carbon. The constant term TE is the mean energy-transfer efficiency between trophic levels, and the average TE value of 14 for temperate shelves and seas (Libralato et al. 2008) was used for each ecosystem. For comparative purposes, the PPR for each system was scaled by dividing by primary production (P_1) estimated from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) data (Behrenfeld & Falkowski 1997) and averaged over the period from 1998 to 2008, to obtain the percent of primary production required (%PPR = PPR/P_1). For a given %PPR, a fishery with higher TL would have less impact than a fishery with a lower TL owing to the much lower catch; however, for a given TL, a lower %PPR would have less impact than one with a higher %PPR, since the removals would be higher (Tudela et al. 2005).

The fishing-in-balance (FIB) index describes the changes in the primary production required by fisheries over time relative to the initial year (Christensen 2000), and is formulated as:

$$FIB = \ln\left[\frac{\sum_i Y_{it} \cdot \mathrm{TE}^{\mathrm{TL}_i - 1}}{\sum_i Y_{i0} \cdot \mathrm{TE}^{\mathrm{TL}_i - 1}}\right]$$

where Y_{it} is the catch of species i during the year t, Y_{i0} is the catch of species i during the year at the start of a time series and TE and TL are as defined above. The indicator FIB is intended to capture changes in fishing strategies and their impact on system productivity: a positive FIB index indicates that the fishery has expanded and/or bottom-up effects are occurring, and there is more catch than expected; a negative FIB index indicates it is likely that the fishing impact is so high that the ecosystem function is impaired and the ecosystem is less productive owing to excessive fishery removals (Christensen 2000).

Ecosystem drivers

We used a suite of drivers (fisheries, trophodynamic and environmental) as predictor variables. Fisheries drivers were all derived from catch time series for each ecosystem, but we examined fishing in the ecosystem context at the level of comparable aggregate groups based on feeding guilds rather than single species. In a few cases we combined related guilds further (e.g. planktivores and zoopivores) to avoid zero values in some ecosystems. Therefore, our fishing drivers included catch in weight and percentage of total catch for 3 combinations of different feeding guilds: planktivores and zoopivores (PZ, %PZ), piscivores and omnivores (PiO, %PiO) and benthivores, piscivores and omnivores (BPiO, %BPiO). These fishery drivers were considered for each ecosystem as they reflect alternative fishing strategies as well as relative abundance of different feeding guild groups over time.

Trophodynamic drivers included time series generally related to prey and predators of fished species to examine potential bottom-up and top-down effects on fisheries production. A number of studies have reported positive relationships between fish production and primary production (Ware & Thomson 2005, Chassot et al. 2007, Sherman et al. 2009), although the effectiveness of primary production as a predictor of fishery catch is reduced at the global scale (Friedland et al. 2012). Friedland et al. (2012) found significant correlations between mesozooplankton productivity and fisheries yields. Accordingly, we evaluated ecosystem-specific biomass indices of zooplankton and/or top-level predators as trophodynamic drivers for 7 out of the 9 ecosystems in our analyses (see Table 1 for descriptions of each index).

Environmental drivers generally represented some form of thermal or broad-scale oceanographic features considered to be influential in each ecosystem. We included some measure of sea surface temperature (SST) for all ecosystems, although winter, summer or annual SST indices were applied in different ecosystems. Broad-scale climate indices were applied where appropriate to specific ecosystems, including the North Pacific Index (NPI) and Pacific Decadal Oscillation (PDO) in the Pacific Ocean, and the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO) in the Atlantic Ocean (Table 1). Additional environmental variables such as stratification, freshwater discharge and sea ice cover were considered important locally and were therefore included for specific ecosystems, similar to Bundy et al. (2012, their Table S2). Having a different set of trophodynamic and environmental drivers for each ecosystem was appropriate for our statistical analyses, as we analyzed each ecosystem's indicators and drivers independently.

Statistical analyses

PLS regression is essentially a dimension reduction technique that extracts a few latent variables called X-scores from predictor matrix X (size: $n \times m$) that maximize the explained variance in the response matrix Y (size: $n \times p$). The X-scores, denoted by matrix T (size: $n \times l$, where l is the number of components), are linear combinations of the matrix X with coefficient matrix W^* (size: $m \times l$), i.e.

$$T = XW^* \tag{1}$$

The X-scores are predictors of X and also Y (Eqs. 2 & 3 below); i.e. both X and Y are assumed to be, at least partly (aside from residuals), modeled by the same latent variables:

$$X = TP' + E \tag{2}$$

and

$$Y = TQ' + F \tag{3}$$

where P and Q are matrices of coefficients (loadings) with the dimensions of $m \times l$ and $p \times l$, respectively, and E and F are residual matrices. For multivariate Y ($p > 1$), they are the combinations of the corresponding Y-scores (denoted by U with size: $n \times l$) and the loading matrix Q along with a residual matrix G:

$$Y = UQ' + G \tag{4}$$

Because $T = XW^*$, from Eq. (1), Eq. (3) can be rewritten as:

$$Y = XW^*Q' + F = XB + F \tag{5}$$

where B is the coefficient matrix of PLS regression.

All calculations were implemented for each ecosystem independently using packages 'pls', 'plspm', and 'mixOmics' in R (R Development Core Team 2011) for the entire period from 1984 to 2006, a period when both biomass and catch data were available for all ecosystems. Before applying PLS regression, the predictor drivers and ecosystem response indicators were normalized (mean = 0, SD = 1) by applying a Z-transformation. For the PLS regression, the first step is to determine the optimal number of components by testing the predictive significance of models with different numbers of components. The root mean squared errors of prediction (RMSEPs) of each ecosystem response indicator were estimated through leave-one-out cross-validation. In addition, the residuals of the ecosystem response indicators were examined for autocorrelations. Once the optimal number of components was determined, the estimates of the regression coefficient of predictor drivers were corrected based on bootstrapped CIs with the coefficient set to zero if the CI contained zero.

RESULTS

Ecosystem response indicator trends

Biomass-based ecosystem indicators showed some similar trends across ecosystems and also highlighted some key dynamics within ecosystems. During the period 1984 to 2006, total biomass of the eastern Bering Sea and the eastern and western Scotian Shelf showed slight declines due to the reduction of gadoid biomass in the eastern Bering Sea and eastern Scotian Shelf and clupeid biomass in the western Scotian Shelf. In contrast, the total biomass of the Barents/Norwegian Seas and Gulf of Maine increased steadily due to the increase of gadoid biomass and particularly clupeid biomass (Fig. 1). Despite the slight increase of total biomass, the Gulf of Maine experienced a dramatic decline in the proportion of predatory biomass and in the mean trophic level in the community, implying that the community has become more dominated by species at lower trophic levels. In contrast, the Gulf of Alaska experienced steady increases in the proportion of predator biomass, mean trophic level of the community and the demersal-to-pelagic biomass ratio, despite the fact that total biomass showed no increase over the entire period, indicating increased dominance of higher trophic level species in this ecosystem.

Trends in catch-based ecosystem indicators were more variable across ecosystems, but showed consistency within ecosystems. The overall exploitation rate for the eastern Scotian Shelf declined after the early 1990s, and the exploitation rate in the Gulf of Maine decreased over the entire study period. The exploitation rate in the Barents/Norwegian Seas declined in the late 1980s and was stable afterwards (~0.15 yr^{-1}), but there were no clear consistent trends in exploitation rate in the other ecosystems (Fig. 2). The fishing-in-balance indices for southern Gulf of St. Lawrence, eastern Scotian Shelf, western Scotian Shelf, Gulf of Maine and Georges Bank were all negative, indicating high fishing impact. In particular, the fishing-in-balance index of the eastern Scotian Shelf showed a dramatic decline in the early 1990s, suggesting a possible decrease in ecosystem productivity. In contrast, the fishing-in-balance indices for the eastern Bering Sea and Gulf of Alaska were 'balanced', while those of the Barents/Norwegian Seas and Hecate Strait gave positive values with slightly increasing trends. The trajectories of mean trophic level of the catch and the percent primary production required to sustain fisheries were similar to those of

Fig. 1. Trajectories of 6 biomass-based response indicators — total biomass (*B*, t km^{-2}), percent of predatory biomass (%pred*B*), demersal-to-pelagic biomass ratio (*D*/*P*), mean trophic level of community (mTLco), biomass of clupeid (t km^{-2}) and biomass of gadoid (t km^{-2}) — for the period from 1984 to 2006 in 9 ecosystems: the Barents Sea and Norwegian Sea (BSNS), eastern Bering Sea (EBS), Gulf of Alaska (GOA), Hecate Strait (HS), southern Gulf of St. Lawrence (sGOSL), eastern Scotian Shelf (ESS), western Scotian Shelf (WSS), Gulf of Maine (GOM) and Georges Bank (GB). Total biomass and biomass of gadoids for eastern Bering Sea were scaled down from original values by half for better presentation

the fishing-in-balance index for each ecosystem. The increasing trend of mean trophic level of the catch in Hecate Strait reflected a fishery targeting higher trophic level species and reduced Pacific herring *Clupea pallasi* abundance and catches. The dramatic reduction of mean trophic level of the catch in the eastern Scotian Shelf after the early 1990s indicated a shift in fishery strategies that targeted lower trophic level species.

PLS regression diagnostics

The first step in PLS regression is to determine the number of significant components, which indicates the complexity of the model and of the system. Ideally, much variation in the data should be explained with few components. Plots of RMSEPs as a function of the number of components showed that RMSEPs were generally minimized at 1 to 3 components for the majority of the indicators (plots not shown). The goodness of fit of PLS regression is given by the cumulative percent of variance explained (R^2), and R^2 was generally significant for the predictor drivers as well as for the majority of response indicators in most of the ecosystems (Fig. 3). There were a few exceptions to this general result for certain ecosystem response indicators. Mean trophic level of community had consistently low R^2 in all but 2 ecosystems, suggesting that alternative predictor drivers should

Fig. 2. Trajectories of 4 catch-based response indicators — exploitation rate (*F*′), fishing-in-balance (FIB), mean trophic level of catch (mTLc) and percent of primary production required to fisheries (%PPR) — for the period from 1984 to 2006 in 9 ecosystems: the Barents Sea and Norwegian Sea (BSNS), eastern Bering Sea (EBS), Gulf of Alaska (GOA), Hecate Strait (HS), southern Gulf of St. Lawrence (sGOSL), eastern Scotian Shelf (ESS), western Scotian Shelf (WSS), Gulf of Maine (GOM) and Georges Bank (GB)

be identified and included in the model to address changes in ecosystem community structure. On the other hand, the percent of predatory biomass and demersal-to-pelagic biomass ratio indicators were well modeled with rather high R^2 using 3 components in all but one ecosystem. The catch-based indicators, fishing-in-balance and percent primary production required to sustain fisheries, had high R^2 at the first component for all but 2 ecosystems, indicating great explanatory capacity of the first component for these 2 indicators.

The residuals of the ecosystem response indicators were analyzed for autocorrelations, and results showed that the majority of response indicators did not have significant autocorrelation (<0.3, plots not shown) in all but 2 ecosystems. To address the autocorrelations in these 2 ecosystems, the eastern Bering Sea and the Gulf of Alaska, the predictor driver matrix was expanded to include variables with time lags of 1 and 3 yr, respectively. As a result, much smaller RMSEPs, higher R^2, and nonsignificant autocorrelations in the indicator residuals were achieved for the eastern Bering Sea. However, the addition of lagged predictors did not render smaller RMSEPs or lower autocorrelations for the Gulf of Alaska. Instead, the addition of transformed catch (inverse) and environmental data (squared) resulted in much reduced RMSEPs and autocorrelations. For comparison purposes, we only focused on results based on the current (unlagged, normalized) predictor arrays.

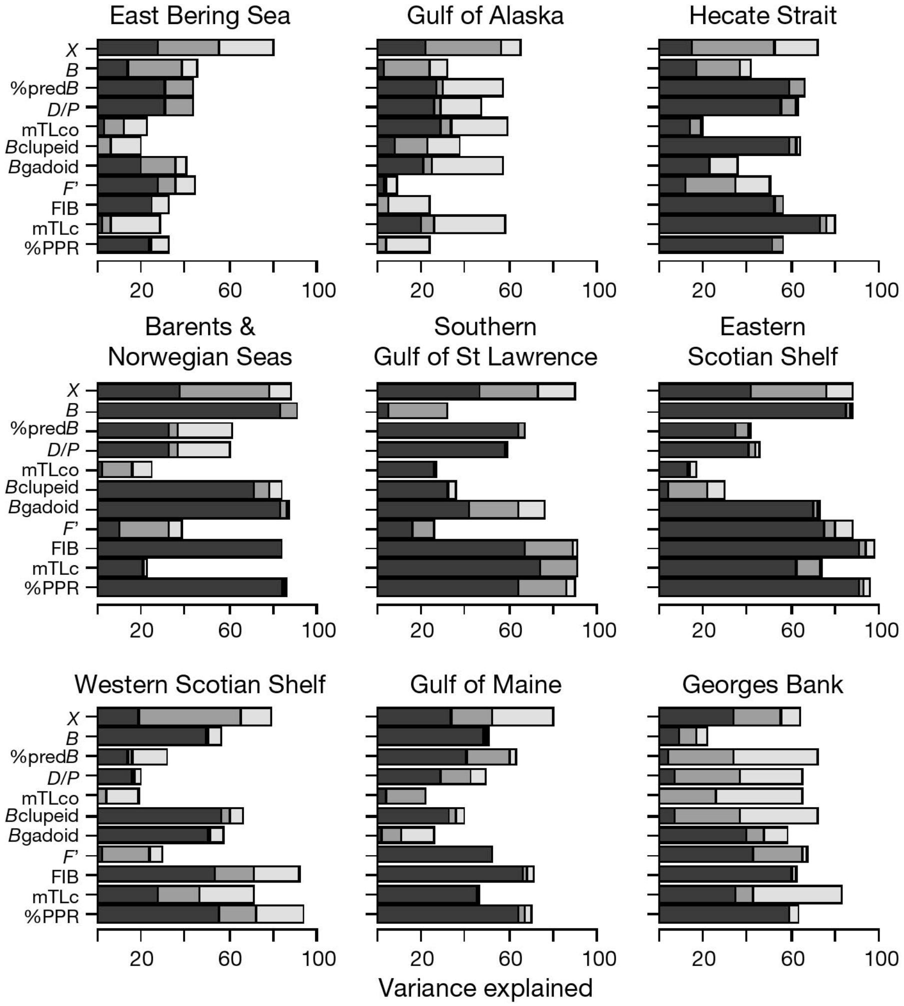

Fig. 3. Percent variance explained by the first 3 components (shown as a stacked histogram, with the first component shown as the darkest shaded bar and the third component as the lightest shaded bar) in overall predictor variables (X) from the PLS analyses and each ecosystem response indicator: total biomass (B), percent of predatory biomass (%pred$B$), demersal-to-pelagic biomass ratio (D/P), mean trophic level of community (mTLco), biomass of clupeids (B_{clupeid}), biomass of gadoids (B_{gadoid}), exploitation rate (F'), fishing in balance (FIB), mean trophic level of catch (mTLc) and percent of primary production required to sustain fisheries (%PPR)

Relative importance of the triad of drivers

The coefficients obtained from PLS regression provide important information on the relative impact (either positive, negative, or none) of each predictor driver on each ecosystem response indicator (results shown in Table 2). The nonzero coefficients show that all of the ecosystems responded to both fisheries and environmental drivers, and all but one responded to available trophodynamic drivers as well. In general, fisheries drivers had the most widespread effect, producing the highest and the most numerous nonzero coefficients in relation to ecosystem response indicators across all systems. However, environmental and trophodynamic drivers were also important to key ecosystem response variables across systems, and some results for biomass-based indicators were surprising. It was particularly striking that in 4 out of the 9 ecosystems (eastern Bering Sea, Gulf of Alaska, southern Gulf of St. Lawrence and western Scotian Shelf), total biomass was not related to any of the fisheries drivers, and in Georges Bank and the Gulf of Maine, total biomass was related only to the percent of piscivores and omnivores in the catch among fisheries drivers. In 3 out of the 9 ecosystems (Barents/Norwegian Seas, southern Gulf of St. Lawrence and Georges Bank), biomass of gadoids was affected by both fisheries and environmental drivers; while in other ecosystems, this indicator was influenced by fisheries and trophodynamic drivers (Gulf of Alaska, Hecate Strait, eastern Scotian Shelf and western Scotian Shelf), by environmental drivers (Gulf of Maine) or not at all (eastern Bering Sea).

Fisheries drivers had the most influence on the catch-based indicators across ecosystems, according to the magnitudes of PLS regression coefficients (Table 2). Of the fisheries drivers, 2 absolute catch indices and 1 catch proportion index appeared most influential across ecosystem response variables and ecosystems: catch of benthivores, piscivores and

Table 2. Corrected coefficients of predictor drivers in relation to ecosystem response indicators including total biomass (*B*), percent of predatory biomass (%pred*B*), demersal-to-pelagic biomass ratio (*D/P*), mean trophic level of community (mTLco), biomass of clupeids ($B_{clupeid}$), biomass of gadoids (B_{gadoid}), exploitation rate (*F'*), fishing-in-balance index (FIB), mean trophic level of catch (mTLc) and percent of primary production required to fisheries (%PPR) for the 9 ecosystems. The predictor drivers for fisheries include percentage and weight of total catch for 3 combinations of different feeding guilds: planktivores and zoopivores (%PZ, PZ), piscivores and omnivores (%PiO, PiO) and benthivores, piscivores and omnivores (%BPiO, BPiO); for trophodynamic and environmental drivers, refer to Table 1 for full names. Nonzero values indicate significance

System	Fisheries driver						Trophodynamic driver		Environmental driver					
Eastern Bering Sea														
Indicator	%PZ	%PiO	%BPiO	PZ	PiO	BPiO	Bcope		sSST	ice	ONI	NPI	ALPI	PDO
B	0	0	0	0	0	0	0		0	0	0	0	0	0
%pred*B*	0	0.56	0	0	0	0	0		0	0	0	0	0	0
D/P	0	0.25	0	0	0	0	0		0.13	0	0	0	−0.19	0
mTLco	0	0	0	0	0	0	0.4		0	0	0	0	0	0
$B_{clupeid}$	−0.26	0	0	0	0.26	0	0		0	0	0	0	0	0
B_{gadoid}	0	0	0	0	0	0	0		0	0	0	0	0	0
F'	0.18	0.29	0	0	−0.18	0	0		0.16	0	0	0	0	0
FIB	0	0.84	0	0	0	0	0		0	0	0	0	0	0
mTLc	0.18	0	0	0	−0.18	−0.18	0		0.14	0	0	0	0	0
%PPR	0	0.93	0	0.26	0	0.37	0		0	0	0	0	0	0
Gulf of Alaska														
Indicator	%PZ	%PiO	%BPiO	PZ	PiO	BPiO			sSST	discharge	ONI	NPI	ALPI	PDO
B	0	0	0	0	0	0			0.63	0	0	0	0	0
%pred*B*	−0.13	0	0.14	0.13	0.13	0.12			0	0	0	0	0	0
D/P	−0.11	0	0.12	0.12	0.11	0.11			0	0	0	0	0	0
mTLco	−0.13	0	0.14	0.13	0.13	0.12			0	0	0	0	0	0
$B_{clupeid}$	0.11	0	−0.12	−0.12	−0.11	−0.12			0	0	0	0	0	0
B_{gadoid}	0.19	0	−0.2	−0.19	−0.19	0			0	0	0	0	0	0
F'	0	0.54	0	0	0	0			0	0	0	0	0	0
FIB	0	0	0	0.31	0	0.33			0	0	0	0	0	0
mTLc	−0.17	−0.17	0.18	0.14	0.17	0.13			0	0	0	0	0	0
%PPR	0	0.81	0	0.46	0	0.5			0	0	0	0	0	0
Hecate Strait														
Indicator	%PZ	%PiO	%BPiO	PZ	PiO	BPiO		Bafl	wSST	wSSH	ONI	NPI	ALPI	PDO
B	0	0.64	−0.37	0	0	0		0	0.54	0	0	0	0	0
%pred*B*	−0.1	0	0.11	0.1	0.1	0.09		0.14	0	0	0	0	0	0.06
D/P	0	0	0	0	0	0		0.76	0	0	0	0	0	0
mTLco	0	0	0	0	0	0		0.55	0	0	0	0	0	0
$B_{clupeid}$	0.12	0.11	−0.14	−0.12	−0.12	−0.11		−0.11	0	0	0	0	0	0
B_{gadoid}	0.08	0.07	−0.1	−0.09	−0.08	−0.07		−0.08	0	0	0	0	0	0
F'	0	0	0	0.61	0	0		0	0	0	0	0	0	0
FIB	−0.13	0	0.13	0.16	0.13	0.17		0.11	0	0.05	0	0	0	0
mTLc	−0.16	−0.13	0.16	0.15	0.16	0.15		0.12	0	0	0	0	0	0
%PPR	0	0.44	0.18	0.52	0	0.51		0	0	0	0	0	0	0
Barents/Norwegian Seas														
Indicator	%PZ	%PiO	%BPiO	PZ	PiO	BPiO	Bzoo	Bseal	BS_SST	NS_SST	ice	NS_NAO		
B	0.13	0.14	−0.1	0	0	0.18	0.09	0.19	0.14	0.26	0	0		
%pred*B*	0	0	0	0	0.7	0	0	0	0	0	0	0		
D/P	0	0	0	0	0.69	0	0	0	0	0	0	0		
mTLco	0	0	0	0	0	0	−0.4	0	−0.36	0	0	0		
$B_{clupeid}$	0	0.15	0	0	0	0.34	0.21	0	0	0	0	0		
B_{gadoid}	0.26	0.22	0	0	0	0.18	0	0	0	0.49	0	0		
F'	0	0	0	0	0	0	−0.14	−0.12	−0.17	−0.19	0	0		
FIB	0.18	0.21	−0.13	0.15	0	0	0	0.17	0	0.18	0.13	0		
mTLc	0	0	0	0	0	0	0	0	0	0.18	0	0		
%PPR	0	0.7	0	0	0	0.21	0	−0.25	0	0.46	0	0		

Table 2 (continued)

System	Fisheries driver						Trophodynamic driver			Environmental driver					
Southern Gulf of St. Lawrence															
Indicator	%PZ	%PiO	%BPiO	PZ	PiO	BPiO	Bcope			sSST	ice	ONI	NPI	ALPI	PDO
B	0	0	0	0	0	0	0	0.24	0	0	0.2				
%pred$B$	0	0	0	0.23	0	0	0	0	−0.31	−0.32	0				
D/P	0	0	0.13	0.14	0	0.12	0	−0.11	−0.17	−0.17	−0.1				
mTLco	0	0	0	0	0	0	0	0	0	−0.49	0				
B_{clupeid}	0	0	0	0	0	0.58	0	0	1.09	0	0				
B_{gadoid}	0	0	0	0.2	0	0.22	0	0	−0.28	0	0.32				
F'	0	0	0	0	0	0	0	−0.18	0	−0.14	0				
FIB	−0.05	0.31	0.21	0.25	0.05	0.21	0	0	−0.25	0	0				
mTLc	−0.12	0	0.17	0.17	0.12	0.16	0.08	0	−0.17	−0.11	0				
%PPR	−0.06	0.38	0.24	0.31	0.06	0.27	0	0	0	0	0				
Eastern Scotian Shelf															
Indicator	%PZ	%PiO	%BPiO	PZ	PiO	BPiO			Bseal	SST	sBT	50mT	100mT	strat	
B	0	0.24	0	0.24	0	0.32			0	0	0	0	0	0	
%pred$B$	0	−0.13	−0.10	−0.11	0	−0.10			0.14	0.09	0.00	0	0	0	
D/P	0	−0.34	0	0	0	0			0.36	0	0	0	0	0	
mTLco	0	0	0	0	0	0			0	0	0	0	0	0	
B_{clupeid}	0	0	0	0	0	0			0	0	0	0	0.15	−0.11	
B_{gadoid}	0	0	0	0.29	0	0.27			0	0	0	0	0	0	
F'	0	0.18	0.18	0.18	0	0.18			−0.16	0	0	0	0	−0.08	
FIB	0	0.21	0.20	0.21	0	0.20			−0.19	0	0	0	0	0	
mTLc	0	0.18	0.17	0.17	0	0.15			−0.19	0	0	0	0	0	
%PPR	0	0.37	0	0.27	0	0.29			0	0	0	0	0	0	
Western Scotian Shelf															
Indicator	%PZ	%PiO	%BPiO	PZ	PiO	BPiO				SST	sBT	50mT	100mT	strat	BoFstrat
B	0	0	0	0	0	0				0	0	0	0	0	0
%pred$B$	−0.1	−0.13	0	−0.13	0.1	−0.13				0	0	0	0	0	0
D/P	0	−0.39	0	0	0	0				0	0	0	0	0	0
mTLco	−0.06	−0.08	0	−0.07	0.06	−0.07				0	0	0	0	0	0
B_{clupeid}	0.14	0.19	0	0.17	−0.15	0.18				0	0	0	0	−0.13	0
B_{gadoid}	0	0	0	0.37	0	0.41				0	0	0	0	0	0
F'	0.14	0.14	0	0.11	−0.14	0.1				0	0	0	0	0	0
FIB	0	0.36	0	0.34	0	0.32				0	0	0	0	0	0
mTLc	0.2	0.19	0.13	0.21	−0.19	0.16				0	0	0	0	0	0
%PPR	0.16	0.25	0	0.24	−0.16	0.25				0	0	0	0	−0.07	0
Gulf of Maine															
Indicator	%PZ	%PiO	%BPiO	PZ	PiO	BPiO	Bzoo			SST	NAO	AMO			
B	0	0.18	0	0	0	0	0			0	0	0			
%pred$B$	0	0	0	0	0	0.43	0			0	0	−0.42			
D/P	−0.13	0	0.09	0.1	0.13	0.15	0			0	0	−0.13			
mTLco	−0.15	−0.17	0.12	0	0.15	0	0			0	0	0			
B_{clupeid}	0.18	0.16	−0.16	0	−0.18	0	0			0	0	0.15			
B_{gadoid}	0	0	0	0	0	0	0			0.39	0	0			
F'	0	0	0	0.24	0	0.24	0			0	0	−0.26			
FIB	−0.12	0	0.14	0.18	0.12	0.17	0			0	0	−0.17			
mTLc	−0.17	−0.16	0.17	0.1	0.17	0.1	0			0	0	−0.13			
%PPR	0	0	0	0.33	0	0.31	0			0	0	−0.31			
Georges Bank															
Indicator	%PZ	%PiO	%BPiO	PZ	PiO	BPiO	Bzoo			SST	NAO	AMO			
B	0	0.88	0	0	0	0	0			0.58	−0.31	0			
%pred$B$	−0.19	−0.18	0.14	0.1	0.19	0.11	0			0	0	0			
D/P	−0.41	0	0	0	0.41	0	0			0	0	0			
mTLco	−0.18	−0.21	0	0	0.18	0	−0.06			0	0	0			
B_{clupeid}	0.24	0.24	−0.21	0	−0.24	0	0			0	0	0			
B_{gadoid}	−0.19	−0.28	−0.11	−0.2	0.19	0	0			0	0	0.3			
F'	0	0	0	0.18	0	0	0			−0.2	0.19	−0.22			
FIB	0	0	0.25	0.33	0	0.34	0			0	0	0			
mTLc	0	0	0.9	0	0	0	0			0	0	0			
%PPR	0	0.19	0	0.64	0	0.41	0			0	0	0			

omnivores; catch of planktivores and zoopivores; and the proportion of piscivores and omnivores in the catch. The percent primary production required to sustain fisheries was always affected by at least 2 of these fisheries drivers, and it was most closely related to the percent of piscivores and omnivores in the catch for 6 out of the 9 ecosystems (Barents/Norwegian Seas, eastern Bering Sea, Gulf of Alaska, eastern Scotian Shelf, western Scotian Shelf and southern Gulf of St. Lawrence). The same set of drivers was also most influential on the fishing-in-balance index, although individual driver effects were mixed. The percent of piscivores and omnivores in the catch influenced this index most in the Barents/Norwegian Seas, eastern Bering Sea, western Scotian Shelf and southern Gulf of St. Lawrence, but the same driver had no influence on the fisheries-in-balance index for another 4 ecosystems (Hecate Strait, Gulf of Alaska, Georges Bank and Gulf of Maine) where the absolute catch of benthivores, piscivores and omnivores was most relevant. In 4 systems (Gulf of Alaska, Hecate Strait, western Scotian Shelf and Gulf of Maine), mean trophic level of catch was affected by all of the fisheries drivers, whereas in Barents/Norwegian Seas, there were no apparent fisheries effects on this index.

Environmental drivers, particularly temperature-related independent variables (e.g. SST) were also important across all ecosystems, with high coefficients in relation to biomass-based ecosystem response indicators. In particular, total biomass (i.e. Barents/Norwegian Seas, Gulf of Alaska, Hecate Strait, southern Gulf of St. Lawrence and Georges Bank), biomass of gadoids (i.e. Barents/Norwegian Seas, southern Gulf of St. Lawrence, Georges Bank and Gulf of Maine), biomass of clupeids (eastern Scotian Shelf, western Scotian Shelf and Gulf of Maine) and percent of predatory biomass (eastern Scotian Shelf, southern Gulf of St. Lawrence and Gulf of Maine) appeared to be at least partially environmentally driven.

Although trophodynamic driver time series were unavailable in several ecosystems, and less numerous across all ecosystems than fisheries or environmental drivers, we note that their coefficients are of similar magnitude to the other drivers in all of the cases where they could be included. Trophodynamic drivers had the highest coefficients in relation to mean trophic level in the community (Barents/Norwegian Seas, eastern Bering Sea and Georges Bank), demersal-to-pelagic biomass ratio (Hecate Strait and eastern Scotian Shelf) and biomass of clupeids (southern Gulf of St. Lawrence).

DISCUSSION

This is the first application of PLS regression for modeling the relationships between ecosystem indicators and the triad of drivers: fisheries, trophodynamic and environmental. The results of our PLS regression modeling have provided important insights into the relative importance of the triad of drivers affecting the dynamics of ecosystem indicators, outlined here and detailed below. First, the full triad of drivers needs to be considered to understand fishery production — across 9 diverse northern hemisphere ecosystems, none were influenced by only a single driver type. We found that fishing is an important driver across all ecosystems, that environmental drivers are often more important to ecosystem biomass indicators than fishing drivers and that trophodynamic drivers can be very influential in individual ecosystems, despite a general lack of time series data for this type of driver. Within individual ecosystems, the relative importance of the triad of drivers is context dependent. This work clearly illustrates the value of long-term ecological time series combined with the comparative approach in ecological investigations.

Empirical evidence that the triad of drivers influence fisheries production

It is clear from our results that fisheries, trophodynamic and environmental drivers shape critical aspects of fishery production. Across 9 ecosystems spanning the north Pacific and Atlantic ocean basins from subarctic to temperate regions, all showed evidence that multiple classes of drivers influence ecosystem responses. While this result may seem intuitive from an ecological standpoint, fisheries production investigations have often focused on a single driver type, most often either fishing or the environment. This dichotomy was illustrated most famously for single-species production in the Thompson–Burkenroad debate of the 1950s, where Thompson maintained that changes in Pacific halibut *Hippoglossus stenolepis* populations were directly attributable to changes in fishing, while Burkenroad argued that 'natural causes' drove population dynamics (Beverton & Holt 1957, Skud 1975). Although most current arguments regarding drivers of production are not this extreme, it is still common to have environmental and fisheries effects on population and ecosystem productivity studied separately (e.g. Link 2010: most standard stock assessments ignore environment/

trophodynamics while biology/ecology investigations ignore fishing). Based on our results and those of many others (e.g. Blanchard et al. 2010, Shannon et al. 2010, Shin et al. 2010a,b, Link et al. 2010b), these lines of investigation should be integrated.

The importance of fishing as a driver of exploited marine ecosystem dynamics is not surprising, but our results show fishing within the context of a full suite of drivers. While fisheries drivers had the most consistent influence on the catch-based ecosystem indicators across all ecosystems, with clear influence on biomass-based indicators in many systems, the coefficients were often of a similar magnitude to those estimated for environmental or trophodynamic drivers on the same indicators, suggesting a similar level of influence. However, the influence of fishing was not always observed at the full-ecosystem level: in 4 out of the 9 ecosystems, total biomass was not related to any of the fisheries drivers (in 2 of those systems, it was unrelated to any of the drivers). While some of these results may arise from differences among ecosystems in the availability of time series for constructing ecosystem response variables, the general implication that fisheries are important but not exclusive drivers of production remains clear.

Despite the clear importance of fisheries as drivers of ecosystem productivity, our results demonstrate that environmental drivers may be even more influential on ecosystem attributes related to biomass. While some environmental drivers showed little influence on the ecosystem response indicators (particularly for the ONI and NPI indices in the Pacific ecosystems), high (>0.3) coefficients showed the strong influence of SST on one or more biomass-based indicators for 6 of the 9 systems. This result suggests that climate-driven changes in SST may have important ecosystem-level effects, reinforcing the need to monitor environmental as well as fishery drivers in assessing marine ecosystems.

Trophodynamic drivers were clearly important in affecting ecosystems, exhibiting some of the highest influence on ecosystem response indicators in several systems. Apex predator time series showed particularly high influence over both biomass and catch-based ecosystem indicators in 3 of the 4 ecosystems where they were included. Although zooplankton time series were rare, when available, they showed an influence on ecosystem response similar to that of fisheries. These results suggest that further work to assemble time series representing major bottom-up and top-down trophodynamic drivers in a wider range of ecosystems will result in better understanding of ecosystem productivity. Further, improving the availability of trophodynamic drivers, including biomass of mesozooplankton and top-level predators, may improve our ability to explain changes in the mean trophic level of the community, an indicator that is regarded as important (Libralato et al. 2008, Shin et al. 2010a), but was largely unexplained in our analysis.

Context dependence of driver importance

While there were similarities across ecosystems with respect to the general importance of all 3 driver types, it was clear from our results that contiguous ecosystems may not always respond synchronously to common drivers, regardless of driver type. This suggests that the relative importance of the triad of drivers will be context dependent, with local histories modulating broad-scale, basin-level drivers, and with key trophodynamic and environmental drivers likely to be system specific. Some basin-scale patterns were apparent from our results, probably owing to some common ecosystem context across the ecosystems, with potential implications for fisheries management. For example, the negative and declining trends in the fishing-in-balance indices of the eastern Atlantic ecosystems in the 1990s provided a warning that the functioning of these ecosystems had been impaired by the impacts of fishing. The reduction of mean trophic level of catch in these 6 ecosystems highlighted an additional concern that the fishing patterns had ‘fished down the foodweb’, which can indicate the loss of higher trophic level species, with consequent impacts on the ecosystem vulnerability (Pauly & Watson 2005, Bundy et al. 2009). Fortunately, the similarly decreasing trend in percent of primary production required to sustain fisheries indicated that more cautious fisheries management strategies have operated in the last decade.

Our results for the remaining ecosystems further demonstrate the context dependence of driver importance. In the Pacific Ocean, ecosystems either showed balanced (i.e. eastern Bering Sea and Gulf of Alaska) or a positive and slightly increasing trend (Hecate Strait) in the fishing-in-balance indices. The increasing trend of mean trophic level of the catch in Hecate Strait indicates that higher trophic level species are being targeted, since catches of Pacific herring declined and no longer comprise the majority of the commercially caught fish, resulting in exploitation that is more balanced across trophic levels. In the Barents/Norwegian Seas, the fishing-in-balance index started to increase after 1990 indicating fishery expansion in the last 2 decades; Atlantic herring *Clupea harengus* in the Norwegian Sea had recovered and the fishery increased to take advantage of this increased productivity (Holst et al. 2002). Also of note is that our analysis suggests the presence of lags in the response of ecosystems to changes in the intensity of any of the drivers. For example fishing activity has been reduced on the eastern Scotian Shelf, yet dramatic reductions of mean trophic level of the catch along with other indicators such as total biomass and percent primary production required in the eastern Scotian Shelf were still observed (Bundy et al. 2005).

Overall, comparisons of 10 indicators across 9 northern hemisphere ecosystems indicated that different ecosystem indicators responded to the triad of drivers differently, and it may be necessary to further include more ecosystem-specific indicators in order to better understand the different impacts from multiple drivers (see below). Each of the triad of drivers was important for all ecosystems; however, the relative importance of each driver and the indicators they most affected varied among ecosystems, reinforcing the finding that an examination of a suite of indicators and drivers is required. Further analyses like PLS regression modeling and exploration is warranted for each ecosystem in order to identify additional driver variables and improve model predictive ability.

Implications for ecosystem-based management

Marine ecosystems are inherently complex, influenced by a triad of fisheries, trophodynamic and environmental drivers, and such complexity requires that the management of marine fisheries adopt a more holistic approach. Correspondingly, ecosystem-based fisheries management (EBFM) has been advocated to account for both fishing and environmental processes, in conjunction with species interactions when formulating fisheries management advice (e.g. Pikitch et al. 2004, Sissenwine & Murawski 2004, Link 2010). To support the implementation of EBFM, it is important to develop and monitor indicators to assess ecosystem status and the effectiveness of management strategies (Cury & Christensen 2005, Shin et al. 2010b). Further, a standardized set of ecosystem indicators that can be applied across ecosystems may be desirable as a basis for EBFM (e.g. Shin et al. 2010b). Travers et al. (2006) showed that indicators did not always vary as predicted from first principles because of indirect effects of fishing on the different components of the ecosystem. Consequently, the fishing configuration (species targeted, fishing intensity) and the type of community should be incorporated into the development and evaluation of ecosystem indicators.

Our results suggest that EBFM should focus on considering the effects of fishing on ecosystem indicators as a standard approach across ecosystems, while component-specific ecosystem indicators should be tailored to individual ecosystems. We explored ecologically oriented, component-specific indicators, such as biomass of gadoids, biomass of clupeids and the demersal-to-pelagic biomass ratio in addition to the commonly used integrative indicators such as total biomass, mean trophic level in the catch, mean trophic level in the community, fishing in balance and percent of primary production required to sustain fisheries. Likewise, we examined component-specific fisheries drivers including the catch and catch percentages of certain aggregate groups (e.g. catch and catch percentage of planktivores and zoopivores). We found that the component-specific biomass indicators were sensitive to the suite of drivers in some ecosystems, but were not universally sensitive indicators across all ecosystems. However, component-specific fisheries drivers did produce significant responses across ecosystems and ecosystem indicators.

Although our main focus was a comparison across ecosystems, EBFM is implemented within particular ecosystems such that further augmentation of the standardized indicator approach and the drivers considered may be necessary. For example, we limited anthropogenic drivers to fishing only, since fishing has been recognized as the predominant factor influencing ecosystem dynamics on a global scale (e.g. Jackson et al. 2001, Pauly et al. 2002). While fishing was clearly influential across ecosystems, on a regional scale, other anthropogenic impacts, such as coastal development and urbanization, pollution or other human uses, should be included as drivers when appropriate for regional EBFM applications, along with any additional ecosystem response indicators appropriate to these drivers.

Finally, this work again shows the importance of developing and maintaining time series for EBFM related not just to fished species but to their key predators and prey and to key environmental drivers that are relevant to each ecosystem. Our convincing empirical evidence for the importance of the triad of drivers to fishery production is based on the long-term scientific monitoring efforts of multiple agencies and institutions across a variety of regions. However, even with this data set it was difficult to explain some proposed universal ecosystem indicators such as trophic level of the community because time series on zooplankton and apex predators were not available in all ecosystems. For EBFM to be successful, maintenance of current ecological data sets is critical. In addition, as key ecosystem indicators are identified, testing the relationships between these indicators and available driving time series may identify new monitoring necessary to support EBFM.

CONCLUSIONS

It is crucial to search for empirical correlations between ecosystem indicators and drivers in the process of EBFM where appropriate indicators have to be selected and applied rigorously, although doing so has largely been neglected (Daan 2005). Through PLS regression modeling of the relationships between ecosystem indicators and the triad of fisheries, trophodynamic and environmental drivers, we identified common themes shared by all the ecosystems studied in terms of the relative importance of the triad of drivers. These common themes were: (1) environmental drivers, particularly temperature-related independent indicators (e.g. SST), affected all systems, as found by Bundy et al. (2012), and were most related to one of 3 biomass indicators; (2) trophodynamic drivers were related to measures of biotic community structure; (3) the fisheries drivers (as would be expected) tended to be most related to the catch-based indicators, yet had no impact on total system biomass in 4 out of the 9 ecosystems. These results suggest that a suite of both standardized and ecosystem-specific indicators are be needed to reflect the different impacts from fisheries, trophodynamic and environmental drivers regardless of the ecosystem being investigated.

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Contribution to the Theme Section 'Comparative analysis of marine fisheries production'

Trophic-level determinants of biomass accumulation in marine ecosystems

Fabio Pranovi[1,*], Jason Link[2], Caihong Fu[3], Adam M. Cook[4], Hui Liu[2], Sarah Gaichas[5], Kevin D. Friedland[6], Kjell Rong Utne[7], Hugues P. Benoît[8]

[1]Department of Environmental Sciences, Informatics and Statistics, University Ca' Foscari, Venice, Castello 2737/b 30122, Venice, Italy
[2]NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, Massachusetts 02543, USA
[3]Pacific Biological Station, Nanaimo, British Columbia V9T 6N7, Canada
[4]Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada
[5]NOAA, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, Washington 98115, USA
[6]NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, Narragansett, Rhode Island 02882, USA
[7]Institute of Marine Research, Nordnesgt 33, 5085 Bergen, Norway
[8]Gulf Fisheries Centre, Fisheries and Oceans Canada, Moncton, New Brunswick E1C 9B6, Canada

ABSTRACT: Metrics representative of key ecosystem processes are required for monitoring and understanding system dynamics, as a function of ecosystem-based fisheries management (EBFM). Useful properties of such indicators should include the ability to capture the range of variation in ecosystem responses to a range of pressures, including anthropogenic (e.g. exploitation pressures) and environmental (e.g. climate pressures), as well as indirect effects (e.g. those related to food web processes). Examining modifications in ecological processes induced by structural changes, however, requires caution because of the inherent uncertainty, long feedback times, and highly nonlinear ecosystem responses to external perturbations. Yet trophodynamic indicators are able to capture important changes in marine ecosystem function as community structures have been altered. One promising family of such metrics explores the changing biomass accumulation in the middle trophic levels (TLs) of marine ecosystems. Here we compared cumulative biomass curves across TLs for a range of northern hemisphere temperate and boreal ecosystems. Our results confirm that sigmoidal patterns are consistent across different ecosystems and, on a broad scale, can be used to detect factors that most influence shifts in the cumulative biomass–TL curves. We conclude that the sigmoidal relationship of biomass accumulation curves over TLs could be another possible indicator useful for the implementation of EBFM.

KEY WORDS: Marine ecosystems · Fishing impact · Trophodynamic indicators · Trophic level · Cumulative biomass curve · Environmental factors

INTRODUCTION

Implementation of ecosystem-based fisheries management (EBFM) requires information pertaining to the structure and function of the biotic communities within an ecosystem. To use such information, metrics representative of key processes are required, as is establishing thresholds for them from which management actions can be triggered. There is a growing body of work on indicators germane to fishing pressures and responses (Degnbol & Jarre 2004, Cury & Christensen 2005, Link 2005, Rice & Rochet 2005, Bundy et al. 2010, Coll et al. 2010, Link et al. 2010a) as well as the establishment of indicators and thresh-

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*Email: fpranovi@unive.it

olds that delineate ecosystem overfishing (EOF; Tudela et al. 2005, Coll et al. 2008, 2010, Libralato et al. 2008, Link et al. 2010a, Shin et al. 2010a). Useful properties of such indicators include being responsive to variation in a diversity of specific pressures including anthropogenic (e.g. exploitation pressure), environmental (e.g. climate), and trophodynamic (ecological interactions). This 'triad' of drivers (Link et al. 2012, this Theme Section [TS]) can significantly impact the production of fisheries in an ecosystem, and developing suites of metrics that would indicate when such production was being altered is valuable.

Among this triad of drivers, 2 are external to a system (anthropogenic and environmental) and can have a strong influence over the third driver, the trophodynamic features of an ecosystem. Often these impacts result from changes to the structure of biotic communities in an ecosystem. Examining modifications in ecological processes induced by structural changes, as caused by these external perturbations, requires caution because of the inherent uncertainty, long feedback times, and nonlinearity of ecosystem responses to external perturbations (Holling et al. 1995). A comparative approach is needed to establish what are normal and what are extreme fluctuations in marine ecosystems, and to establish ranges of thresholds in response to these fluctuations such that they are useful for EBFM (Piatt et al. 2007, Murawski et al. 2009, Link et al. 2010b). Ideally, such a comparative approach should encompass a multi-species, multi-region, and multi-trophic level set of conditions.

Since Odum & Heald (1975) described fractional trophic levels (TLs), the use of an energetic context for evaluating ecosystem function has been widely developed. Trophodynamic studies have elucidated important responses in marine ecosystem functioning as community structure has been altered (e.g. Pitcher & Cochrane 2002, Coll et al. 2010, Shannon et al. 2010, Shin et al. 2010b). Many of these papers have specifically examined such responses with respect to the impacts of fishing, serving as first attempts to delineate EOF (e.g. Pauly et al. 2000, Gascuel et al. 2005, 2008, Coll et al. 2008, Libralato et al. 2008). These trophodynamic measures show notable promise of being robust EOF measures that capture changes to the dynamics of the major processes constituting ecosystem function.

In this trophodynamic context, accumulation of biomass has been documented for many marine food webs, with the middle TLs exhibiting the largest increase in cumulative biomass for a system (Gascuel et al. 2005, Link et al. 2009a). Changes to this accumulation may reflect shifts in ecosystem structure and function, as well as represent important considerations for management thresholds. How robust and consistent this accumulation of biomass is as a general feature of marine ecosystems is unknown. Here we compared such cumulative biomass curves across TLs for a range of northern hemisphere temperate and boreal ecosystems. Our objectives were to evaluate the consistency of this suspected pattern across different ecosystems and, if the pattern held, to examine those broad-scale factors that most influence temporal shifts in the cumulative biomass–TL (cumB–TL) curves.

MATERIALS AND METHODS

Ecosystems and data sets

The key characteristics of the 10 compared ecosystems, in terms of type of system, main changes over the time, and key environmental factors, are listed in Table 1, along with their abbreviations, and a map of their location is given in Fig. 2 of Link et al. (2012). Annual biomass for each species is contained in the CAMEO database (Link et al. 2010b), and the species included in the calculation for each ecosystem are listed in Table 2. It is worth noting that for some ecosystems, the database comprises not just fish species, but also different groups of invertebrates. Biomass estimates were obtained from stock assessments when available or from research surveys. Stock assessment estimates of biomass typically corresponded to the exploitable portion of total biomass, assuming knife-edge recruitment. Swept-area estimates of survey biomass were expanded to the total area of the ecosystem and were corrected for catchability when possible (for major details, refer to Link et al. 2010b).

Trophic spectra

The trophic spectra analysis, i.e. the distribution of an ecological property, such as biomass, along TLs, has been proposed as an indicator to assess the effect of fishing activities on the ecosystem structure (Gascuel et al. 2005). Studying the trophic structure of fish communities (but also of taxonomically larger biological communities) involves species aggregation based on trophic similarities (Bozec et al. 2005). As highlighted by Libralato & Solidoro (2010), a possible critical issue in the trophic spectra analysis is related to the method used to distribute the biomass value of each species/group over a continuum of TLs. Due to variability in species diet that generally changes during life history (e.g. Jennings et al. 2002a) and the lack of dietary information for many fish species, the trophic position of a species is better characterized by a range of fractional TLs rather than a single value.

Table 1. Key characteristics of 10 ecosystems; for references about ecosystem changes over time and key environmental influences, see Fu et al. (2012, this Theme Section, their supplementary material). References reported here refer to EwE models.TL: trophic level

Ecosystem (Source)	Important changes	Key environmental influences
Transitional between Arctic and sub Arctic		
EBS: Eastern Bering Sea, USA (Aydin et al. 2007)	A majority of commercial fishery tonnage depends on walleye pollock production, which in turn is hypothesized to be closely tied to climate and sea ice dynamics. A recent stretch of anomalously warm years with early ice retreat resulted in low zooplankton biomass and poor pollock production 2001–2005, while cooler years with late ice retreat 2007–2010 resulted in higher zooplankton biomass, improved pollock production.	This region is influenced by the El Niño-Southern Oscillation (ENSO) and the Arctic Oscillation. These climate drivers combined with local conditions influence the timing of ice formation and retreat on the Bering Sea shelf, which is critical to setting up conditions for biological productivity across most TLs. Warm conditions associated with early ice retreat and late water column stratification favor later zooplankton blooms and more pelagic production, while in cold years with late ice retreat, stratification happens immediately, promoting blooms that sink to the benthic energy food web.
Downwelling		
GOA: Gulf of Alaska (Aydin et al. 2007)	Large-scale groundfish and crab fishing began in 1960; groundfish fishing continues to the present, while crab and shrimp fisheries declined around 1980 and never recovered. A major change in community composition at multiple TLs was observed around 1977 and has been attributed to a climate regime shift. However, physical mechanisms driving dynamics have proven elusive in the GOA. Arrowtooth flounder populations have increased since the 1960s, while pollock peaked and declined in that time.	The Pacific Decadal Oscillation is an atmosphere–ocean pattern observed across the North Pacific and linked to zooplankton and salmon productivity in the oceanic GOA. Local weather patterns are also influenced by ENSO. Locally varying conditions lead to complex and dynamic influences in various regions of the continental shelf.
HS: Hecate Strait, Canada (Ainsworth et al. 2002)	Groundfish fisheries were introduced in the 1970s. Most groundfish species of limited commercial value that are caught primarily as bycatch in groundfish fisheries showed an increasing trend over the entire time series with an approximate 4-fold increase in biomass. Two other groups (12 groundfish species) showed an initial period of increase, followed by a decline to the late 1990s, and an increase in the early 2000s. A final group that included Pacific cod and spiny dogfish showed a downward trend throughout the time series. Trends in biomass of commercially important groundfish species generally correspond to trends in fishing effort and a continuing increase in primary and secondary production.	Enrichment: wind-driven upwelling (weakening downwelling), estuarine flow of FW runoff, tidal and wind mixing. Initiation: shallow banks limit depth of mixing (localized effect). Southerly winds dominate in winter; conversely, in summer, relaxation of downwelling winds produces a surface offshore flow and a deep onshore flow.
Temperate-boreal		
NL: Newfoundland & Labrador (Pitcher et al. 2002)	The 1985–1993 fish collapses led to a fishing moratorium in 1992. At the same time, other fisheries (notably crab) are experiencing record yields.	Characterized by a wide and relatively shallow continental shelf transected in places by deeper trenches. Ocean circulation is dominated by the southerly flowing and cold Labrador current and its interaction with the warm Gulf Stream.

Table 1 (continued)

Ecosystem (Source)	Important changes	Key environmental influences
SGOSL: Southern Gulf of Saint Lawrence (Morissette et al. 2003)	Since the 1950s, exploitation of groundfish has been intense. In the early 1990s, the cod stock collapsed, other groundfish species experienced serious declines, and the ecosystem switched from one dominated by demersal fish to one dominated by forage species such as sand lance, herring, and invertebrates such as shrimp, snow crab, and clams. There have been significant fishing impacts with decreases in fish size, TL, and proportion of predatory fish.	The Gulf of St. Lawrence is considered an inland sea. With a drainage basin that includes the Great Lakes, the gulf receives more than half of the freshwater inputs from the Atlantic coast of North America. The SGOSL has the farthest regular annual extension of sea ice in the north Atlantic during winter, yet largely the warmest surface water temperatures in Atlantic Canada during the summer.
Temperate		
ESS: Eastern Scotian Shelf (Bundy 2005)	In the early 1990s, the cod stock collapsed, other groundfish species experienced serious declines, and the ecosystem switched from one dominated by demersal fish to one dominated by forage species such as sand lance, herring, and invertebrates such as shrimp, snow crab, and clams. In addition, the grey seal population increased exponentially since the early 1970s. There have been significant fishing impacts with decreases in fish size, TL, and proportion of predatory fish.	The hydrographic environment of the Scotian Shelf is governed largely by its location near the confluence of 3 major currents, a Shelf current, which brings cool fresh water primarily from the Gulf of St. Lawrence; the Labrador Current, which brings cold fresh water from the north along the edge of the shelf; and the Gulf Stream, which brings warm salty water from the south. Shelf bottom is also an important factor affecting the hydrographic environment.
WSS: Western Scotian Shelf (Araújo & Bundy 2011)	This system has seen changes in species composition, with reductions in the biomass of groundfish and flatfish and increases in some invertebrates. These changes have been accompanied by reductions in mean weight and length at age for some key commercial stock. These changes are not as severe as those observed on the ESS.	The WSS is subject to a similar hydrographic environment to the ESS. However, it is more subject to the influence of the Gulf Stream, which brings warm salty water from the south.
GB: Georges Bank (Link et al. 2006, 2008)	The system changed from one dominated by flatfish and gadids to one dominated by small pelagics and elasmobranchs. Also, the community shifted from demersal to pelagic. The major perturbations were the arrival and subsequent departure of the distant water (international) fleets with an estimated 50% decline in fish biomass during this time period; and the 200 mile (~320 km) limit extended jurisdiction in 1977 combined with modernization and increased capacity of the domestic fleet-reducing groundfish to historically low levels. Recently there has also been a documented shift in some fish populations, likely due to change in temperature. Zooplankton composition shifted between the 1980s and 1990s coinciding with a major change in surface layer salinity.	Offshore upwelling along the shelf–slope break, vigorous tidal mixing, and the generally clockwise pattern of its currents concentrates nutrients on GB, making it highly productive. Periods of stratification can occur seasonally and in localized areas, which can temporarily interrupt the nutrient cycle.
GOM: Gulf of Maine (Link et al. 2006, 2008)	As in GB above	Movement of deep slope water into the GOM through the northeast channel which carries a steady supply of nutrients, which is interrupted by summer stratification. Nutrient-poor Labrador Shelf water is occasionally transported from the north by intense negative North Atlantic Oscillation (NAO), and intrusion of fresh water from ice melting in the Gulf of St. Lawrence and Arctic has recently occurred.

Table 1 (continued)

Ecosystem (Source)	Important changes	Key environmental influences
Upwelling		
BSNS: Barents Sea/ Norwegian Sea (Gaichas et al. 2009, Skaret & Pitcher 2012)	The herring stock collapsed in the late 1960s and did not recover fully until the 1990s. There have been 3 collapses of the capelin stock (1985, 1993, 2003), all followed by a rapid recovery of the stock. There was increased abundance of pelagic fish in the Norwegian Sea from 1995 to 2006 concurring with an increase in water temperature.	The NAO determines the inflow strength of Atlantic water, which affects the water temperature and salinity. This affects the amount of ice in the Barents Sea.

Table 2. Species included in each ecosystem (abbreviations as in Table 1). NS: species not specified

	EBS	GOA	HS		NL	SGOSL	ESS	WSS	GOM	GB	BSNS
Pacific Ocean				**Atlantic Ocean**							
Alaska plaice	X	X		Aesop shrimp	X						
Alaska skate	X			Alewife		X	X				
Arrowtooth flounder	X	X	X	American lobster		X	X	X			
Atka mackerel	X	X		American plaice	X	X	X		X	X	
Big skate		X		Arctic cod	X						
Bivalves (NS)	X			Atlantic argentine			X				
Bocaccio			X	Atlantic butterfish					X	X	
Copepods (NS)	X			Atlantic cod	X	X	X	X	X	X	X
Crabs other (NS)	X			Atlantic hagfish			X	X			
Crustaceans other (NS)	X			Atlantic halibut	X	X	X		X	X	
Curlfin sole			X	Atlantic herring	X	X		X	X	X	X
Dover sole	X	X	X	Atlantic mackerel			X	X	X	X	X
Dusky rockfish	X	X		Atlantic redfishes (NS)	X	X	X	X	X	X	
English sole			X	Atlantic tomcod				X			
Eulachon	X	X	X	Atlantic wolffish	X	X			X	X	
Fish other (NS)	X			Barndoor skate				X			
Flathead sole	X	X	X	Blue hake	X						
Forage fishes other (NS)	X	X		Blue whiting							X
Gelatinous filter feeders (NS)	X			Common alligatorfish	X						
Greenlings (NS)	X	X		Common grenadier	X						
Grenadiers (NS)		X		Cunner		X					
Hermit crabs (NS)	X			Cusk			X	X			
Kamchatka flounder	X			Daubed shanny	X						
King crab	X			Fourline snakeblenny	X						
Large sculpins (NS)	X	X		Fourspot flounder					X	X	
Lingcod			X	Goosefish			X	X	X	X	
Longnose skate		X		Greenland cod		X					
Northern rock sole	X	X		Haddock	X	X	X	X	X	X	X
Northern rockfish	X	X		Halibut				X			
Pacific cod	X	X	X	Jonah crab			X				
Pacific halibut	X	X	X	Longfin hake	X	X					
Pacific herring	X	X	X	Longfin squid					X	X	
Pacific ocean perch	X	X		Longhorn sculpin		X					
Pacific salmon	X	X		Longnose eel	X						
Pacific sand lance	X	X		Lumpfish	X		X	X			
Pacific sanddab			X	Lumpfishes (NS)	X						
Pandalid shrimps (NS)	X	X		Marlin-spike grenadier		X					
Octopuses (NS)	X	X		Northern alligatorfish	X						
Petrale sole			X	Northern prawn	X						
Quillback rockfish			X	Northern sand lance	X				X	X	

Table 2 (continued)

	EBS	GOA	HS		NL	SGOSL	ESS	WSS	GOM	GB	BSNS
Rex sole	X	X	X	Ocean pout			X	X	X	X	
Rougheye rockfish	X	X		Offshore hake			X				
Sablefish	X	X	X	Perciformes		X					
Salmon shark		X		Pollock			X	X	X	X	
Sand sole			X	Rainbow smelt		X					
Sculpins other (NS)	X	X		Red hake			X	X	X	X	
Scyphozoid jellies (NS)	X			Rock crab		X	X				
Sebastes other (NS)		X		Roughhead grenadier	X						
Sharpchin rockfish		X		Roundnose grenadier	X						
Shortraker rockfish		X		Saithe							X
Shortspine thornyhead		X		Scorpaeniformes		X					
Silvergray rockfish			X	Sculpin			X	X			
Sleeper shark	X	X		Sculpins (NS)	X						
Slender sole			X	Scup					X	X	
Southern rock sole		X	X	Sea raven	X	X					
Spotted ratfish			X	Shad			X				
Tanner crab	X			Shortfin squid		X			X	X	
Walleye pollock	X	X	X	Shorthorn sculpin		X					
Yellowfin sole	X	X		Silver hake			X	X	X	X	
Yellowtail rockfish			X	Small pelagics				X			
				Smooth dogfish						X	
				Snake blenny	X						
				Stone crab			X				
				Summer flounder					X	X	
				Thorny skate	X						
				Threebeard rockling (NS)	X						
				Threespine stickleback		X					
				Toad crabs (NS)		X					
				White hake	X	X	X	X	X	X	
				Windowpane			X		X	X	
				Winter flounder		X	X		X	X	
				Witch flounder	X	X	X		X	X	
				Wolffishes (NS)	X		X	X			
				Yellowtail flounder		X	X		X	X	
Both oceans											
Butter sole			X	Butter sole							X
Capelin	X	X		Capelin	X	X					
Eelpouts (NS)	X	X		Eelpouts (NS)	X	X					
Flatfishes (NS)	X	X		Flatfishes (NS)				X			
Greenland halibut	X			Greenland halibut	X	X	X				X
Shrimps (NS)	X			Shrimps (NS)		X					
Skates (NS)	X	X	X	Skates (NS)		X	X	X	X	X	
Snails (NS)	X			Snails (NS)	X						
Snow crab	X			Snow crab	X	X	X				
Spiny dogfish		X	X	Spiny dogfish		X	X	X	X	X	
Squids (NS)	X	X		Squids (NS)			X	X			

Here we assumed that the probability distribution of TLs is normal with the mean being set at the species-specific mean TL and coefficient of variation (CV) being set arbitrarily at 0.1. The mean TL for each species in each ecosystem was obtained either from Ecopath models, if available (Table 1), or from FishBase (Froese & Pauly 2011). The TL distribution was truncated within an arbitrary range of ±0.7 and then scaled by the sum before it was multiplied by the species- and year-specific biomass (see the previous description of data) to distribute the biomass over the range of TLs. For each year from 1984 to 2007, the biomass at each TL interval (0.1) was aggregated over all species to obtain a system biomass–TL spectrum from which absolute cumB–TL curves were obtained. These curves were used to obtain a first description of trophic structure modifications in each system through time.

Analysis

Temporal variations of the total biomass and its distribution among the different TLs within each system was tested by using a Kolmogorov-Smirnov test applied to the absolute curves, allowing us to perform a preliminary assessment of possible modifications in the general curve shape.

In order to improve the comparative analysis, within and among different ecosystems, the raw data were then fitted according to a 4-parameter logistic nonlinear regression model, with the form:

$$\text{Biomasses} = \frac{A - D}{1 + \left(\frac{TL}{C}\right)^{B}} + D \tag{1}$$

where A and D are the minimum and maximum asymptotes (here set to 0 and 1, respectively); B is the slope factor/steepness of the curve; and C is the inflection point in terms of TL. The parameters B and C were determined as nonlinear weighted least-squares estimates of the parameters of the nonlinear model (Bates & Chambers 1992).

Possible relationships between the temporal trends of curve parameters (B and C) and external drivers, such as environmental variables including latitude, sea surface temperature (SST), Pacific Decadal Oscillation (PDO), Siberian/Alaskan Index (SAI), Arctic Oscillation (AO), Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO), chlorophyll *a* (chl *a*) and its flux (in terms of sum of anomalies over the year), and fishing pressure, as total catches, were investigated by means of generalized additive models (GAMs; Hastie & Tibshirani 1990). All drivers are represented by a complete time series (1984–2007), except for the shorter chl *a*/flux time series (1998–2007). Analyses were carried out for all systems combined and for each individual system independently.

GAMs represent a collection of nonparametric and semi-parametric regression techniques for exploring relationships between response and predictor variables, having greater flexibility for drawing out the long-term nonlinear trends than chain or linear modeling methods. Indeed, some predictors can be modeled non-parametrically, using a cubic spline as the smoothing function, in addition to linear and polynomial terms, allowing the response shape to be fully determined by the data.

The following additive formulation was used:

$$\mathrm{Y} = a + s_1\,(V_1) + \ldots + s_\mathrm{n}(V_\mathrm{n}) + \varepsilon \tag{2}$$

where a is the intercept, s is the thin-plate smoothing spline function (Wood 2003), $V_1 \ldots V_\mathrm{n}$ are the predictors, and ε is the random error. Calculations were carried out using the MGCV package (Wood 2006) in R v 2.13 (R Development Core Team 2011).

The strength of the link between curve parameters and external drivers was assessed by quantifying the probability density distribution of the correlation coefficients obtained by bootstrap resampling. This analysis involved a random pairwise sampling with replacement where each time series was resampled 5000 times. The number of elements in each bootstrap sample equals the number of elements in the original dataset. The probability density distribution of the corresponding correlation coefficients was then computed using nonparametric kernel smoothing (Casini et al. 2010).

RESULTS

The absolute cumB–TL curves for each system are reported in Fig. 1. The analysis of temporal trends of the total biomass highlighted different patterns in different regions (Table 3), but, in spite of different characteristics of each system, a consistent pattern both in terms of geographical areas and latitudes emerged. The Pacific systems (EBS, GOA, HS) showed a decreasing total biomass trend over time, though less pronounced in the Gulf of Alaska (GOA). The western Atlantic systems (GB, GOM, WSS, ESS, SGOSL, NL) showed different patterns in relation to latitude, with a decreasing biomass in the higher latitude systems (WSS, ESS, SGOSL, NL) and either an increasing or a fluctuating pattern in the lower ones (GB, GOM). The eastern Atlantic system (BSNS) showed a consistently increasing pattern. In all systems, with the exception of the GOA, differences between the extremes of the curves were statistically significant (Kolmogorov-Smirnov test; Table 3), confirming a modification of the curve shape during the period analyzed.

In order to better describe the observed temporal trends, steepness (B) and TL inflection points (C) of each curve were estimated (Figs. 2 & 3). Differences highlighted in the absolute curve analyses were also reflected in the analyses of steepness and inflection point parameters of the relative curves, as can be seen for the within-system estimates of the standard deviation of B (Table 4).

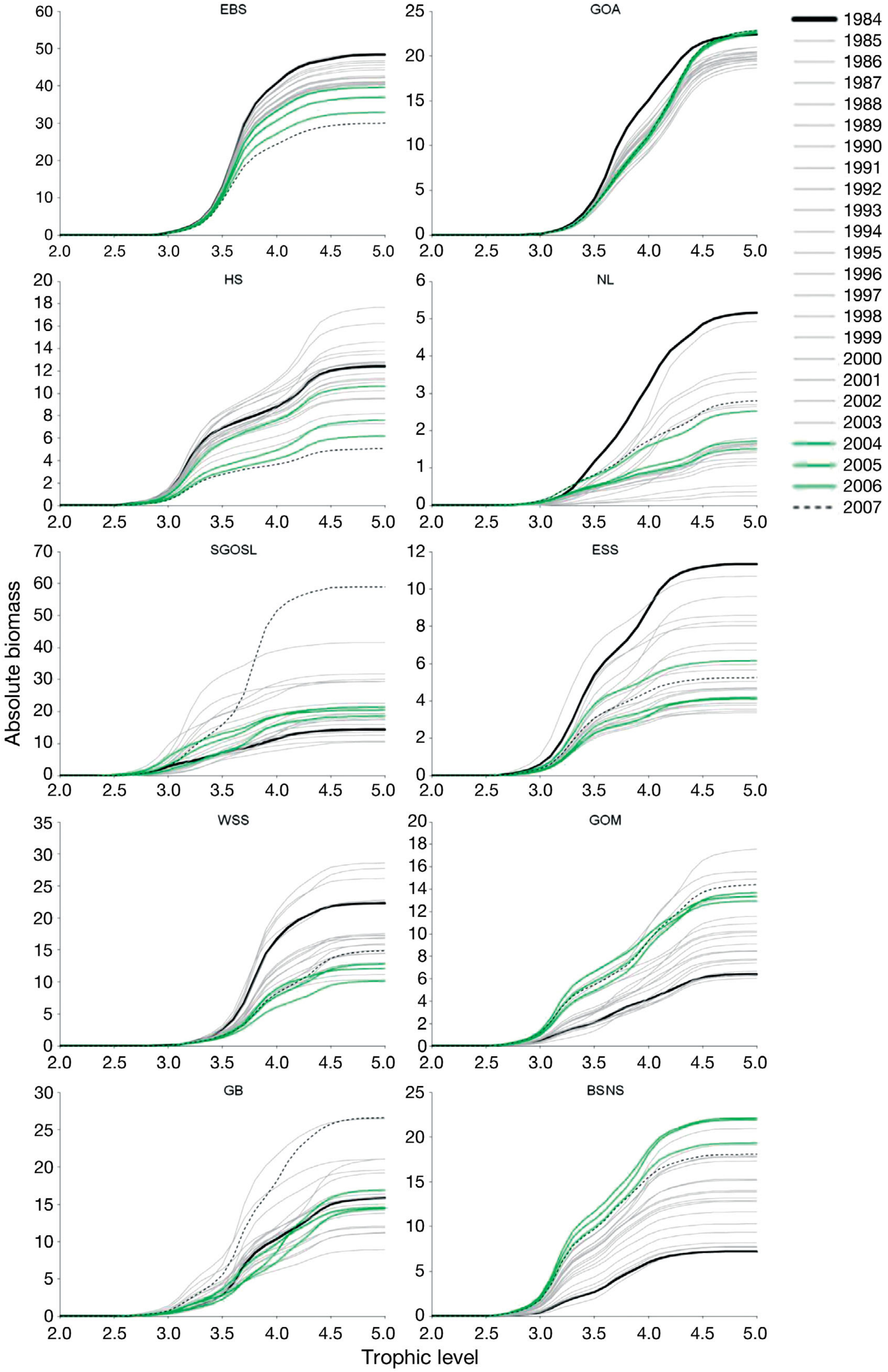

Fig. 1. Absolute cumulative biomass–trophic level curves. Ecosystem abbreviations as in Table 1

Table 3. Temporal evolution analysis of the absolute cumulative biomass–trophic level curves in different years for each study system; years used in the test are shown in parentheses. Ecosystem abbreviations as in Table 1

Ecosystem	Trend	Kolmogorov-Smirnov test p (years)	Notes
EBS	Decreasing	0.005 (1986–2007)	2007 the lowest value
GOA	Slightly decreasing (stable)	>0.1	Pattern quite stable
HS	Decreasing	<0.001 (1989–2007)	2007 the lowest value
NL	Mixed	<0.05 (1984–2007)	1984 the highest value, the early 1990s the lowest (when the collapse was recorded, see Table1)
SGOSL	Mixed	<0.001 (1998–2007)	2007 the highest value, but a generally stable pattern
ESS	Decreasing	<0.001 (1984–2007)	2003 the lowest value, then a partial recovery
WSS	Decreasing	<0.01 (1986–2004)	2004 the lowest value
GOM	Increasing	<0.001 (1987–2002)	2002 the highest value, 1987 the lowest
GB	Mixed	<0.025 (1984–2007)	2001 and 2007 the highest values, mid-1990s the lowest
BSNS	Increasing	<0.001 (1984–2007)	A constant increasing trend, 2005 the highest value, 1986 the lowest

The time series of *B* and *C* allowed for the exploration of the role that external drivers, such as environmental parameters and fishing pressure, have on the TL of systems. The analysis of all systems combined (both without and with the chl *a*, which is represented by a shorter time series) highlighted that SST, latitude, chl *a* (when considered), and fishery (landings) all played an important role in shaping the cumB−TL curves, whereas the other atmospheric parameters had minimal to no influence (Figs. 4 to 7; Table 5). Latitude and fishery showed contrasting effects: increasing latitude decreased the steepness of the cumB−TL curve and the inflection point to shift towards higher TL, whereas increasing fishing pressure resulted in an increase of the steepness and a reduction of the TL inflection point, as would be expected. In contrast, chl *a* and SST positively affected both parameters. The general pattern holds when ecosystems were analyzed individually except that SST was replaced by regional atmospheric indices (Table 6); the AMO and PDO, often coupled with the fishing pressure, were significantly correlated with the curve parameters.

DISCUSSION

We assert that the results shown here represent a fundamental feature of marine ecosystems. In either absolute or relative curves, the accumulation of biomass is a consistent feature across a wide range of ecosystems characterized by distinctive taxa and as influenced by distinct drivers. This is consistent with prior studies that have examined size spectra (Jennings et al. 2002b, Piet & Jennings 2005) or food web model outputs (Link et al. 2009a, Pranovi & Link 2009). That we consistently observed a sigmoidal relationship, with the highest accumulation of biomasses at middle TLs, is not a trivial finding. The resultant pattern was robust both in terms of the

Table 4. Mean values of curve parameters (average 1984–2007), obtained by fitting raw data; *B*: steepness; *C*: trophic level inflection point (see Eq. 1). Ecosystem abbreviations as in Table 1

	mean *B*	SD	mean *C*	SD
EBS	38.49	10.65	3.56	0.01
GOA	17.58	4.42	3.90	0.05
HS	13.51	0.76	3.65	0.05
NL	9.09	4.88	3.49	0.27
SGOSL	30.79	31.51	3.42	0.11
ESS	25.74	28.43	3.54	0.21
WSS	32.03	38.71	3.73	0.12
GOM	18.71	2.58	3.76	0.06
GB	38.52	33.19	3.73	0.05
BSNS	25.47	1.69	3.65	0.03

Table 5. Correlation between parameters of the cumulative biomass–trophic level curves and external drivers (only parameters showing significant relationships are reported). The analysis was carried out for all systems combined with and without the chlorophyll *a* (chl *a*)/flux chl *a* time series. +: significant positive relationship; −: significant negative relationship. SST: sea surface temperature; AMO: Atlantic Multidecadal Oscillation; TC: Total catches

Parameter	SST	AMO	Latitude	Chl *a*	TC
All systems					
Steepness	+		−	Without	+
Inflection	+	−	+	Without	−
All systems					
Steepness			−	+	+
Inflection			+	+	−

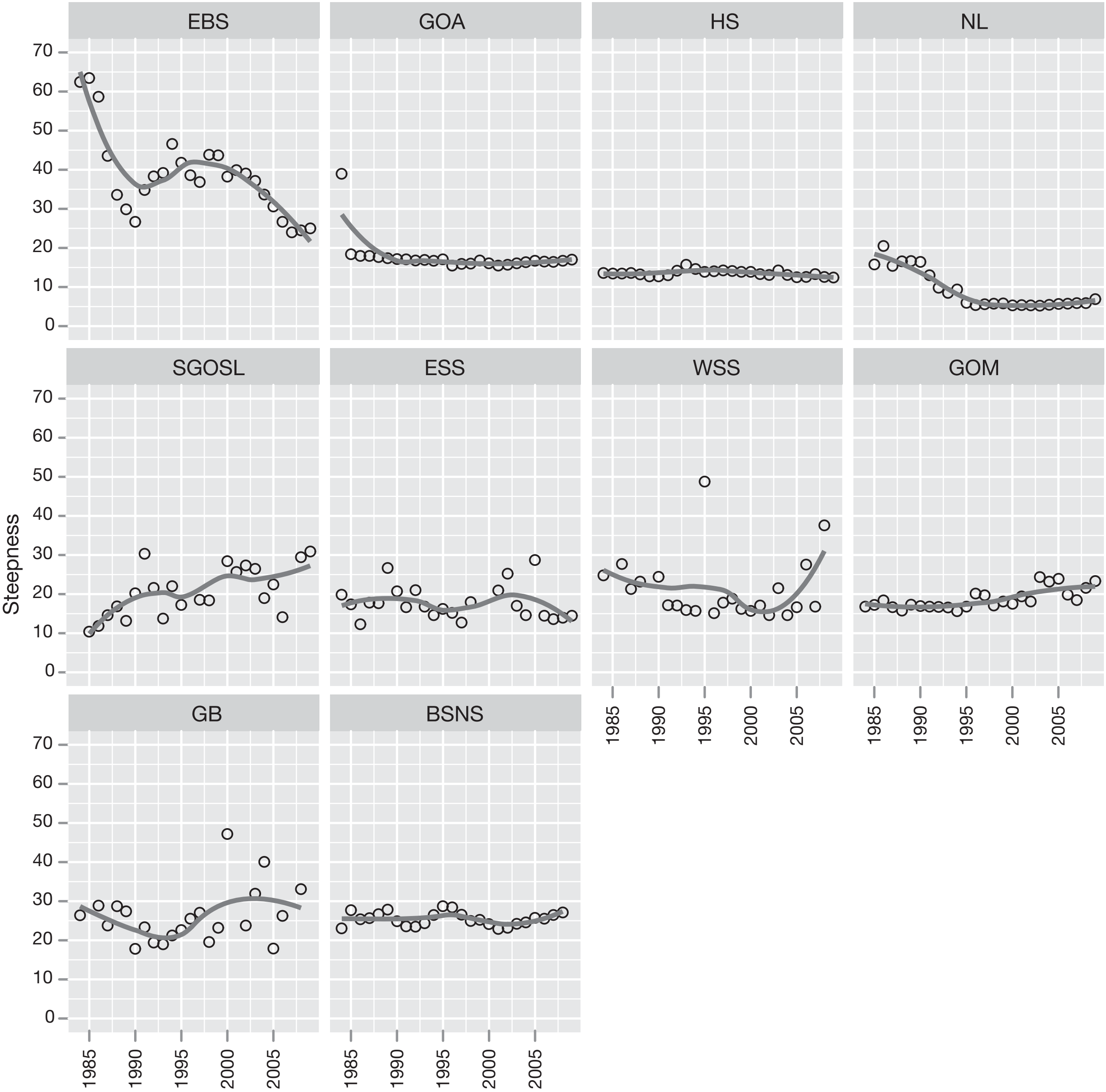

Fig. 2. Steepness (*B*) time series (see Eq. 1), for each analyzed ecosystem. Ecosystem abbreviations as in Table 1

methodology applied to construct the trophic spectra and the taxonomical composition of the analyzed database, resulting in the fact that it is not a simple property of the fish community (see also Link et al. 2009a). One could readily leverage this fundamental feature of marine ecosystems to both further elucidate ecosystem dynamics and establish systemic management thresholds.

In terms of absolute curves, the dynamics of the emergent pattern also seem to be consistent both in terms of the geographic area and latitude of the analyzed systems. Higher-latitude systems (both in the Pacific and Atlantic) exhibit a decrease in total biomass over time, whereas mid-latitude systems (in both the Eastern and Western Atlantic) exhibited an increase or at least a fluctuating trend. These dynamics represent a change in realized production and may be indicative of structural shifts in lower TL community structure in response to broad-scale phenomena (see, for example, changes recorded in the

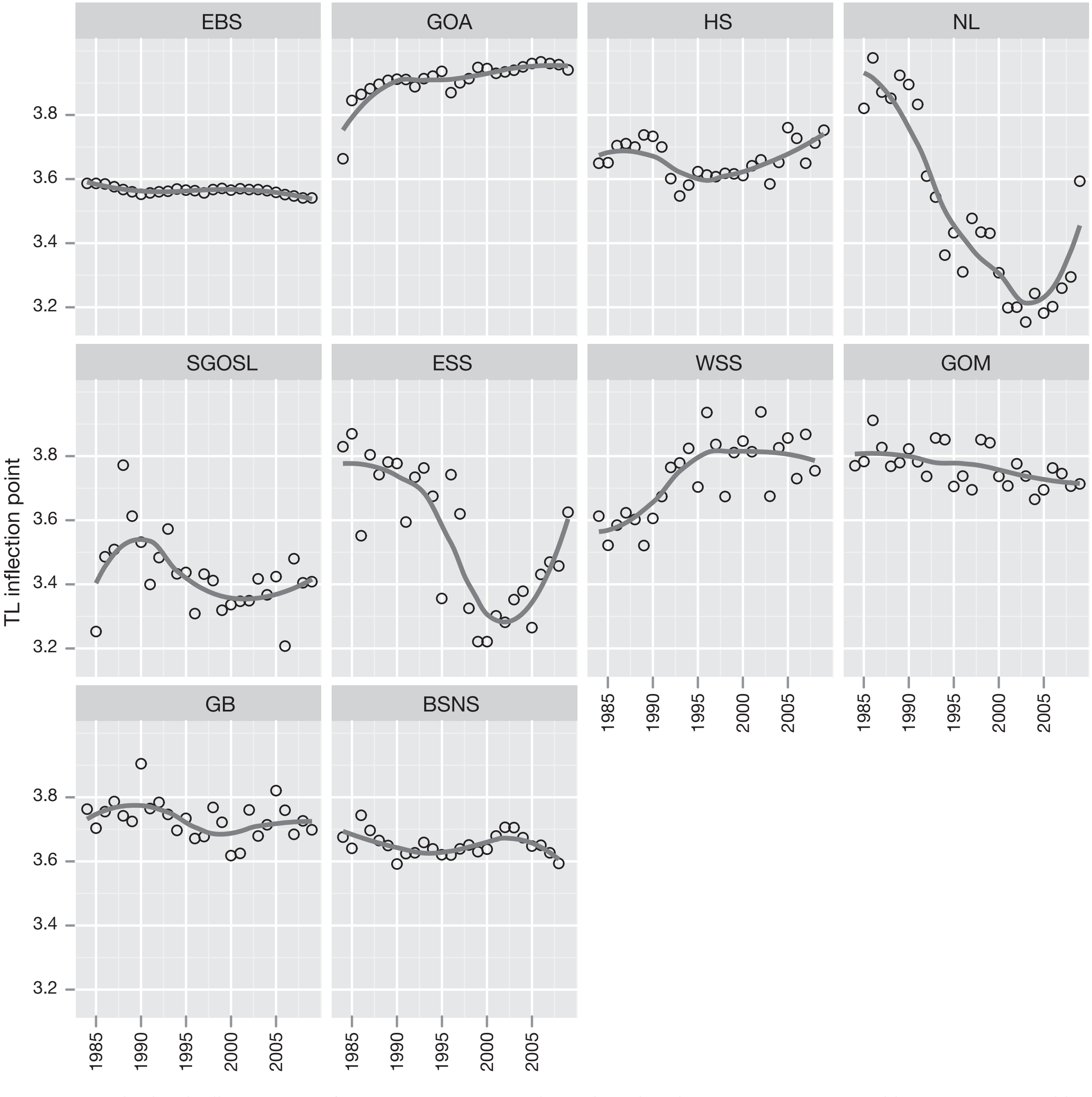

Fig. 3. Trophic level inflection point (*C*) time series (see Eq. 1), for each analyzed ecosystem. Ecosystem abbreviations as in Table 1

Newfoundland–Labrador system, Table 1). Suggestions of this have been implied in prior studies (Drinkwater et al. 2009, Gaichas et al. 2009, Link et al. 2009b, 2010a, Megrey et al. 2009, Pranovi & Link 2009, Blanchard et al. 2010, Coll et al. 2010).

The relative curves exhibit lower biomass accumulation for higher-latitude systems, which are reflected in a lower steepness and consequently a higher TL inflection point. This observation may be a result of the somewhat lower primary productivity of those high-latitude systems, although on an areal basis and as annually integrated, some of those higher latitude systems can be quite productive (Gaichas et al. 2009, Lucey et al. 2012, this TS) and have supported significant fisheries production (Mueter & Megrey 2006, Link et al. 2009b, Bundy et al. 2012, this TS). That there are differences in ecosystems across latitudes is not surprising; what is surprising is the minimal difference between ocean basins.

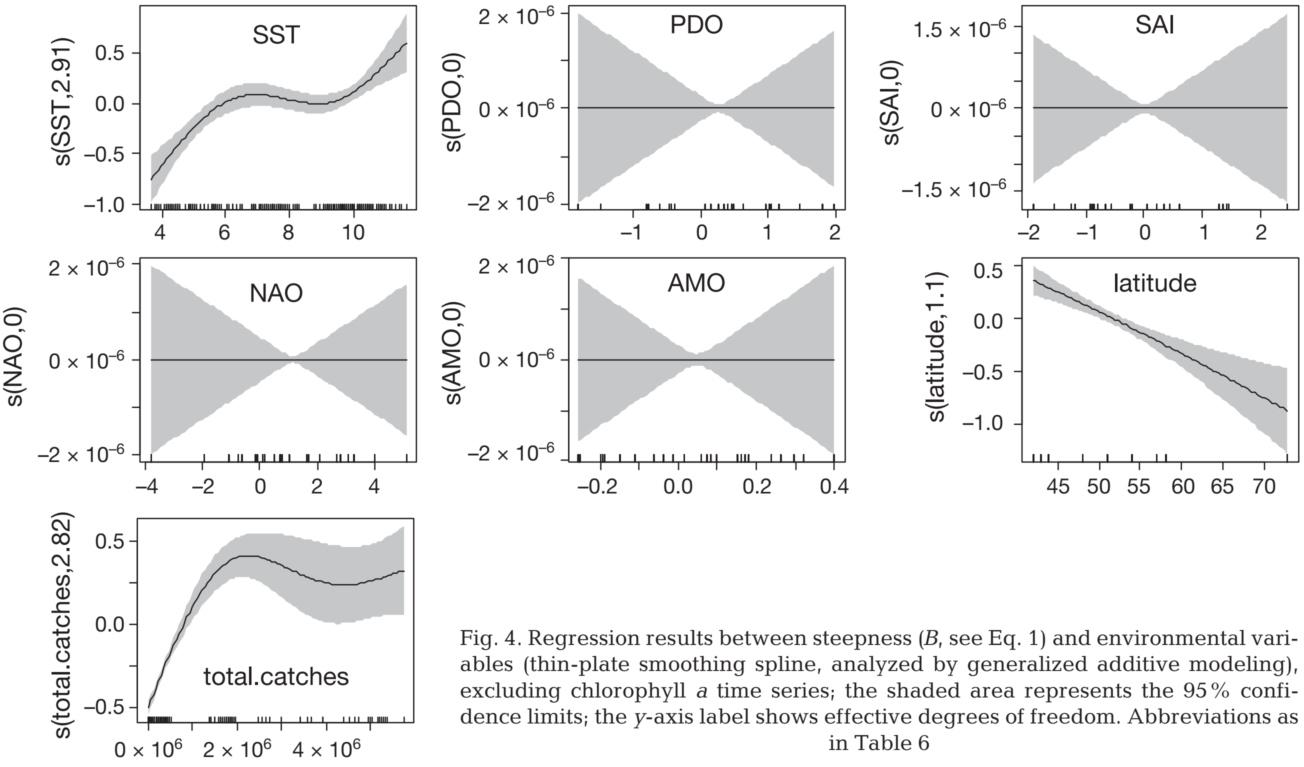

Fig. 4. Regression results between steepness (*B*, see Eq. 1) and environmental variables (thin-plate smoothing spline, analyzed by generalized additive modeling), excluding chlorophyll *a* time series; the shaded area represents the 95% confidence limits; the *y*-axis label shows effective degrees of freedom. Abbreviations as in Table 6

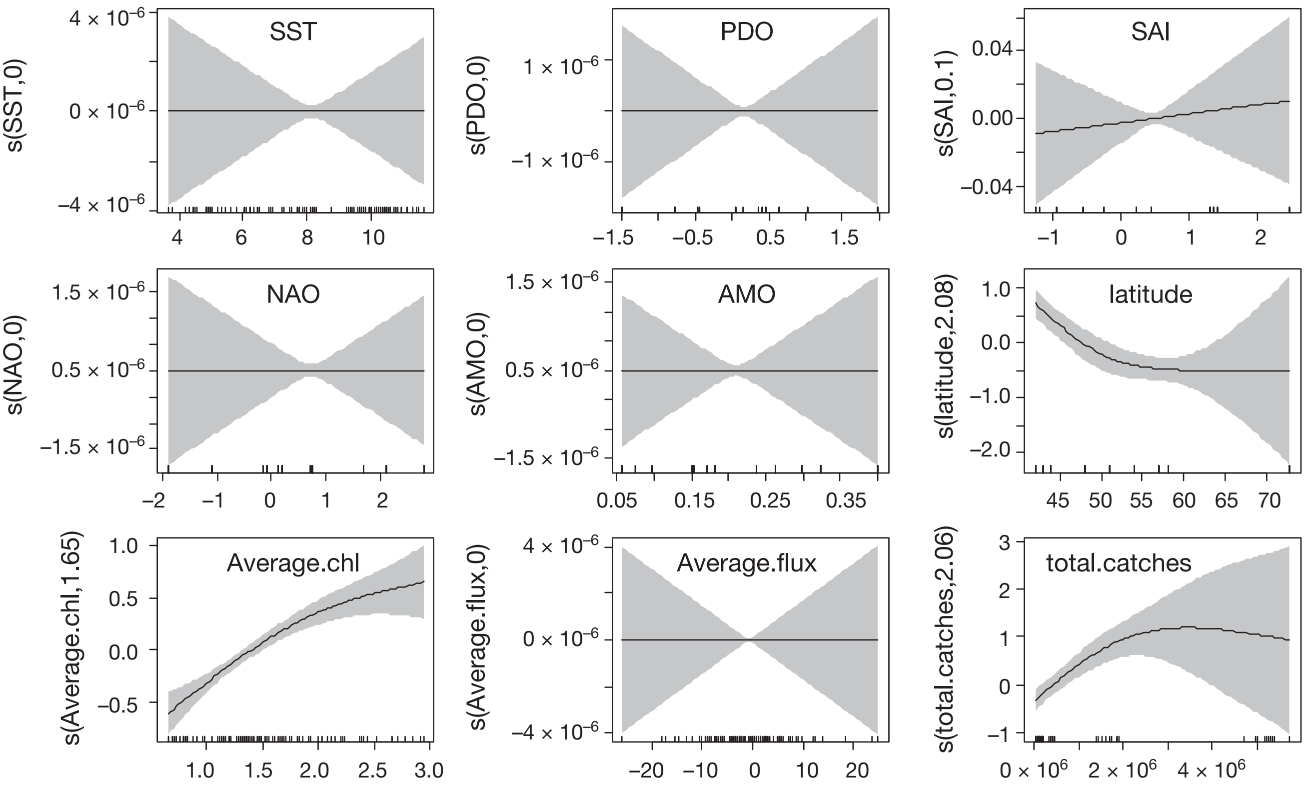

Fig. 5. Regression results between steepness (*B*) and environmental variables (thin-plate smoothing spline, analyzed by generalized additive modeling), including chlorophyll *a* time series; the shaded area represents the 95% confidence limits; the *y*-axis label shows effective degrees of freedom. Abbreviations as in Table 6

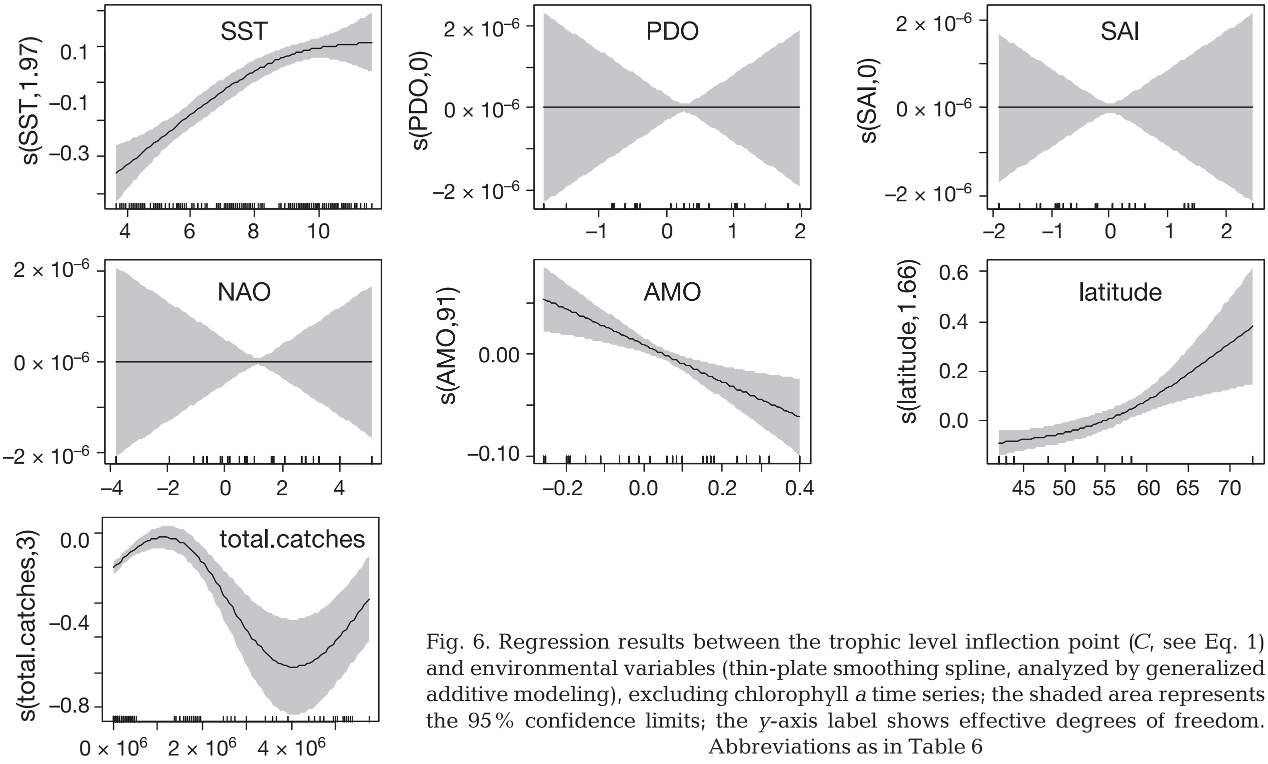

Fig. 6. Regression results between the trophic level inflection point (*C*, see Eq. 1) and environmental variables (thin-plate smoothing spline, analyzed by generalized additive modeling), excluding chlorophyll *a* time series; the shaded area represents the 95% confidence limits; the *y*-axis label shows effective degrees of freedom. Abbreviations as in Table 6

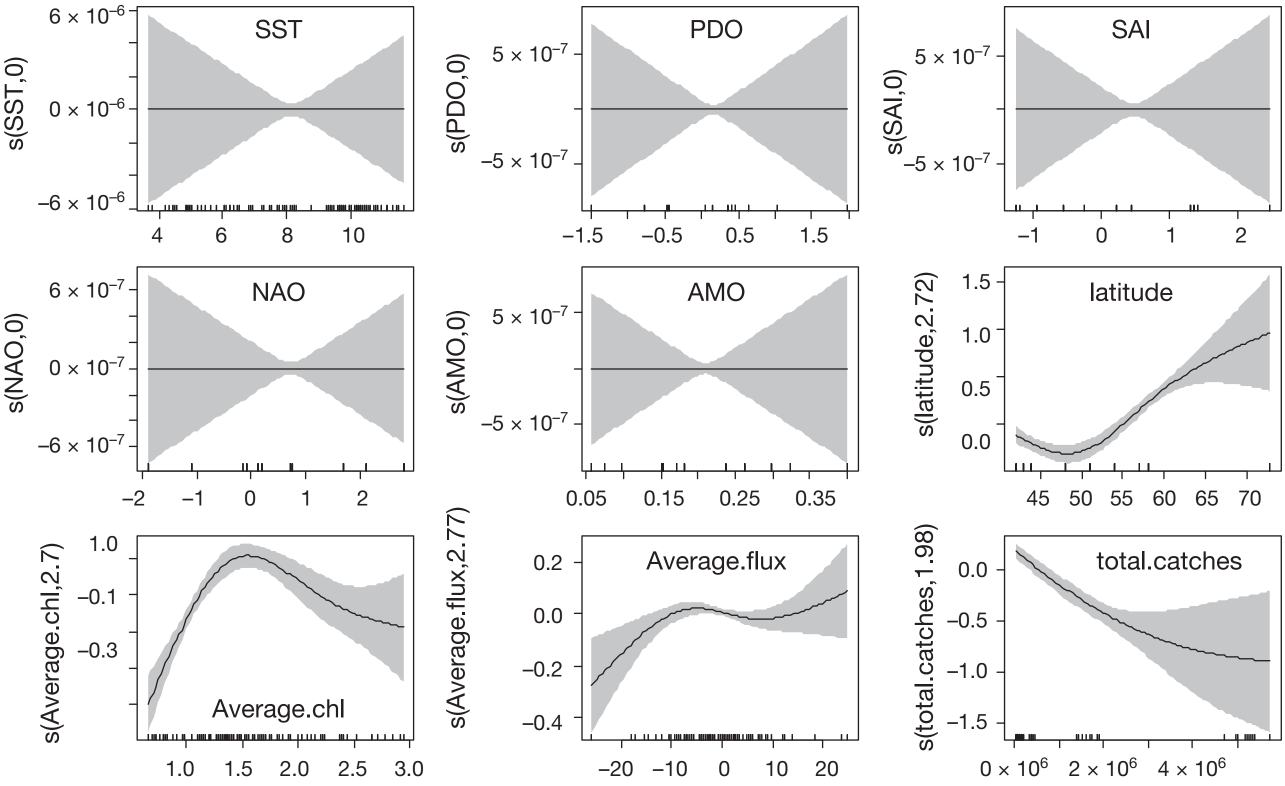

Fig. 7. Regression results between the trophic level inflection point (*C*) and environmental variables (thin-plate smoothing spline, analyzed by generalized additive modeling), including chlorophyll *a* time series; the shaded area represents the 95% confidence limits; the *y*-axis label shows effective degrees of freedom. Abbreviations as in Table 6

Table 6. Correlation between parameters of the cumulative biomass–trophic level curves and external drivers (only systems/parameters showing significant relationships are reported), with analysis carried out on individual systems. +: significant positive relationship; −: significant negative relationship; ( ): almost significant (0.1 > p > 0.05); ±: significant relationship inverse U-shaped. Ecosystem abbreviations as in Table 1. SST: sea surface temperature, PDO: Pacific Decadal Oscillation, SAI: Siberian/Alaskan Index; AO: Arctic Oscillation; NAO: North Atlantic Oscillation; AMO: Atlantic Multidecadal Oscillation

System	Parameter	SST	PDO	SAI	AO	NAO	AMO	Total catches
EBS	Steepness		+					
GOA	Steepness		+	(+)	+			+
	Inflection							−
GB	Steepness							−
GOM	Inflection						−	±
SGOSL	Steepness						+	
	Inflection							+
NL	Steepness						−	+
	Inflection						(−)	+
ESS	Steepness	+						
	Inflection						−	(+)
WSS	Steepness					+		
	Inflection						−	−
BSNS	Inflection	−						+

If these cumB−TL curves and their associated parameters are to be used as potential indicators of EOF, their relation to the major triad of drivers needs to be established. Across all of the ecosystems we examined, measures of exploitation can influence the curves, producing a consistent pattern, with an increase of steepness at lower exploitation levels and then a decrease at higher levels and a downward shift in the TL inflection point. This could be related on one hand to a direct effect of fishing activities on higher TLs, exporting biomass from the system, thereby producing a reduction in TL. This could also be combined with predation release whereby decreases in higher TL fish results in less predation on those at lower TLs, which in turn increase, thereby lowering the mean TL (Benoît & Swain 2008). On the other hand, exploitation can indirectly affect higher TLs by reducing the energy flowing from the lower TLs when the exploitation targets lower TL species, such as forage fish (Gascuel et al. 2008, Libralato et al. 2008). Either way, the resulting change in the curve would be a flatter profile with a lower total biomass. These results are consistent with the pattern reported by Sosa-López et al. (2005), who described a flattening of biomass cumulative curves in relation to an increase of anthropogenic impacts.

Environmental metrics are also related to the features of the relative cumulative biomass curves. On a global scale, taking into the account all of the systems, both an increase in SST and chl *a* resulted in a downward shift in the inflection point and an increase in steepness, thereby making the cumB−TL curves more pronounced. This does not directly imply the presence of a positive relationship between the 2 environmental parameters, since this issue is still debated (see also Chavez et al. 2011 and Friedland et al. 2012), but simply indicates the possible presence of a similar mechanism driving the ecological processes, in relation to both SST and chl *a*. The positive effect of chl *a* on the cumB−TL curve shape is in agreement with very recent findings by Friedland et al. (2012).

In the individual ecosystem based analysis, patterns in the cumB−TL curves over time confirmed a strong effect of fishing pressure on the structure and functioning of the system, as was also shown in the global-scale analysis. This is seen via an effect of fishing on the TL inflection point and a flattening out of the curve (reflected in the lower steepness values). At this level of analysis, moreover, SST is replaced by atmospheric variables as the significant environmental driver. AMO (which almost always had negative effects) played a significant role in the Atlantic systems and PDO (always positive effects) in the Pacific systems, although the same pattern of the cumB−TL curves is seen. Both results confirm the observations regarding the key environmental influences (as reported in Table 1).

Collectively across systems, within systems, and considering both exploitation and environmental effects, what our results show is that positive ecosystem responses are exhibited as a ‘stretching’ or heightening of the sigmoidal curves. Conversely, negative effects on an ecosystem are exhibited as a flattening of these sigmoidal curves (Fig. 8). An example from our analysis is the flattening of the

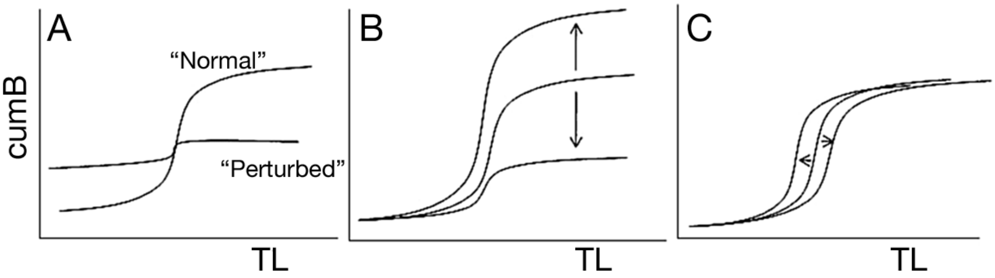

Fig. 8. Conceptual diagram illustrating (A) expected variations in the cumulative biomass–trophic level (cumB–TL) curve shape in relation to external drivers; (B) effects on the absolute curves; (C) effects on the relative curve

curves in the NL system due to the collapse recorded in the 1990s. A corollary would be that as ecosystems are degraded, their patterns on these curves would flatten out, but as they recover their patterns would be clearly demonstrable. Examples from our analyses show that the GOM, NSBS, and GB ecosystems exhibited some recovery in fishery resources, which has been confirmed by more detailed studies on the component species in those ecosystems (Drinkwater et al. 2009, Link et al. 2009b).

Thus, this fundamental sigmoid feature could potentially be used as a system-level biological reference point of EOF. For instance, as changes occurred in a given ecosystem, the inflection point and steepness parameters also reflected those changes, indicative of potential system-level thresholds similar to other attempts to define ecosystem overfishing (Tudela et al. 2005, Coll et al. 2008, 2010, Libralato et al. 2008, Link et al. 2010a, Shin et al. 2010a). The value of this approach is that it is a relatively simple derivation of readily available survey data and does not require extensive multi-species, food web, or ecosystem modeling, other than to obtain reasonable values for TL. Indeed, while in the previous application (Link et al. 2009a) the cumB–TL method was applied to an extensive multi-species food web database, in the present study it was applied to data from surveys or assessments.

By establishing the cumB–TL curves and then calculating steepness and inflection parameters, a robust set of 2 simple metrics could be monitored to detect when a shift in community structures was beyond normal ranges of the data. Clearly further work is warranted on developing methodological features (e.g. sensitivity to the TL attribution could be a critical issue) and establishing probabilistic thresholds, but as a first-order attempt to examine EOF from an empirically-based, trophodynamic perspective, this approach holds some promise.

Obviously, some caveats have to be taken into the account. Giving a picture of the state of the ecosystem, in the present version the method requires for comparison at least 2 different temporal points, in order to assess the direction of changes. Moreover, as previously shown, there could be different external drivers which produce similar effects on the cumB–TL curve shape; for this reason, some cautions are required in determining causes of a detected change.

Robust ecological indicators of the trophic structure of marine communities, and long-term changes therein, are now available (Sosa-López et al. 2005). The sigmoidal relationship of cumB–TL curves is another possible indicator, among many in development (Libralato et al. 2008, Coll et al. 2008, Link et al. 2009a, 2010a, Shannon et al. 2010, Shin et al. 2010a), that could be used to delineate EOF. Moving towards fuller implementation of EBFM will necessarily require a suite of robust indicators. We trust that what we propose here is a useful step towards that end as these ecological indicators continue to develop.

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Contribution to the Theme Section 'Comparative analysis of marine fisheries production'

Common patterns, common drivers: comparative analysis of aggregate surplus production across ecosystems

Alida Bundy[1,*], Erin C. Bohaboy[2,7], Dag O. Hjermann[3], Franz J. Mueter[4], Caihong Fu[5], Jason S. Link[6]

[1]Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada
[2]Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA
[3]Department of Biology, Center of Ecological and Evolutionary Synthesis, University of Oslo, 0316 Oslo, Norway
[4]Fisheries Division, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau, Alaska 99801, USA
[5]Pacific Biological Station, Marine Ecosystems and Aquaculture Division, Fisheries & Oceans Canada, Nanaimo, British Columbia V9T 6N7, Canada
[6]National Atmospheric and Oceanic Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, Massachusetts 02543, USA

[7]*Present address:* RPS ASA, South Kingstown, Rhode Island 02879, USA

ABSTRACT: Marine ecosystems are dynamic, often have open boundaries, and their overall productivity responds nonlinearly to multiple drivers acting at multiple temporal and spatial scales, under a triad of influences: climatic, anthropogenic, and ecological. In order to further our understanding of how the structure and functioning of marine ecosystems influence and regulate patterns of fisheries production, and how they are affected by this triad of drivers, a comparative approach is required. We apply a system-level surplus production modeling approach to the total aggregated catch and biomass of all major targeted fish species in 12 exploited Northern Hemisphere ecosystems. We use 2 variations of a surplus production model: a regression model and a dynamic model, each fit with and without environmental and biological covariates. Our aims were to explore (1) the effects of common drivers at the basin scale and their relative influence within the triad of drivers among systems, (2) the impact of covariates on biological reference points and implications for fisheries management, and (3) the relationship between maximum sustainable yield (MSY) and production. Our results show that the environment affects estimates of system-level MSY across all ecosystems studied and that specifically water temperature is a major influence on productivity. Emergent properties of northern hemisphere systems suggest that MSY values and optimal exploitation rates are relatively consistent: MSY ranges between 1 and 5 t km^{-2} and optimal exploitation rate between 0.1 and 0.4 yr^{-1}. Finally, we suggest that the relationship between fisheries yield and primary production is not as simple as suggested in other studies. These results put fisheries in a broader ecosystem context and have implications for an ecosystem approach to management.

KEY WORDS: Multiple ecosystem drivers · Surplus production models · Comparative analysis

INTRODUCTION

Living marine resources inhabit a complex world, influenced by multiple physical, environmental, anthropogenic, and biotic drivers that operate and interact over multiple scales (deYoung et al. 2004) that can result in nonlinear or abrupt responses to perturbation (e.g. Hare & Mantua 2000, Hunt et al.

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*Email: alida.bundy@dfo-mpo.gc.ca

2002, Scheffer & Carpenter 2003, Steele 2004). Trophodynamically, marine food webs are dynamic, often have open boundaries, and respond nonlinearly to climatic, anthropogenic, and ecological influences (Hsieh et al. 2005). Until relatively recently, management of living marine resources largely ignored this complexity, focusing on single-species stock assessment. This is one of the many contributing factors to the series of fisheries crises (stock collapses and fisheries closures) witnessed over the last 2 decades (e.g. Smith 1994, Mullon et al. 2005, Smith & Link 2005, Murawski 2007, Branch et al. 2011, Pinsky et al. 2011). While the solution and the way forward towards successful resource management does not rest in science alone (Frid et al. 2006, Bundy et al. 2008, Fulton et al. 2011), robust science advice, grounded in an ecosystem context, is an essential component. The inherent complexity and the large scale of marine ecosystems suggests that progress toward an understanding of how the structure and functioning of marine ecosystems influence and regulate patterns of fisheries production will be most effective if researchers adopt a comparative approach (Link et al. 2010a, Murawski et al. 2010), since this is similar to the replication method traditionally used in experimental science. This approach has been amply demonstrated in empirical studies (e.g. Bundy et al. 2009, 2010, Gaichas et al. 2009, Link et al. 2009, 2010b, Shackell et al. 2012). However, there is an additional need to explore mechanistic understandings and drivers of ecosystem structure, functioning, and production as revealed by such comparisons.

Mechanistic approaches vary from the simple to the complex. However, comparative analyses require standardized methods that can be applied across multiple ecosystems and that produce standardized results for comparison. Complex methods are usually developed or tailored for a specific system and are time-consuming to parameterize and fit. Hence such models are challenging to use in a comparative approach since they require far more time, resources, and co-ordination. Rather, comparative approaches, especially over a broad range of ecosystems, are most readily addressed using simpler methods such as production models (Walters & Hilborn 1976, Jacobson et al. 2001, Mueter & Megrey 2006, Gaichas et al. 2012a, this Theme Section). These models relate the production of a population to current population size, given an intrinsic rate of productivity and a finite carrying capacity to account for density-dependent effects. As for all models, they are reductionist representations of complex processes, and though there has been some debate about their utility in specific applications (Mohn 1980, Ludwig & Walters 1985, 1989, Punt 2003), there is consensus that they play a useful and important role in ecology in general (Mangel 2006) and fisheries science in particular (Ludwig & Walters 1985, 1989, NRC 1998).

Production models are a useful method to compare fish communities across ecosystems and drivers because: (1) data requirements are relatively simple and data are readily available, (2) they are robust to various assumptions (Ludwig & Walters 1989), (3) they can sometimes outperform more complicated (i.e. stage or age-structured) fisheries models (Ludwig & Walters 1985, 1989, Hilborn & Walters 1992), (4) they produce standard outputs that are readily comparable, (5) they can be scaled to different spatial and organizational levels, and (6) they can incorporate drivers as covariates (Jacobson et al. 2005, Mueter & Megrey 2006). In addition, the outputs of these models can be readily related to commonly used fishery management biological reference points (BRPs) such as maximum sustainable yield (MSY) and the biomass (B_{MSY}) or fishing mortality rate (F_{MSY}) corresponding to MSY (Restrepo et al. 1999, Mueter & Megrey 2006).

Here we use surplus production modeling to compare the influence of a triad of drivers (fishery exploitation, trophic interactions, and environmental drivers) on fishery production. We apply 2 system-level surplus production models (regression and dynamic) to the total aggregated biomass of all targeted fish species in 12 exploited northern hemisphere ecosystems. We do so with and without environmental and biological covariates to explore the effects of selected drivers on production.

We take an aggregate, system-level approach (e.g. Mueter & Megrey 2006) for the following reasons. (1) Fundamentally, the energy available to all fish and invertebrates originates from lower trophic levels and is limited and shared by the entire marine community (Pauly & Christensen 1995, Pauly et al. 1998, 2002). Lower-trophic-level production has been shown to limit fisheries production (Iverson 1990, Ware & Thomson 2005, Chassot et al. 2007, 2010). These analyses suggest that the production potential for marine resources in any given area of the ocean is, within ranges of natural variation, relatively fixed due to lower-trophic-level production. (2) Due to species interactions, and differences in productivity among fish stocks, the aggregate management objective is not the simple sum of the single-stock objectives (e.g. Brown et al. 1976, Walters et al. 2005, Mueter & Megrey 2006, Tyrrell et al. 2011). Therefore an average or aggregate quota may sometimes be more appropriate, especially when managing suites of stocks (May 1975, Pope 1975, 1979, Fukuda 1976, Mayo et al. 1992), and provides additional precaution (in addition to stock-specific quotas) when used to constrain total removals from a system (Witherell et al. 2000, Mueter & Megrey 2006). (3) Aggregate surplus production models often fit better than production models applied on a species-by-species basis (FAO 1978, Ralston & Polovina 1982).

Comparing responses in aggregate production across multiple ecosystems elucidates both common, generic patterns and those processes that are unique to particular ecosystems. Our aims are to use total, system-level estimates of BRPs based on production models to explore (1) the effects of common drivers at the basin scale and their relative influence within the triad of drivers among systems, (2) the impact of covariates on BRPs and implications for fisheries management, and (3) the relationship between MSY and production.

METHODS

Data

Biomass, landings, and relevant environmental data were compiled for 12 temperate and sub-arctic marine ecosystems in the northern hemisphere (Table 1) (see Fu et al. 2012, this Theme Section, for further descriptions). The principal marine species were selected for each ecosystem based on prevalence in the landings and biomass data as well as importance in the marine community. These species together comprise a large majority of total trawlable fish biomass in each system. We used biomass estimates from stock assessments when available and survey-based estimates otherwise. Stock assessment estimates of biomass typically corresponded to the exploitable portion of total biomass, assuming knife-edge recruitment. Swept-area estimates of survey biomass were expanded to the total area of the ecosystem and were corrected for catchability when possible. Biomass was summed by year over all selected species to obtain time series of aggregated biomass for each ecosystem. Similarly, reported landings were summed by year over all selected species to obtain time series of aggregate landings for each ecosystem. The landings represent the majority, if not all, recorded catch, but do not account for non-recorded by-catch or discards. Principal species, years, data types, and sources of biomass and landings data for each system are detailed in Table S1 in the supplement at www.int-res.com/articles/suppl/m459p203_supp.pdf.

Environmental and biological covariates for each system were selected by regional experts who were asked to identify those regional and basin-scale variables that are generally considered to be important drivers of productivity in a given ecosystem. Available time series data were compiled for each system that included water temperature, stratification, large-scale climatic indices, freshwater discharge, and abundances of important top-level predators (Table S2 in the supplement). All covariates were standardized to have mean = 0 and standard deviation (SD) = 1 over the time series.

Models

The productivity of each of the 12 ecosystems and the influence of environmental covariates on productivity were compared using a surplus production modeling approach. Since we don't know the true dynamics of these systems, we used 2 different approaches to examine surplus production dynamics: a regression approach that models empirical estimates of annual surplus production as a quadratic function of biomass (Graham-Schaefer functional form with additive errors); and a dynamic surplus production model of the Graham-Schaefer form with multiplicative errors.

Table 1. Marine ecosystems in the present study. 'Species' means principal marine species (see Table S1 in the supplement at www.int-res.com/articles/suppl/m459p203_supp.pdf)

System	Abbreviation	Area (km^2)	No. of species
Eastern Bering Sea	EBS	430 829	8
Gulf of Alaska	GOA	238 439	13
Hecate Strait	HS	23 501	20
Georges Bank	GB	42 154	18
Gulf of Maine	GOM	76 483	19
Western Scotian Shelf	WSS	73 344	23
Eastern Scotian Shelf	ESS	113 704	24
Newfoundland/Labrador	NL	388 204	13
Southern Gulf of St. Lawrence	GOSL	74 137	20
Norwegian Sea	NS	728 331	3
Barents Sea	BS	747 893	8
North Sea	Nort	609 748	9

Regression models

The observed annual surplus production in year t (ASP_t) was calculated as:

$$\text{ASP}_t = B_{t+1} - B_t + C_t \tag{1}$$

where B_t is the biomass summed across all ages in year t, B_{t+1} is the following year's biomass, and C_t is the catch in year t. The Graham-Schaefer model describes ASP_t as a quadratic function of B_t and a linear function of a covariate as:

$$\text{ASP}_t = \alpha B_t + \beta B_t^2 + \delta X_{t-l} + \varepsilon_t \tag{2}$$

where α, β, and δ are regression parameters, X_{t-l} is an environmental or biological covariate measured in year $t - l$, normalized to mean 0 with SD = 1 (Table S2 in the supplement), and l represents the time lag (in years, ranging from $l = 0$ to $l = 7$) before effects on ASP are realized. Parameter δ represents the magnitude and sign of the effect of the biological or environmental covariate on ASP_t and can be directly compared across different standardized covariates. If residuals from the model (ε_t) had significant autocorrelation (Durbin-Watson test, $p < 0.10$), the model was refit under the assumption that residuals follow a first-order autoregressive process:

$$\varepsilon_t = \varphi \cdot \varepsilon_{t-l} + \nu_t \tag{3}$$

with coefficient φ and independent, normally distributed annual deviations (ν_t) with mean = 0 and variance = σ_ν^2:

$$\nu_t \sim N(0, \sigma_\nu^2) \tag{4}$$

All parameters were estimated using a generalized least-squares regression approach as implemented in the 'nlme' package (Pinheiro & Bates 2000) in R (R Development Core Team 2011). Maximum surplus production was taken to represent MSY and was calculated as follows (for models with covariates, MSY corresponds to average environmental conditions):

$$\text{MSY} = -\alpha^2/4\beta \tag{5}$$

We also calculated the biomass at which MSY occurs (B_{MSY}) and defined the optimal exploitation rate F'_{MSY} as the ratio MSY/B_{MSY}. (Note that F'_{MSY} expresses an exploitation rate, i.e. landings as a fraction of the total biomass, rather than the instantaneous fishing mortality, as is the common usage of F_{MSY}.) The potential effects of covariates on ASP were estimated separately for each covariate and at each of multiple lags, and the resulting coefficients, t-statistics, and p-values were summarized and examined.

Biomass dynamic models

Following Walters & Hilborn (1976), the predicted biomass in year $t + 1$ ($\hat{B}_{t+1}$) was calculated as

$$\hat{B}_{t+1} = \hat{B}_t + r_t \hat{B}_t \left(1 - \frac{\hat{B}_t}{k}\right) - C_t + \varepsilon_t \tag{6}$$

where $\hat{B}_t$ is the predicted biomass in year t, and C_t is the observed catch in year t. The intrinsic population growth rate in year t (r_t) and the equilibrium population size in the absence of catch (k, also referred to as the carrying capacity) are parameterized quantities. The initial biomass ($B_{t=0}$ or B_0) is also an estimated parameter.

For any year t, r_t can be expressed as a function of an environmental or biological covariate in year t (X_{t-l}), where l represents a time lag (in number of years, ranging from $l = 0$ to $l = 7$) before effects on r are realized (Mueter & Megrey 2006):

$$r_t = r_m e^{\gamma X_{t-l}} \tag{7}$$

Covariates were standardized to have mean = 0 and SD = 1 over the time series; hence the expected value of r_t under average environmental conditions ($X_{t-l} = 0$) is r_m. Parameter γ represents the magnitude and sign of the effect of the biological or environmental covariate on r_t and can directly be compared across different standardized covariates.

The model residuals (ε_t) are assumed to follow a log-normal distribution with mean = 0 and variance = σ_ν^2, i.e.:

$$\varepsilon \sim \ln N(0, \sigma_\nu^2) \tag{8}$$

The model was implemented in AD Model Builder, a C++ software language extension and automatic differentiation library (ADMB Project 2009), and all parameters were estimated by maximizing the likelihood. MSY and B_{MSY} were calculated as

$$\text{MSY} = \frac{r_m k}{4} \tag{9}$$

and

$$B_{\text{MSY}} = k/2 \tag{10}$$

When comparable, the relative value of each model (e.g. with versus without a particular environmental covariate) was evaluated using the small sample Akaike information criterion AIC (AIC_c; Hurvich & Tsai 1989).

$$\text{AIC}_\text{c} = -2 \times \text{LL}(\theta|B) + 2K\left(\frac{n}{n-K-1}\right) \tag{11}$$

where LL(θ|B) is the loglikelihood of a particular set of parameter values (θ) given the observed biomass data (B), and K is the number of parameters estimated in the model.

$$\text{LL}(\theta|B) = -\frac{1}{2} n \ln \sum_{t=1}^{n} \left(\ln \hat{B}_t - \ln B_t\right)^2 \tag{12}$$

The number of years of observed biomass is denoted by n.

For each modeling approach, we report 2 sets of results: the model fitted without covariates and the model fitted with the covariate giving the largest improvement in model fit. Thus, for each ecosystem we obtain 4 estimates of biological parameters, including MSY, B_{MSY}, and F'_{MSY}. For comparing among systems, MSY and B_{MSY} were standardized to t per km^2 by dividing by the area of each system (Table 1).

Comparative analysis of ecosystem parameters

Estimates of MSY, F_{MSY}, and B_{MSY} were compared across systems and across models — regression and biomass dynamic model (hereafter referred to the dynamic model), each with and without covariates — using a weighted least-squares regression (2-way ANOVA) with weights that were inversely proportional to their estimated variances (Jennrich 1995). To investigate how potential fish productivity varies among ecosystems, MSY per unit area was analyzed using simple linear regressions and multiple linear regressions with the following variables as potential explanatory variables: mean chlorophyll *a* (chl *a*) concentration from NASA's SeaWiFS Project (we used the monthly level-3 processed data averaged over each large marine ecosystem [LME] for the period 1998–2009 to compute an annual mean concentration in mg m^{-3}; http://oceancolor.gsfc.nasa.gov); mean primary production (PP) as estimated from SeaWiFS data (Behrenfeld & Falkowski 1997); mean mass flux index (a measure of the vertical mass flux of particulate organic carbon [POC]; estimates of normalized annual flux of organic carbon [FCo, mmol m^{-2} yr^{-1}] were derived from a model developed from globally observed fluxes [Honjo et al. 2008, Friedland et al. 2012] and remotely sensed chl *a* and sea surface temperature [SST] [K. Friedland pers. comm.]); mean wind speed (Kalnay et al. 1996); and ecosystem area (Table 1).

RESULTS

Regression (ASP) models

There was large variation in biomass among time series (Fig. 1); for the regions with large variation in biomass, there were typically long-term trends such as overall declining (e.g. Hecate Strait) or increasing biomass (e.g. Norwegian Sea), or prolonged periods of both increases and declines (e.g. eastern Scotian Shelf). Similarly, landings data often showed long-term trends (Fig. S1 in the supplement). In contrast, ASP was characterized by high interannual variability rather than long-term trends, even for ecosystems with relatively stable biomass such as the Gulf of Alaska (Fig. 2).

Estimates of maximum production (MSY per unit area), B_{MSY}, and F'_{MSY} varied considerably among regions (Fig. 3; see Table S3 in the supplement for model parameters). The limited contrast in biomass in some regions (Gulf of Alaska, North Sea) resulted in unreliable estimates of B_{MSY} below the minimum observed biomass, while B_{MSY} was close to the maximum observed biomass in the Norwegian Sea due to an increasing trend in biomass throughout most of the time series. Neither the regression nor the dynamic model was able to produce credible estimates of MSY for the Gulf of St. Lawrence, likely due to the highly variable input biomass data (Fig. 1), so this system was dropped from further analysis.

Including environmental covariates improved model fits significantly in most systems, with temperature or temperature-related indices resulting in the best model fits in most cases (Table 2; see Table S4 in the supplement for model parameters). One to 3 different covariates significantly improved the fit, according to $\Delta\mathrm{AIC}_c$ (Table 2). Time lags between environmental variables and regression for the best-fit models spanned the range, but most were 4 yr or less. The estimated environmental effects helped capture the trends in the observed ASP series, such as the declining trend in ASP on the eastern Scotian Shelf, multi-year variability off Newfoundland-Labrador and in the Barents Sea, and interannual variability in the Norwegian Sea (Fig. 3).

Biomass dynamic models

The dynamic Graham-Schaefer model captured the major trends in biomass over time in most systems, but resulted in poor fits in some regions (e.g. Georges Bank, eastern Scotian Shelf, western Scotian Shelf, North Sea; Fig. 4). Including environmental covariates considerably improved the fit of the estimated biomass trajectories in most, but not all systems. The estimated biomass trajectories for the western Scotian Shelf and eastern Scotian Shelf differed substantially between the model with and without environmental covariates, but neither model resulted in a satisfactory fit to the observed time series. Both models (with and without covariates) also failed to capture biomass trends in the North Sea or on Georges Bank. For the Gulf of Alaska and Newfoundland models, although adding environmental covariates did improve the model fit based on the sum of squares (SSQ) (also see Fig. 4), the low value of the $\Delta\mathrm{AIC}_c$ (Table 2) indicates that the addition of this parameter is not justified. Similar to the regres-

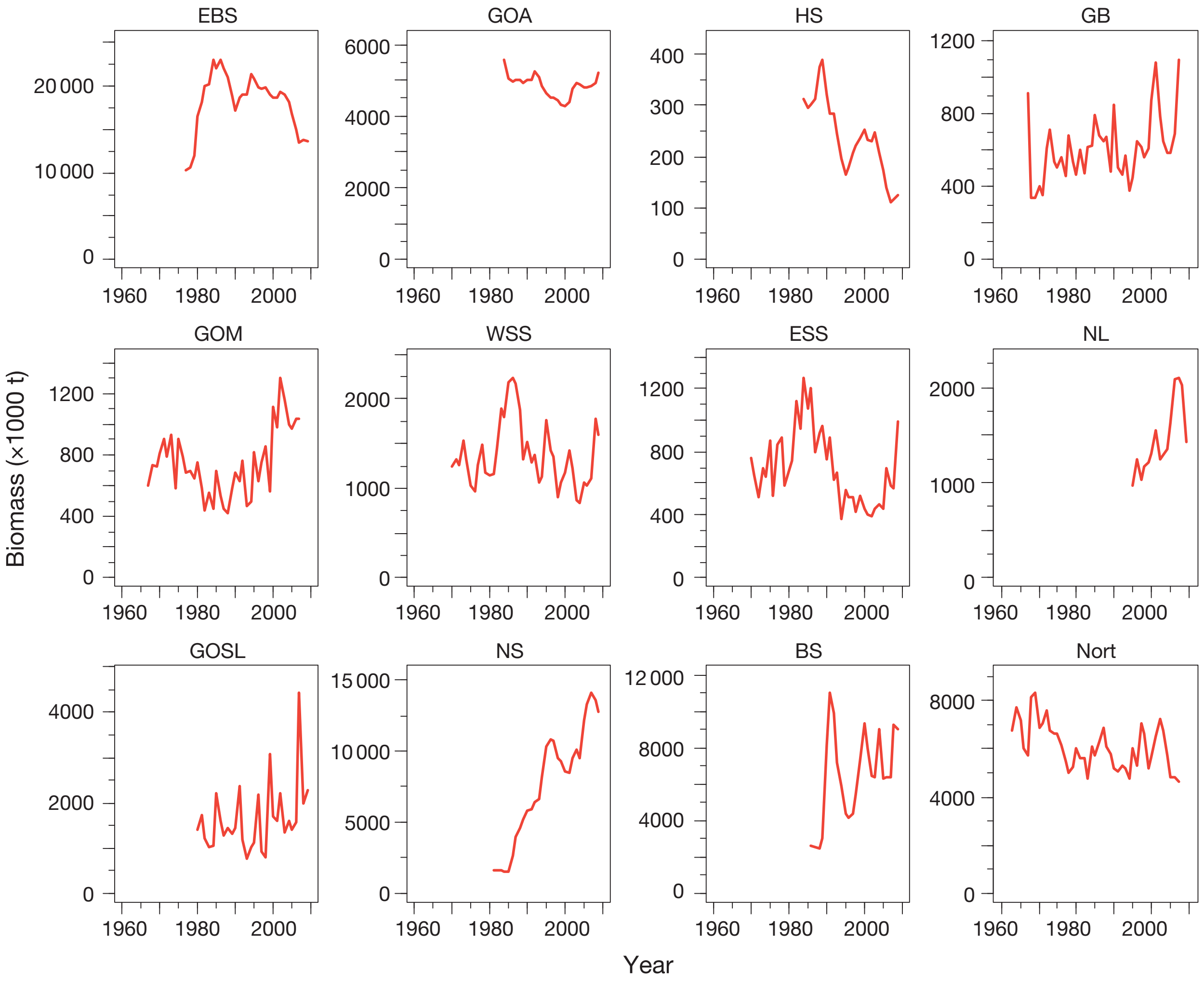

Fig. 1. Total aggregate biomass in each system. See Table 1 for system abbreviations

sion models, time lags before effects on *r* were realized for the best-fit models were typically 4 yr or less. In this case, only 1 to 2 covariates improved the model fits in each system, most of which reflect temperature conditions.

Comparison of regression (ASP) and dynamic model results, with and without covariates

In most cases where the inclusion of a covariate improved the model fit to the data (Table 2), the best environmental covariates for the dynamic models were the same as or similar to those for the regression models (Table 2). In 3 cases they were different — Gulf of Maine, western Scotian Shelf, and Norwegian Sea; on the western Scotian Shelf, for example, the biomass index of grey seals provided the best fit for the dynamic model, but was not included among the 2 covariates that improved the fit of the regression model ($p < 0.05$).

With the exception of the Gulf of Alaska, water temperature was an important covariate in all systems and most models in Table 2, either as SST or temperature at depth. Large-scale climatological signals such as the North Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO), or Atlantic Multidecadal Oscillation (AMO) increased the fit of the model to the data for 7 ecosystems, and were the most important covariate in 4 of the regression models and 1 dynamic model. In some systems, local covariates were important, such as a measure of sea ice in the Barents Sea, the Siberian/Alaskan Index in the eastern Bering Sea, a composite index in Newfoundland-Labrador, winter average sea surface height in Hecate Strait, and water stratification on the western and eastern Scotian Shelf. In 3 ecosystems, a biological predator covariate improved the

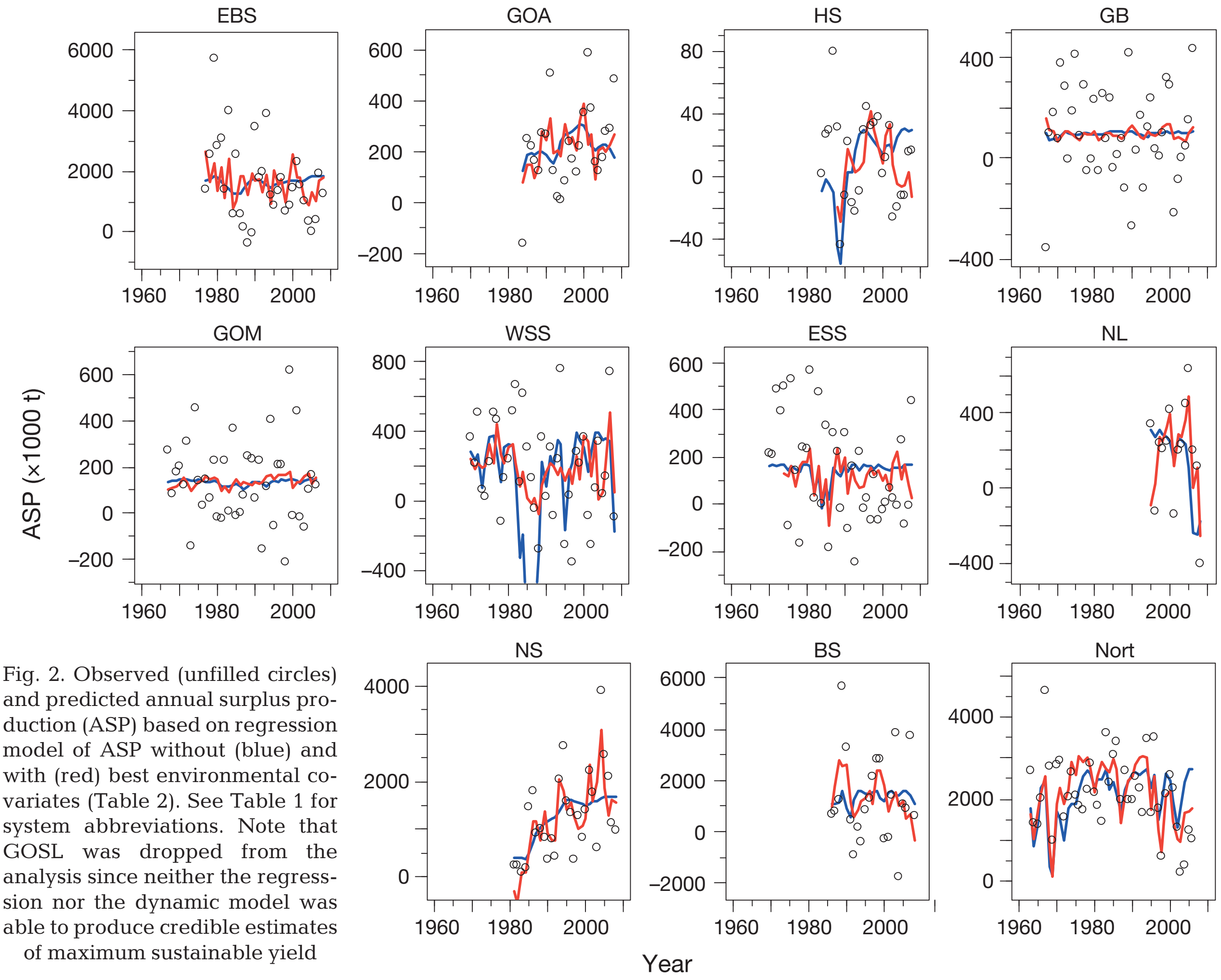

Fig. 2. Observed (unfilled circles) and predicted annual surplus production (ASP) based on regression model of ASP without (blue) and with (red) best environmental covariates (Table 2). See Table 1 for system abbreviations. Note that GOSL was dropped from the analysis since neither the regression nor the dynamic model was able to produce credible estimates of maximum sustainable yield

model fit: the biomass index of grey seals on the eastern Scotian Shelf (both models) and on the western Scotian Shelf (dynamic model), and biomass of arrowtooth flounder in Hecate Strait (both models).

When compared across all 4 models, the estimated MSY per unit area (Fig. 5a) differed statistically among systems (weighted 2-way ANOVA: $F_{11,33}$ = 43.9, p < 0.001) as well as among models ($F_{3,33}$ = 8.18, p < 0.001). Overall estimates largely ranged between 1 and 5 t km^{-2} (20th percentile = 1.22, 80th percentile = 5.28). Furthermore, in several cases, MSY per unit area estimates were relatively consistent across the 4 models, i.e. Barents Sea, Norwegian Sea, and Gulf of Maine. In other cases, the addition of the covariate term made a large difference to MSY, such as Hecate Strait (38 %, regression model), western Scotian Shelf (56 %, dynamic model), eastern Scotian Shelf (63 %, dynamic model), and Newfoundland-Labrador (43 %, dynamic model). However, the sensitivity of the results to the method used was moderate, as the rank of the ecosystems' MSY per area was largely independent of the method: North Sea, eastern Bering Sea, and western Scotian Shelf were always in the top 50 %, and Hecate Strait, Newfoundland-Labrador, eastern Scotian Shelf, and Gulf of Alaska were always in the bottom 50 %; other systems were intermediate.

Estimates of F'_{MSY} also differed statistically across ecosystems ($F_{11,33}$ = 48759, p < 0.001), but not across models (F = 0.0563, p = 0.982; Fig. 5b). Estimates of F'_{MSY} were substantially higher for Georges Bank and North Sea than for the other systems, which ranged between 0.1 and 0.4 yr^{-1}.

Estimates of B_{MSY} generally range between 5 and 15 t km^{-2}, although lower values occurred in Newfoundland-Labrador and the highest values occurred in eastern Bering Sea (Fig. 5c).

Thus, variability notwithstanding, the biological parameter estimates from each method, with or without covariates (Fig. 5), indicate that MSY is largely between 1 and 5 t km^{-2}, that the optimal exploitation rate (F'_{MSY}) is between 0.1 and 0.4 yr^{-1}, and B_{MSY} gen-

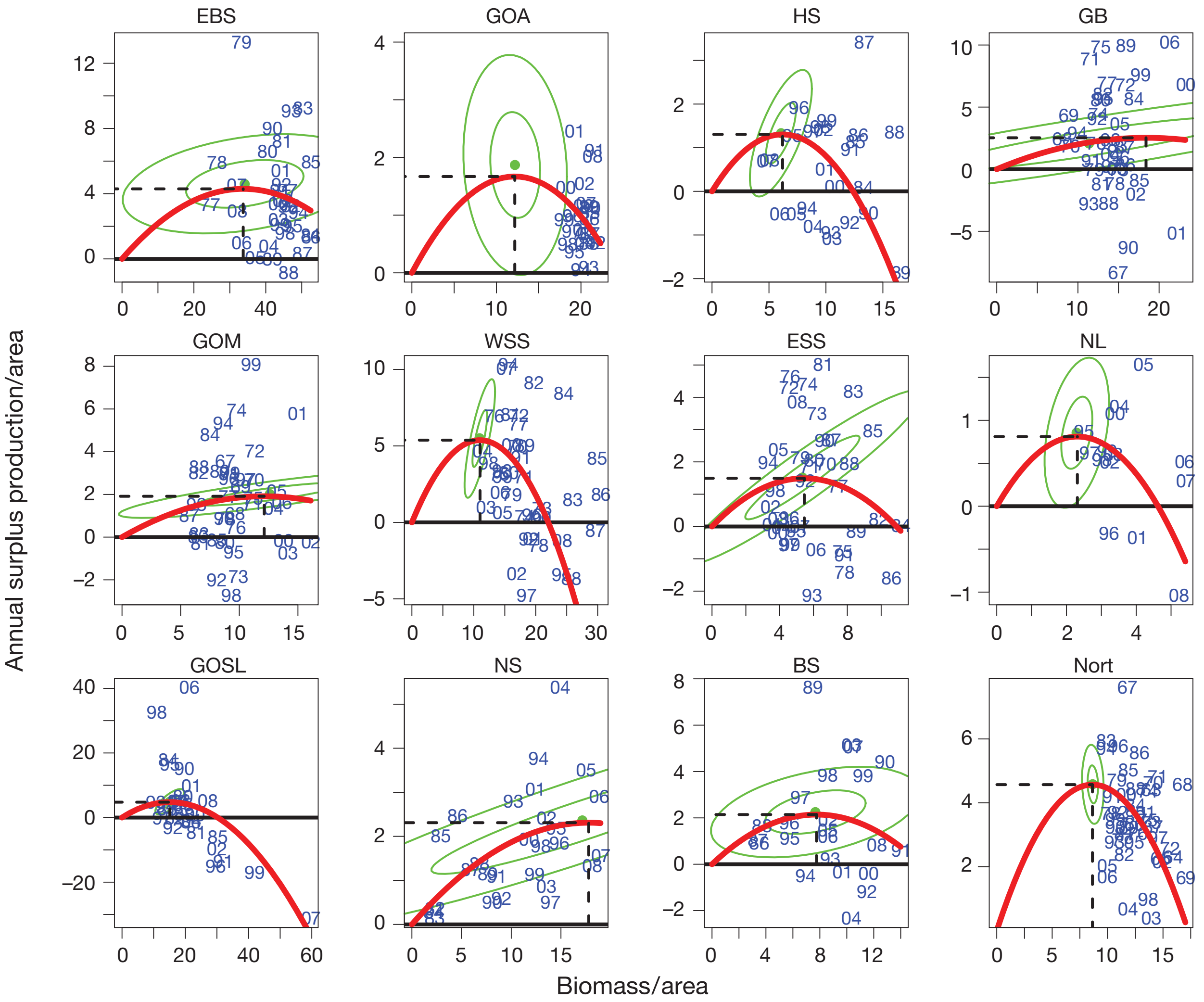

Fig. 3. Observed (blue numbers, labeled by year) and predicted annual surplus production (ASP) from the regression model (red line). All models includes a first-order autocorrelation term, except ESS for which the model failed when including such a term. The horizontal and vertical dotted lines represent, respectively, the MSY (the maximum sustainable yield) and the B_{MSY} (the biomass at which MSY occurs). Green ellipses represent uncertainty of B_{MSY} and MSY, calculated based on the variance-covariance matrix of the model; the inner and the outer ellipse is expected to contain the real B_{MSY} and MSY with a probability of 0.5 and 0.95, respectively. See Table 1 for system abbreviations

erally ranges between 5 and 15 t km^{-2}. An exception is the Norwegian Sea, which shows a considerably higher optimal exploitation rate (0.6 to 1.2 yr^{-1}, depending on the method).

MSY and number of species

In order to exclude the possibility that MSY was influenced by the number of species included in each model (Table 1; Table S1 in the supplement), we tested the relationship between MSY per area and the number of species represented in each modeled ecosystem, but found no relationship (regression model without covariates: $R^2 < 0.001$, with covariates: $R^2 = 0.029$; dynamic model without covariates: $R^2 = 0.008$, with covariates: $R^2 = 0.041$).

MSY and productivity

We found no relationship between MSY per unit area and ordinary measures of productivity (chl *a* concentration and PP); nor did MSY seem to be related to mean wind speed (Fig. S2 in the supplement). There was a possible positive relationship between the flux of chlorophyll and MSY for 3 out of 4 MSY estimates, but the relationships were not sta-

Table 2. Best environmental covariates (based on improved model fit as well as most reasonable or least uncertain parameter values) for regression models of annual surplus production (ASP) and for biomass dynamic models. The best fitting covariate is listed first. Covariates in **bold** improved the fit of both models. Column *l* shows time lag between the covariate and the effect in the model, which was varied between 1 and 7 yr, fitted model parameters are δ (magnitude and sign of effect of the covariate on ASP) and γ (magnitude and sign of effect of the covariate on population growth), and ΔAIC_c is the difference in Akaike information criterion (AIC_c) between models with covariates and models without (Hurvich & Tsai 1989, Burnham & Anderson 2002). AMO: Atlantic Multidecadal Oscillation, avg.: average, NAO: North Atlantic Oscillation, nd: not determined, PDO: Pacific Decadal Oscillation, SST: sea surface temperature, temp.: temperature. See Table 1 for system abbreviations

System	Regression model				Dynamic model			
	Covariate	*l*	δ	ΔAIC_c[a]	Covariate	*l*	γ	ΔAIC_c[a]
EBS	**Summer avg. SST**	1,7	−517.3	−3.43	Siberian/Alaskan Index	1	−0.82	−7.1
	PDO	7	−502.0	−2.03	**Summer avg. SST**	1	−0.63	−6.9
GOA	PDO	0	−68.8	−3.33				
HS	**Biomass index of arrowtooth flounder**	4	−21.3	−6.69	**Biomass index of arrowtooth flounder**	4	−1.48	−13.5
	Winter avg. SST	4	10.3	−2.86	**Winter avg. surface height**	1	−2.11	−3.9
GB	**Annual avg. SST**	2	−21.1	−2.58	**Annual avg. SST**	5	0.24	−12.3
GOM	NAO index	3	21.5	−4.24	Annual avg. SST	3	−0.18 0.11	−2.0
WSS	Annual avg. water temp. at 50 m	1	103.9	−3.25	Biomass index of grey seals	0	−0.62	nd[b]
	Annual avg. stratification	3	−93.6	−2.28				
	NAO index	7	−91.0	−2.06				
ESS	Annual avg. water temp. at bottom	4,6	56.7	−4.11	**Biomass index of grey seals**	0	−1.92	nd[b]
	Biomass index of grey seals	0,1,2	−101.5	−3.47				
	Annual avg. water temp. at 50 m	3	81.8	−3.29				
NL	Composite of environmental indices	1	230.0	−6.02				
	NAO index	5	189.7	−4.20				
	Avg. SST (Stn 27)	2	237.8	−3.76				
NS	AMO	6	638.3	−12.58	Annual avg. SST	5	0.65	nd[b]
					NAO index	1	−0.30	−3.3
BS	**Annual avg. temp.**	2,3	−893.0	−7.4	Index of sea ice cover	6	0.76	−19.5
					Annual avg. temp.	4	−0.57	−17.5
Nort	**AMO**	0	−513.7	**−8.32**	NAO index	1	−0.12	−24.4
	Annual avg. surface water temp.	0,1	−384.2	−6.55	**AMO**	0	−0.24	−24.4

[a] For covariates with >1 time lag, best improvement in % fit is shown

[b] Cannot compare AIC with and without environmental covariates because the years of data were different between the 2 models

tistically significant (p-values from 0.07 to 0.18). Since we observed a tendency for larger areas to have higher MSY per area in these results, we further explored the potential relationship between MSY and productivity using multiple linear regression with ecosystem area as a second covariate. There appeared to be a joint effect for the mass flux index with ecosystem area; mass flux had a significant positive effect ($p < 0.05$) on MSY for 3 of the 4 MSY estimates (Fig. 6).

DISCUSSION

Our results highlight several novel findings: (1) MSY is largely between 1 and 5 t km^{-2}, (2) the optimal exploitation rate F'_{MSY} is between 0.1 and 0.4 yr^{-1}, (3) B_{MSY} varies between 5 and 15 t km^{-2}, (4) the environment, specifically water temperature, notably affects estimates of MSY across most ecosystems studied, and (5) the relationship between fisheries yield and PP is not as simple as suggested in other studies (Iverson 1990, Ware & Thomson 2005, Chassot et al. 2007). Our analyses give some new insights into the similarities and differences among ecosystems, and suggest that reasonable and consistent estimates of system-level MSY can be obtained, which can provide useful ecosystem-level reference points. We discuss each of these findings in further detail below.

A reasonably consistent picture

Although there was surprising consistency in the estimated reference points, there was some variation

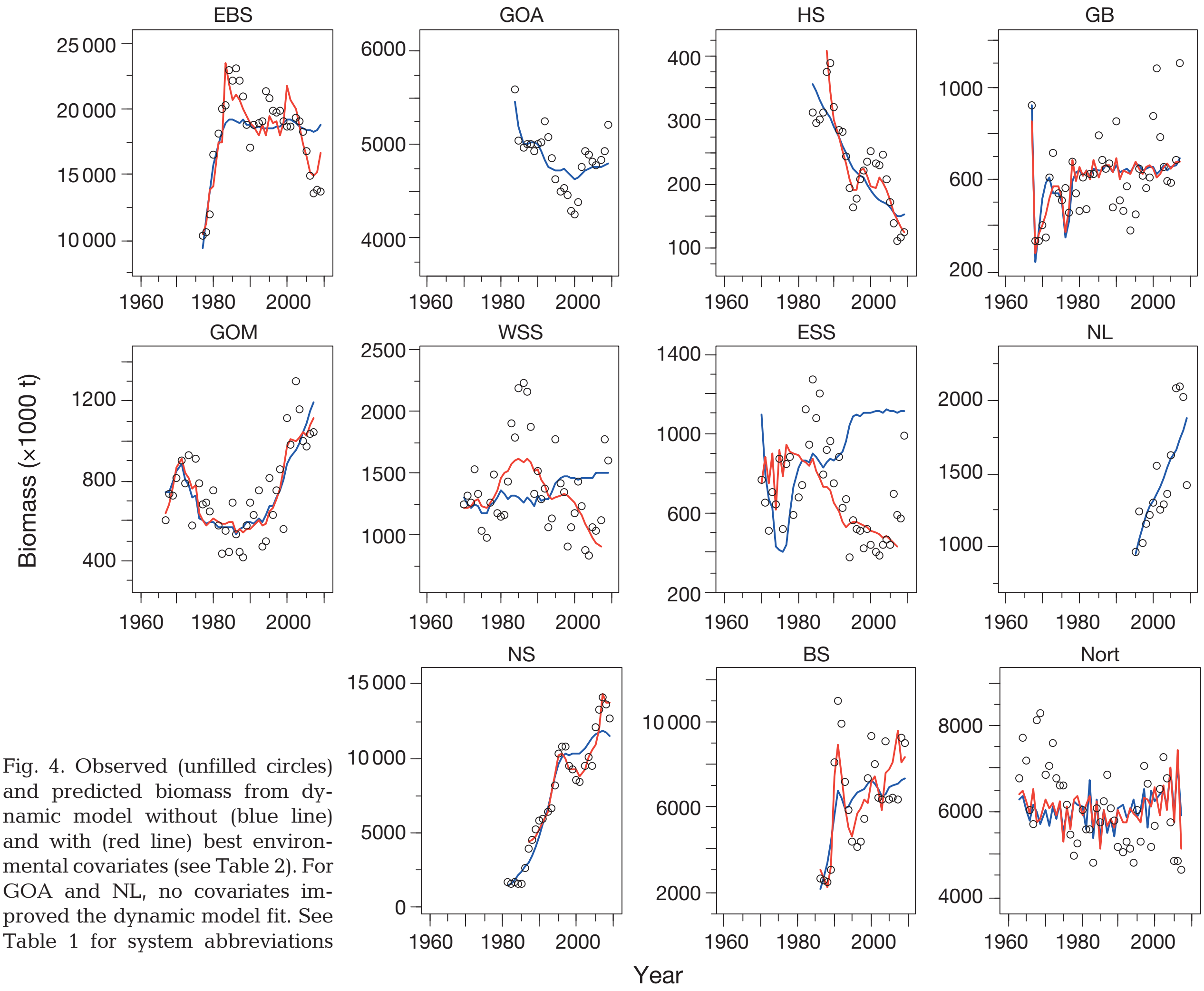

Fig. 4. Observed (unfilled circles) and predicted biomass from dynamic model without (blue line) and with (red line) best environmental covariates (see Table 2). For GOA and NL, no covariates improved the dynamic model fit. See Table 1 for system abbreviations

among models and ecosystems. This is to be expected because the ecosystems modeled had different fishing histories, different data sources (assessment or survey-based), and different lengths of time series. The regression and dynamic models yielded different results for a few ecosystems, which increased when covariates were added, but overall provided a reasonably consistent picture across methods, strengthening our conclusions. We note that including or excluding covariates had a significant effect on parameter estimates. However, the sensitivity of the results to the method used was moderate, as the relative magnitude and rank of the ecosystems' MSY per area was largely independent of the method. Where there were differences, the data pattern may have had a large influence on the robustness of the estimates.

We recognize that the aggregated surplus production models, like all models, are oversimplifications because they treat the entire fish community as a single, aggregated 'population', model the dynamics of this aggregate 'population' using an average growth rate and carrying capacity that is invariant to age structure and species composition, and assume that there is no change in productivity or carrying capacity over time. The latter point is important for the eastern Canadian systems, which have all undergone a potential regime shift (Benoît & Swain 2008, Bundy et al. 2009, Shackell et al. 2010, DFO 2011). An examination of empirical estimates of surplus production provides a useful tool to detect and better understand such changes in productivity (Walters et al. 2005). Future work should explore the effect of changes in productivity on MSY and other BRPs or harvest control rules (Mohn & Chouinard 2007, Brunel et al. 2010).

Common drivers at the basin scale

In most ecosystems, the model fits to the data were improved by adding a covariate. Water temperature improved either or both model fits for all ecosystems, except the Gulf of Alaska. At a basin scale, in the North Pacific the PDO improved the fit of the eastern Bering Sea (regression) and Gulf of Alaska (regression) models, and the Siberian/Alaskan Index, reflecting ice conditions in the Bering Sea, was significant only in the eastern Bering Sea dynamic model. In the NW Atlantic, the NAO improved the model fits for 3 of the 5 ecosystems (Gulf of Maine, eastern Scotian Shelf, Newfoundland-Labrador regression models), but the AMO did not improve the fit for any NW Atlantic ecosystem. In the NE Atlantic, the NAO and AMO also improved the fit for 2 of the 3 ecosystems. Thus these large-scale oceanographic indices (that largely reflect water temperature variability) may influence ecosystem dynamics and productivity over the whole North Atlantic basin. In addition, more local environmental influences were important for most ecosystems. In particular, the Hecate Strait models were most influenced by the predator biomass and winter average sea surface height, a local composite index (Colbourne et al. 2010) improved the fit of the Newfoundland-Labrador regression models, and sea ice was the most important covariate in the Barents Sea (dynamic model). Since the inclusion of a covariate had a substantial effect on MSY in some cases (e.g. western Scotian Shelf), understanding the importance of different environmental covariates on system productivity could lead to improved management by developing robust models, such as those developed here, to take environmental effects into consideration when determining reference points and setting overall quotas.

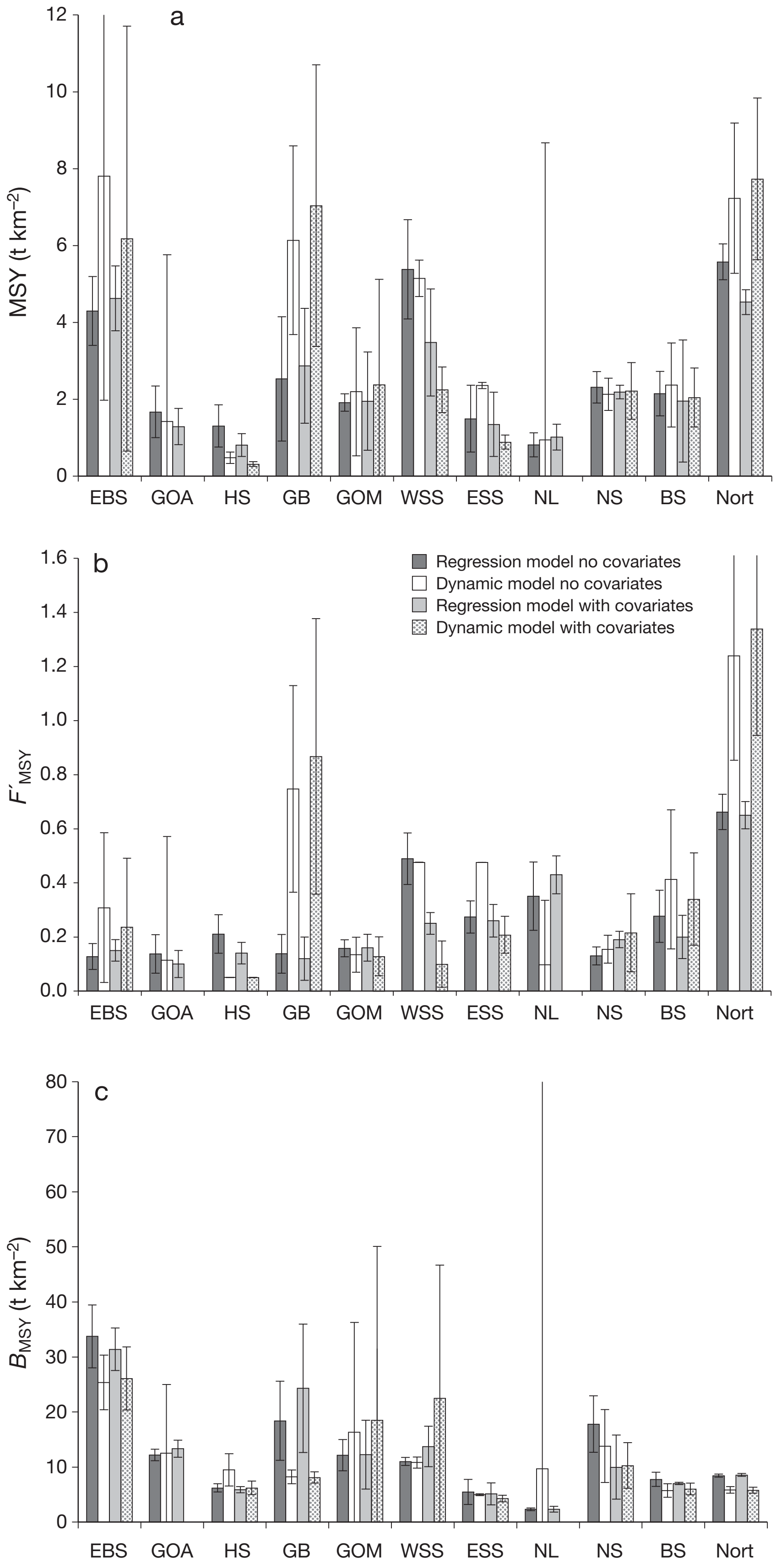

Fig. 5. (a) Maximum sustainable yield (MSY) per area, (b) exploitation rate at MSY (F'_{MSY}), and (c) biomass at MSY (B_{MSY}) per area, for each region and for each method. Results (a,c) from the best-fitting covariates for each model (see Table 2). Error bars indicate 1 SD. See Table 1 for system abbreviations

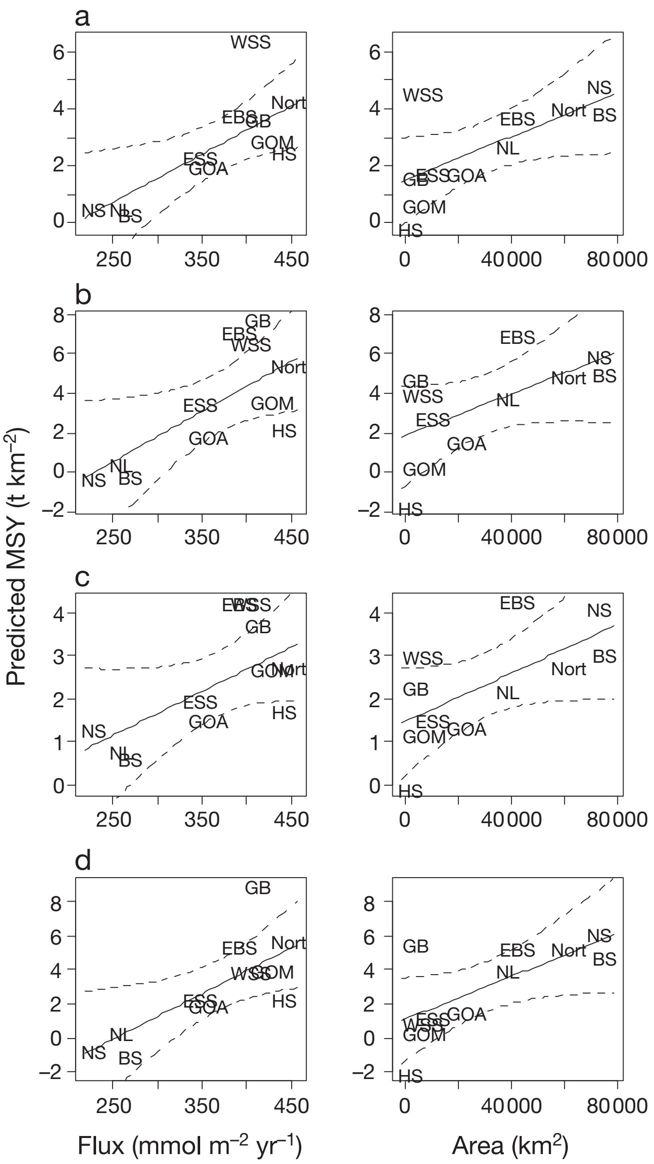

Fig. 6. Multiple linear regression results for maximum sustainable yield (MSY) per area as a function of ecosystem area (right panels) and mass flux index (left panels) under (a) regression model (no covariates), (b) dynamic model (no covariates), (c) regression model (with covariates), and (d) dynamic model (with covariates). Solid and dotted lines represent linear regressions and their 95% confidence intervals, respectively. See Table 1 for system abbreviations

Impact of covariates on BRPs and implications for fisheries management

Surplus production models, like most stock assessment models, assume stationarity in productivity. Violations of this assumption are common and can lead to biases in BRPs estimated from stock-recruitment dynamics (Parma 1990) or from surplus production dynamics (Walters et al. 2005). Empirical estimates of surplus production such as those used here can provide insights into processes causing non-stationarity (Walters et al. 2005), and environmental covariates can be included into surplus production models to account for non-stationarity and to obtain improved reference points (Jacobson et al. 2005). In the absence of *a priori* hypotheses, we used an exploratory approach to assess the influence of selected environmental variables of surplus production dynamics and found strong evidence that aggregate surplus production is linked to environmental variability.

In those cases where the covariate improved the model's fit to the biomass data for the dynamic model (i.e. eastern Bering Sea, Hecate Strait, western Scotian Shelf, and eastern Scotian Shelf), the inclusion of a covariate resulted in a lower MSY (under average conditions) than in the model without a covariate. In the case of the eastern Bering Sea, increased temperatures after the 1976–1977 regime shift were associated with reduced sea ice cover, and both temperatures and sea ice conditions have shown pronounced variability in the last decade (Hunt et al. 2011). Recent high-temperature, low-ice conditions had a negative impact on the recruitment of species such as cod and pollock in the eastern Bering Sea and Gulf of Alaska (Mueter et al. 2009, 2011), which will affect overall fish production and may result in decreased MSY if temperatures increase in the future. In the other 3 models, the addition of a major predator as the covariate improved the fit of the model and decreased MSY. In Hecate Strait, arrowtooth flounder is a voracious predator whose diet consists of 75% fish (Pearsall & Fargo 2007). For the period from 1984 to 2009, it comprised 41% of the predator biomass of herring (Schweigert et al. 2010). The fit of the western Scotian Shelf and eastern Scotian Shelf models was improved with the addition of grey-seal biomass as a covariate. Grey seals are a top predator on the eastern Scotian Shelf (Bundy 2005, Trczinski et al. 2009) and their distribution is expanding to the western Scotian Shelf (Trzcinski et al. 2009, DFO 2011). The trophic role of grey seals and the extent to which they are responsible for the non-recovery of groundfish stocks has been the subject of considerable controversy on the Scotian Shelf (DFO 2011), in the Gulf of St. Lawrence, and in Newfoundland-Labrador. Interestingly, seal biomass did not improve the model fits in Newfoundland-Labrador.

The time lag of the environmental variables was in most cases less than 3 to 4 yr. Time lags of 1 yr indicate that the environment affects the somatic growth of fish, while time lags >1 yr can be the result of the environment affecting recruitment. In the latter case we would expect the environment to have the largest impact on the early juvenile stages, hence changes in biomass will be apparent 2 to 4 yr later when a cohort first becomes fully or largely vulnerable to the survey gear or is first included in the assessment. A few time lags were somewhat longer than expected from this mechanism and further examination is warranted to tease apart the mechanisms underlying them.

We recommend that aggregate MSY could be considered an overall limit for total removals from an ecosystem, and that the cumulative MSY of individual stocks should not exceed it, as suggested by other studies (Brown et al. 1976, Walters et al. 2005, Mueter & Megrey 2006, Tyrrell et al. 2011) and similar to the existing caps on total removals in the Bering Sea and Gulf of Alaska (Witherell et al. 2000). Further, we would suggest that the aggregate MSY should be exploited in a 'balanced' way, across stocks in relation to their productivity (Bundy et al. 2005, Zhou et al. 2010, Garcia et al. 2011, 2012). This could first be explored using surplus production models at different levels of aggregation (see Fogarty et al. 2012, this Theme Section, Gaichas et al. 2012b, this Theme Section, Holsman et al. 2012b, this Theme Section, Lucey et al. 2012, this Theme Section). Aggregate limits can provide an additional tool for managers to prevent ecosystem overfishing, in combination with single-species limits that are required to prevent the loss of the least common (or most easily caught) fish species, or those with lower intrinsic growth rate (Worm et al. 2009, Garcia et al. 2011, Gaichas et al. 2012b).

MSY and PP

Our results suggest a useful rule of thumb for MSY in the northern hemisphere: MSY appears to vary between 1 to 5 t km^{-2} for these ecosystems. This variation is approximately as large as the variation in average phytoplankton concentrations (which varies up to 7-fold among systems), but contrary to what we expected, MSY does not vary consistently with phytoplankton concentration nor with estimated PP. However, if we exclude Hecate Strait from the analysis (an obvious outlier), a positive relationship between chlorophyll concentration and MSY emerged, but most of the variation in MSY is still unexplained. This contrasts with the findings of Iverson (1990), Ware & Thomson (2005), and Chassot et al. (2007), who found that realized fisheries yield per area varies linearly with PP and/or with chlorophyll concentration. However, other studies (e.g. Sherman et al. 2009, Chassot et al. 2010, Conti & Scardi 2010, Friedland et al. 2012) also failed to find a close relationship between PP and fisheries yield; Chassot et al. (2010) found that 3 additional factors — the probability of an ecosystem being sustainably fished (P_{sust}; Libralato et al. 2008), average maximum length of fish, and ecosystem type — were required to explain 77% of the variability in catch across LMEs globally (measured as PP required, PPR; Pauly & Christensen 1995). They found a tighter relationship between catch and PP when catch was expressed as PPR. It is possible that if we calculated MSY as PPR, we might find similar results: however, it is not possible to disaggregate the aggregate production estimate of MSY into MSY per trophic level with the models used here. Friedland et al. (2012) also noted that the relationship between lower-trophic-level dynamics and pathways with fisheries yield is not a straightforward linear relationship with standing phytoplankton biomass.

We challenge previous findings that suggest a simple linear relationship between catch and PP (see also Frank et al. 2006). Our exploratory analyses suggest that MSY increases with total ecosystem area and the mass flux index. The latter index measures the mass flux of POC (Honjo et al. 2008, Friedland et al. 2012); a high value indicates that much of the energy produced by primary producers is transferred to mesozooplankton and thereby to higher trophic levels. Ecosystems characterized by strong thermal transitions and pronounced blooms will tend to have high values of POC flux. Thus, a positive relationship between maximum production and the mass flux index is consistent with the hypothesis that efficient energy transport from primary producers to higher trophic levels is more important than high PP per se.

In conclusion, we compared aggregate system production models across 12 northern hemisphere ecosystems to explore likely production caps for aggregate commercial species. We assert that total species-specific MSYs should be managed within this aggregate limit to reduce the risk of ecosystem overfishing (Murawski 2000), using a balanced harvesting approach (Garcia et al. 2012). That the triad of drivers explored here influences MSY and productivity is not surprising; that environmental drivers were almost always important was surprising. Importantly, although in some cases the 2 models (regression and dynamic) produced different estimates, there was reasonable consistency among the covariates that were important for model fit, relative magnitude of outputs, and the rank ordering of systems by each model. Since in most cases where the inclusion of a covariate significantly improved model fit it resulted in reduction of MSY, we strongly recommend that environmental and trophic covariates be explored when estimating MSY for management purposes (see also Link et al. 2012). These results have implications for fisheries management (Walters et al. 2005) and an ecosystem approach to management (Murawski 2007, Link 2010, Belgrano & Fowler 2010), particularly in the context of changing sea water temperatures as a result of climate change (Belkin 2009).

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Contribution to the Theme Section 'Comparative analysis of marine fisheries production'

Comparative analyses of surplus production dynamics of functional feeding groups across 12 northern hemisphere marine ecosystems

Sean M. Lucey[1,*], Adam M. Cook[2], Jennifer L. Boldt[3], Jason S. Link[1], Timothy E. Essington[4], Thomas J. Miller[5]

[1]National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, Massachusetts 02543, USA
[2]Fisheries and Oceans Canada, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada
[3]Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, British Columbia V9T 6N7, Canada
[4]School of Aquatic and Fishery Sciences, University of Washington, UW Box 355020, Seattle, Washington 98195, USA
[5]Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, PO Box 38, Solomons, Maryland 20688, USA

ABSTRACT: Progress on ecosystem approaches to fisheries management requires comparative studies with standardized methods that incorporate readily available data. This precludes complex ecosystem models in favor of simpler models such as surplus production models. Surplus production models for individual species can provide estimates of common biological reference points such as maximum sustainable yield (MSY) and the corresponding stock biomass level (B_{MSY}). For ecosystem approaches, summing multiple single-species surplus production models to estimate the ecosystem MSY ignores potential biological and fishery interactions among species. Improved estimates of ecosystem-level MSY can be obtained by aggregating species, thereby accounting for known interactions among species. Here, we fit surplus production models to 3 different types of aggregations for 12 northern hemisphere marine ecosystems. Aggregations were based on habitat (benthic/pelagic), foraging guild (planktivore/zoopivore/benthivore/piscivore) and size class (small/medium/large). The objectives of this work were to explore, compare and contrast model outputs across the various types of aggregations and among ecosystems. We found that regardless of the type of aggregation, aggregate production never exceeded 6 t km^{-2} and was generally less than 3 t km^{-2}. Patterns of production varied among ecosystems with no particular pattern with respect to ocean basin, latitude or component species. Aggregated surplus production models can provide biological reference points that are familiar to fishery managers and can be used to set overall removals with respect to aggregate group as long as less productive stocks are protected.

KEY WORDS: Biological reference point · Ecosystem · Fisheries · Maximum sustainable yield · Species aggregation · Surplus production · Trophodynamic

INTRODUCTION

There is a growing emphasis in using comparative ecosystem studies to foster broader, ecosystem approaches to fisheries management (Murawski et al. 2010). Recognized as a way to provide ad hoc replication that is otherwise impossible owing to the large spatial scale and overall complexity of marine ecosystems, comparative studies have been at the core of international programs such as Global Ocean Ecosystem Dynamics (GLOBEC), European Research on Ocean Ecosystems under Anthropogenic and Natural Forcings (EUR-OCEANS), Indicators for the Seas (IndiSeas) and Comparative Analysis of Marine

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*Email: sean.lucey@noaa.gov

Ecosystem Organization (CAMEO) (Megrey et al. 2009). Comparative studies have been used to gain insights on individual species, such as Atlantic cod *Gadus morhua* via ICES/GLOBEC's Cod and Climate program (e.g. Brander 1995, Planque & Fredou 1999, Dutil & Brander 2003, Ratz & Lloret 2003, Drinkwater 2005), and groups of species such as small pelagics (Checkley et al. 2009), as well as whole ecosystems (e.g. Hunt & Drinkwater 2005, Shannon et al. 2008, Gaichas et al. 2009, Link et al. 2009). Comparing similar ecosystems allows us to improve our understanding of and draw generalizations about ecosystem structure (ICES 2001, Megrey et al. 2009, Murawski et al. 2010). The implementation of these generalizations in the form of decision support tools (Kangas et al. 2008) will be an important step in supporting ecosystem-based fisheries management (EBFM; Murawski et al. 2010).

In order to facilitate comparative studies, approaches must be standardized using methods that can be readily applied to existing data. This precludes using complex ecosystem models, which, although powerful, are usually tailored to specific ecosystems. Models of lower complexity can often outperform more complicated models in terms of forecast ability (Costanza & Sklar 1985, Walters 1986, Fulton et al. 2003, Fogarty et al. this volume). Therefore, a preferred solution would be to use simpler models such as surplus production models as the foundation for comparative ecosystem studies. Surplus production models relate a population's production to its current size accounting for fishery removals. This approach relies on readily available data (biomass and landings) and is relatively robust to breach of assumptions (Restrepo et al. 1999). Although surplus production models have their strengths (e.g. limited data demands, ability to generate biological reference points) and weaknesses (e.g. lack of population structure, limitations on time lags), they have generally been deemed useful in fisheries science (Ludwig & Walters 1985, 1989, NRC 1998).

When considering production at the ecosystem level, exploring aggregated properties of biotic communities has value. Current single species reference points are derived from assessments that consider each species in isolation from the ecosystem; however, individual species catches cannot be considered independently in multispecies fisheries as a result of both biological and fishery interactions (McHugh 1959, Murawski 1984, 1991). When such interactions are ignored, the sum of single species maximum sustainable yields (MSYs) is often greater than that sustainable by the ecosystem. Yet, evaluations of overall potential yield from multispecies fisheries assessments suggest that system- or aggregate-level MSY is generally less than the sum of the individual species MSYs (Pope 1975, Brown et al. 1976, May et al. 1979, NEFSC 2008). By aggregating the species within ecosystems into functional groups or aggregate system biomasses, reasonable multispecies equivalents to single species reference points can be obtained (Mueter & Megrey 2006, Sparholt & Cook 2010).

There are multiple reasons for using an aggregated approach to evaluate production at the ecosystem level. First, the energy available from lower trophic levels is limited and shared by the entire suite of living marine resources (LMR), including all fishes and invertebrates. That is, the production available to LMR for any given area of the ocean is constrained by lower trophic level production (Pauly & Christensen 1995, Pauly et al. 1998, 2002). Second, because fish stocks have different productivities, it is often difficult to simultaneously attain single stock objectives in multispecies fisheries (May et al. 1979). Third, there are biological and/or technological interactions that may not always be directly accounted for in single species assessments (Pope 1975, 1979, Fukuda 1976, May et al. 1979, Mayo et al. 1992). However, aggregate models account for all of these interactions without having to explicitly estimate them as in multispecies models (Hollowed et al. 2000, Livingston & Jurado-Molina 2000). In addition, the aggregate approach provides reference points that are familiar to both fishery scientists and LMR managers, but in an ecosystem context.

Here we explore, compare and contrast production model outputs across both various aggregation schemes and multiple ecosystems. This work is part of a hierarchy of studies in which surplus production models were used to undertake comparative ecosystem studies. Holsman et al. (2012, in this Theme Section) present simple surplus production models of cod and herring to examine the potential for biophysical, trophodynamic and exploitative drivers to explain patterns in production. In contrast, Bundy et al. (2012, in this Theme Section) conducted an examination of full system-level aggregate production using surplus production modeling. Here we aggregated species using 3 different aggregation types — habitat, feeding guild and size class — thereby examining processes at a resolution intermediate between Holsman et al. (2012) and Bundy et al. (2012). The aggregation types define functional roles without regard to taxonomy, highlighting important trophodynamic and functional ecological groups and habitat representations within the ecosystems (Werner & Gilliam 1984, Ross 1986, Hawkins & Macmahon 1989, Austen et al. 1994, Fogarty & Murawski 1998, Piet et al. 1999, Garrison & Link 2000, Brose et al. 2006). Species within these aggregations should share similar life history traits and respond similarly to perturbations to the system. Interactions within these aggregations tend to result in compensatory dynamics, which are more stable than individual species dynamics (e.g. Duplisea & Blanchard 2005, Auster & Link 2009). Because of this, management based on single species dynamics may not have the desired results and, hence, the need for decision support tools based on broader ecosystem dynamics merits exploration (Walters & Kitchell 2001, Walters et al. 2008).

MATERIALS AND METHODS

The best available information for landings data and biomass estimates were assembled for all commercial species across 12 northern hemisphere ecosystems (Link et al. 2010 and are described in further detail in Fu et al. 2012, in this Theme Section). The ecosystems investigated were the Baltic Sea, Barents Sea, eastern Bering Sea, eastern Scotian Shelf, Georges Bank, Gulf of Alaska, Gulf of Maine, Hecate Strait, North Sea, Norwegian Sea, southern Gulf of St. Lawrence and western Scotian Shelf (see Fig. 2 in Link et al. 2012, in this Theme Section). The longest available time series for both landings and biomass from each ecosystem were used for the analyses (Table 1). Biomass estimates were acquired from stock assessments, fishery independent surveys corrected for catchability (q) or minimum trawlable swept-area estimates from fisheries independent surveys, depending on the ecosystem and species. Though very infrequent, data for years with missing biomass estimates were linearly interpolated (Fu et al. 2012).

Data were combined based on 3 different species aggregation types within each ecosystem. The first type of aggregation was based on the habitat in which species primarily spend their time foraging: demersal or pelagic habitats. The second type of aggregation was based on specific diet information and species were grouped according to their feeding guild. Originally, there were 7 feeding guilds identified for this project (Link et al. 2010, Fu et al. 2012); however, only 4 of those had sufficient numbers of species across multiple ecosystems for analyses here: planktivores, zoopivores (those animals that consumed zooplankton, shrimp and fish), benthivores and piscivores. The final type of aggregation accounted for size-dependent differences in trophic position. Fish species (excluding invertebrates) were aggregated into 3 size class groups based on the 30th and 70th percentiles of the cumulative frequency histogram of maximum fish lengths across all species. The 3 size categories were: 'small' (<55 cm), 'medium' (≥55 cm and <100 cm) and 'large' (>100 cm).

Aggregate annual surplus production (ASP) was calculated for each aggregate group (agg) and ecosystem (j) as:

Table 1. The 12 northern hemisphere ecosystems analyzed in this study. Length of the time series for each aggregation per ecosystem is listed as well as the physical area of the ecosystem. nd: no data for that aggregation within that ecosystem. Ecosystems are: Baltic Sea (BALT), Barents Sea (BS), eastern Bering Sea (EBS), eastern Scotian Shelf (ESS), Georges Bank (GB), Gulf of Alaska (GoA), Gulf of Maine (GoM), Hecate Strait (HS), North Sea (NORT), Norwegian Sea (NS), southern Gulf of St. Lawrence (GSL), and western Scotian Shelf (WSS)

Region	Area	Length of time series (year–year)								
	(km^2)	Demersal	Pelagic	Planktivore	Zoopivore	Benthivore	Piscivore	Small	Medium	Large
BALT	211 069	1974–2008	1974–2008	1974–2008	nd	nd	1974–2008	1974–2008	nd	1974–2008
BS	747 893	1946–2009	1950–2009	1950–2009	1964–2009	1950–2009	1946–2009	1950–2009	1986–2009	1946–2009
EBS	430 829	1954–2009	1964–2009	1964–2009	nd	1954–2009	1976–2009	1954–2009	1964–2009	1977–2009
ESS	113 704	1970–2008	1970–2008	1970–2008	1970–2008	1970–2008	1970–2008	1970–2008	1970–2008	1970–2008
GB	42 154	1963–2009	1963–2009	1963–2009	1963–2009	1963–2009	1963–2009	1963–2009	1963–2009	1963–2009
GoA	238 439	1950–2009	1950–2009	1950–2009	1960–2009	1977–2009	1950–2009	1961–2009	1961–2009	1950–2009
GoM	76 483	1963–2009	1963–2009	1963–2009	1963–2009	1963–2009	1963–2009	1963–2009	1963–2009	1963–2009
HS	23 501	1984–2009	1951–2009	1951–2009	1984–2009	1984–2009	1984–2009	1951–2009	1984–2009	1984–2009
NORT	609 748	1963–2007	1963–2007	1963–2007	nd	1963–2007	1963–2007	1963–2007	1963–2007	1963–2007
NS	728 331	nd	1950–2009	1950–2009	nd	nd	nd	1950–2009	1972–2009	nd
GSL	74 137	1971–2009	1971–2009	1971–2009	1971–2009	1971–2009	1971–2009	1971–2009	1971–2009	1971–2009
WSS	73 344	1970–2008	1970–2008	1970–2008	1970–2008	1970–2008	1970–2008	1970–2008	1970–2008	1970–2008

$$\mathrm{ASP}_{\mathrm{agg},j,t} = B_{\mathrm{agg},j,t+1} - B_{\mathrm{agg},j,t} + C_{\mathrm{agg},j,t} \quad (1)$$

where $B_{\mathrm{agg},j,t}$ is the total biomass of all species within aggregation in ecosystem j for year t and $C_{\mathrm{agg},j,t}$ is the corresponding total catch. We examined the relationship between ASP and annual biomass by plotting $\mathrm{ASP}_{\mathrm{agg},j,t}$ against $B_{\mathrm{agg},j,t}$. We fit both a null model and a Graham-Schaefer surplus production model. The null model assumed that aggregate annual surplus production was linearly related to the aggregate biomass:

$$\mathrm{ASP}_t = \beta B_t \quad (2)$$

where the intercept is 0 (no production at no biomass) and β is the slope of the relationship. While the surplus production model (hereafter the process error model) estimated surplus production as a quadratic function of biomass (Graham-Schaefer functional form with additive error; e.g. Quinn & Deriso 1998) given by:

$$\mathrm{ASP}_t = \alpha B_t + \beta B_t^2 + \varepsilon_t \quad (3)$$

where α and β are regression parameters. The process model assumed deterministic biomass and first-order autocorrelation error structure [$\varepsilon_t = \varphi\varepsilon_{t-1} + V_t$, where $V_t \approx \mathrm{N}(0,\sigma^2)$]. Parameters were estimated with a generalized least squares regression using the package 'nlme' in R (v. 2.14.1, R Foundation for Statistical Computing). This model assumes that observations are made without error and that all of the error occurs in the change in population size (process error). Biological reference points (BRPs) were calculated directly from the process error model parameters; $\mathrm{MSY} = \alpha^2/4\beta$ and $B_{\mathrm{MSY}} = \alpha/2\beta$.

We compared the 2 models using Akaike's information criterion with correction for small sample size (AIC_c; Anderson 2008). Differences in AIC_c between the null and process error models ($\mathrm{diffAIC}_c$) were calculated as:

$$\mathrm{diffAIC}_c = \mathrm{AIC}_{c_{\mathrm{null}}} - \mathrm{AIC}_{c_{\mathrm{process}}} \quad (4)$$

This is similar to ΔAICc, which in typical AIC notation is the difference between a candidate model and the best model, where high ΔAICc values indicate less credibility for the candidate model, with values less than 14 having at least some credibility (Anderson 2008). However, since we used the equation above, we defined diffAICc values of 2 or greater to indicate a better fit by the process error model over the null model, values of between 2 and −2 to indicate equal support for both models and values of −2 or less to indicate a better fit by the null model. Independent of model selection, overall fit of the models to the data was also determined with R^2 value and p-values of regression coefficients.

Finally, comparisons were made across ecosystems by aggregation type. To facilitate comparisons, we standardized the BRPs by the area of the ecosystem (Table 1). Observed variation within aggregate groups was quantified with coefficients of variation (CVs). We then conducted a 2-factor ANOVA to test whether there were significant differences between ecosystems or aggregate groups. Further analysis was done with Tukey's HSD test to make multiple comparisons of means between ecosystems as well as between aggregate groups. Based on these tests, we identified patterns with respect to overall aggregate production across ecosystems and relative production between aggregation types.

RESULTS

There was substantial variation in physical size and fish biomass density among the 12 ecosystems examined. There was a greater than 30 times difference in area between the smallest ecosystem (Hecate Strait, 23 501 km^2) and the largest ecosystem (Barents Sea, 747 893 km^2) (Table 1). Despite these differences, the average annual biomass estimates per unit area from 1984 to 2008 for all aggregate groups were generally $\leq 13\ \mathrm{t\ km}^{-2}$ (0.001 to 31.200 $\mathrm{t\ km}^{-2}$); the one consistent exception was the eastern Bering Sea ecosystem, which had high estimates of biomass per unit area for several of the aggregate groups (Fig. 1). For most aggregate groups, the top species (or species group) contributed over 50 % of the biomass per unit area (Fig. 1, striated area of bars).

Generally, the process error model was more informative than the null model. Some ecosystems lacked species in certain aggregate groups, leaving a total of 98 combinations of ecosystems and aggregate groups for which comparisons could be made. Of the 98 combinations, there was substantial evidence in favor of the process error model being a better fit in 78 instances (79.6 %; Table 2). There was equal support for both models in 17 combinations (17.3 %). Substantial support for the null model was found in only 3 instances (3.1 %). General fit of the process error model to the data was good with a range of R^2 values from 0.031 to 0.928, while 85.7 % and 73.5 % of the α and β parameters were significant at the 0.05 level, respectively (Fig. 2, Table S1 in the supplement at www.int-res.com/articles/suppl/m459p219_supp.pdf). Hecate Strait on average had the lowest R^2 values while the Baltic Sea had the highest. For all eco-

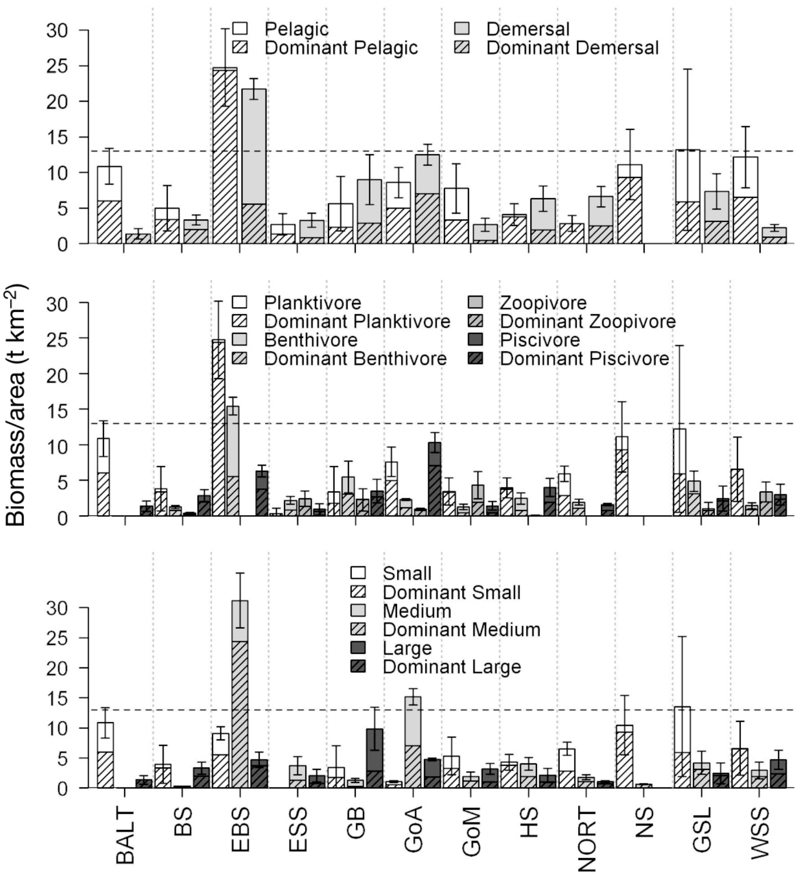

Fig. 1. Average (±SE) biomass per unit area (t km^{-2}) of each aggregation for 12 ecosystems during 1984–2008. Each bar is divided into 2 sections. The bottom striated section of each bar represents the top ranked species or species group (i.e. highest proportion of total biomass). The top section of each bar represents the rest of the species in that group. For reference purposes a horizontal line is shown at 13 t km^{-2}. See Table 1 for definition of ecosystem abbreviations

systems, these R^2 values were generally higher than similar values for the null model.

There were similarities and differences between ecosystems and aggregations with respect to BRPs estimated by the process error model (Figs. 3–5). Estimates of both MSY and B_{MSY} varied between aggregate groups (Table 3). The 2-factor ANOVA showed significant difference between ecosystems and aggregate groups (Table 4). Comparing the differences in means with Tukey's HSD test, we found that most of the differences between ecosystems arose from the 2 systems: the eastern Bering Sea and southern Gulf of St. Lawrence (Tables S2 & S3 in the supplement). Most other ecosystems were not significantly different. As expected, there were more significant differences between aggregate groups (Tables S4 & S5 in the supplement).

Mean values for both MSY and B_{MSY} were larger for the pelagic aggregate group than the demersal aggregate group with values ~1.5 and 1.3 times larger, respectively (Table 3). Estimates of MSY had approximately the same amount of variation for the pelagic and demersal aggregate groups (CVs, 62.9 and 62.2%, respectively; Table 3). There was slightly more vari-

Table 2. Values of diffAIC$_c$ (AIC$_{c_{\mathrm{null}}}$ – AIC$_{c_{\mathrm{process}}}$; see text for explanation). Negative values indicate where the null model fit the data better than the process model. Values that are not shaded indicate combinations for which the process error model had substantially more support than the null model. Light grey boxes show where there is equal support for both models ($-2 < \mathrm{diffAIC_c} < 2$). Dark grey boxes show where there is substantial support for the null model over the process error model. nd: data missing for individual levels of aggregation within ecosystems. See Table 1 for definition of ecosystem abbreviations

Aggregate	Ecosystem											
group	BALT	BS	EBS	ESS	GB	GoA	GoM	HS	NORT	NS	GSL	WSS
Pelagic	0.7	7.4	12.2	9.9	12.2	13.5	9.3	–1.6	44.3	20.4	14.5	–0.4
Demersal	4.0	20.9	20.2	–1.1	17.8	5.7	10.8	4.4	3.5	nd	5.9	51.8
Planktivore	0.7	4.4	12.2	10.8	13.8	8.8	8.8	–1.7	13.6	20.4	13.3	27.2
Benthivore	nd	16.2	18.9	10.5	13.0	2.3	12.2	2.5	6.3	nd	5.4	23.7
Zoopivore	nd	6.5	nd	11.0	16.4	0.8	17.7	–2.7	nd	nd	4.6	14.2
Piscivore	4.0	29.4	–0.5	6.4	16.5	1.6	14.2	4.8	–1.4	nd	0.7	27.3
Small	0.7	4.8	11.5	–2.9	13.9	–1.2	7.3	–1.8	14.6	20.3	14.5	25.7
Medium	nd	8.9	13.5	13.4	27.6	29.8	15.0	5.1	6.2	27.6	2.8	12.6
Large	4.0	23.2	30.3	–0.1	23.6	–3.7	16.6	1.1	7.9	nd	0.7	31.5

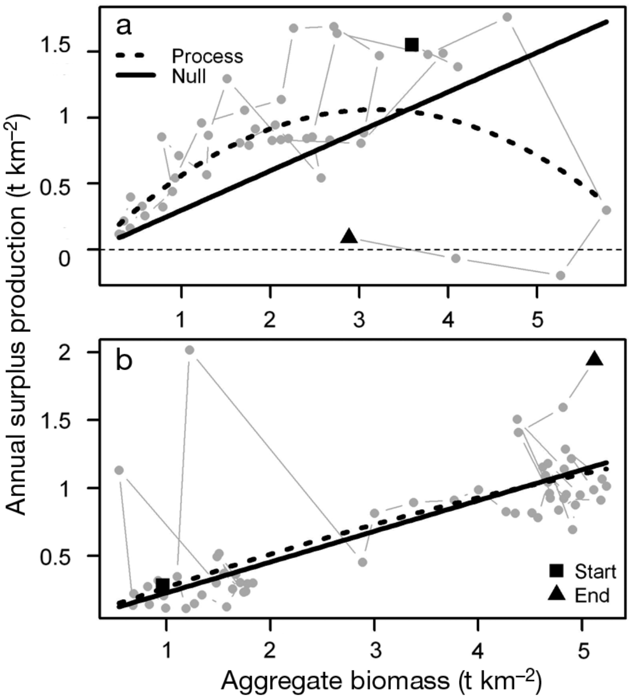

Fig. 2. Examples of the fit by the models to the data. (a) Example where the process error model (thick dashed line) fits the data well (North Sea pelagic aggregate group). This occurs for the majority of the aggregate groups across the ecosystems. (b) Example of where the null model (solid line) fits the data well (Gulf of Alaska 'large' aggregate group). This occurred in only 3 aggregate groups. The thin dashed line shows where annual surplus production equals 0

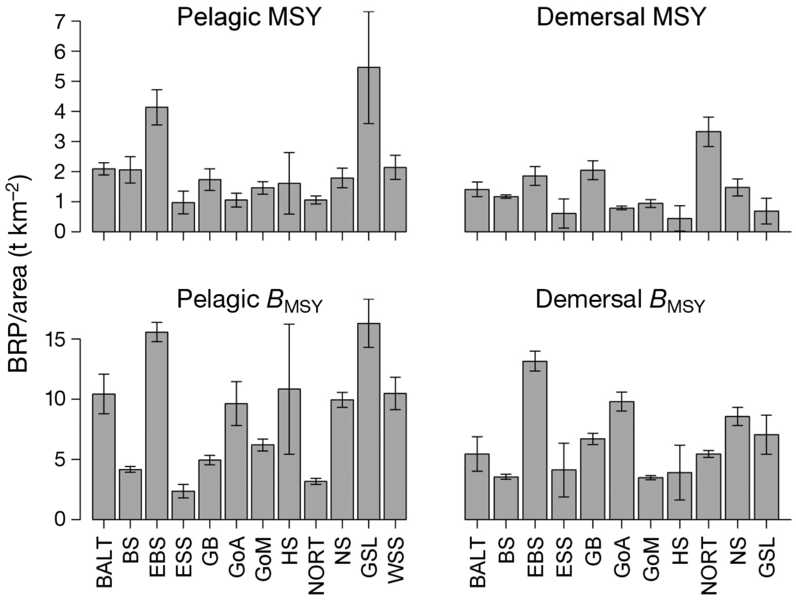

Fig. 3. Area-corrected maximum sustainable yield (MSY) and biomass at maximum sustainable yield (B_{MSY}) derived from the process error model for the habitat aggregation type by ecosystems. See Table 1 for definition of ecosystem abbreviations

ation in the pelagic estimate of B_{MSY} (CV, 52.7%) than the demersal estimate (CV, 46.9%) (Table 3). Estimates of MSY for the pelagic aggregate groups ranged from 0.97 to 5.46 t km^{-2}, while estimates of B_{MSY} ranged from 2.36 to 16.31 t km^{-2} (Table 3). The highest estimates for MSY and B_{MSY} for the pelagic aggregate group were from the eastern Bering Sea and southern Gulf of St. Lawrence (Fig. 3). For both systems, the pelagic productivity was much larger than production from their demersal aggregate groups (2.6 and 4.2 times larger for the eastern Bering Sea and southern Gulf of St. Lawrence, respectively). In contrast, estimates of MSY for the demersal aggregate groups ranged from 0.45 to 3.32 t km^{-2} while estimates of B_{MSY} ranged from 3.49 to 13.16 t km^{-2} (Table 3). The most productive demersal aggregate group was from the North Sea ecosystem. The North Sea's demersal aggregate group was 3.1 times more productive than its pelagic aggregate group (Fig. 3). However, unlike the pelagic aggregate group, the ecosystem with the highest estimate of B_{MSY} (eastern Bering Sea) was not the most productive (Fig. 3).

Similar patterns were observed in the other 2 aggregation types, although CVs for the majority of the aggregate groups within the feeding guild and size aggregation types showed more variation than with the habitat aggregation type (Figs. 3–5, Table 3). Ranges for aggregate groups usually associated with 'forage' fish (pelagic, planktivore and 'small') were similar (Table 3). The 'forage' fish aggregations were also more productive than the other aggregate groups (Table 3). Based on Tukey's HSD test, differences in means were significantly different for all 3 'forage' fish aggregate groups against the benthivore aggregate group. Means were also significantly different for the pelagic and planktivore aggregate groups against the zoopivore, piscivore, medium and large aggregate groups (Tables S4 & S5 in the supplement).

There were also similarities with regards to relative differences in production as well as dominate ecosystems. The greatest variability among functional groups was observed in the feeding guild aggregation type, of which the planktivore aggregate group's mean MSY was 2 to 5 times greater than the other feeding groups (Table 3). Similar to the pelagic aggregate group, the east-

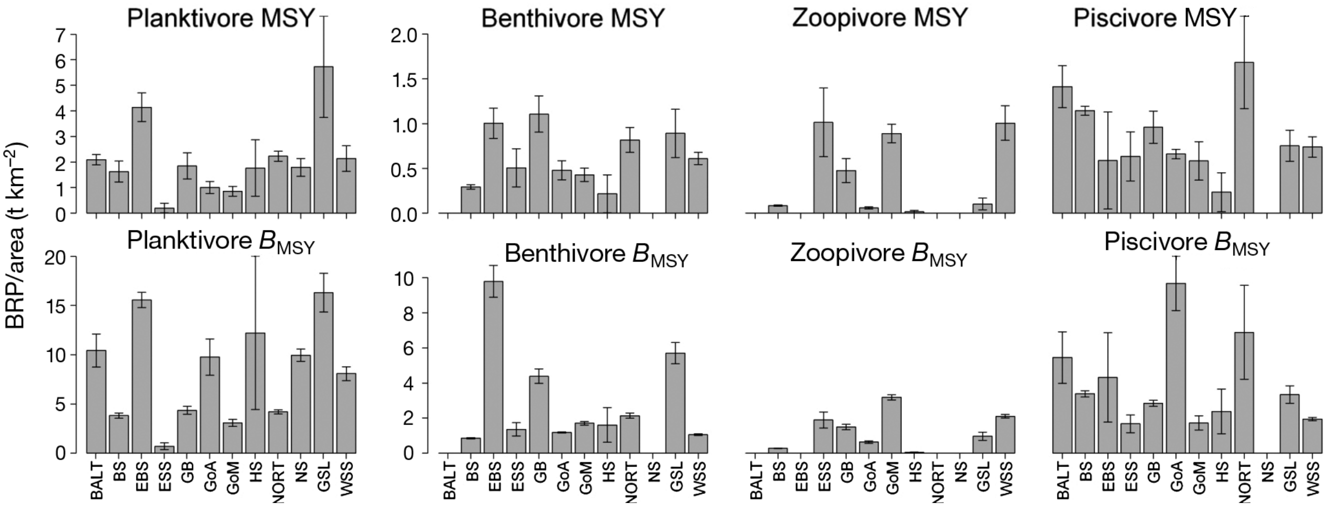

Fig. 4. Area-corrected maximum sustainable yield (MSY) and biomass at maximum sustainable yield (B_{MSY}) derived from the process error model for the feeding guild aggregation type by ecosystems. Note the different scale for the planktivore aggregate group than the other 3 aggregate groups. See Table 1 for definition of ecosystem abbreviations

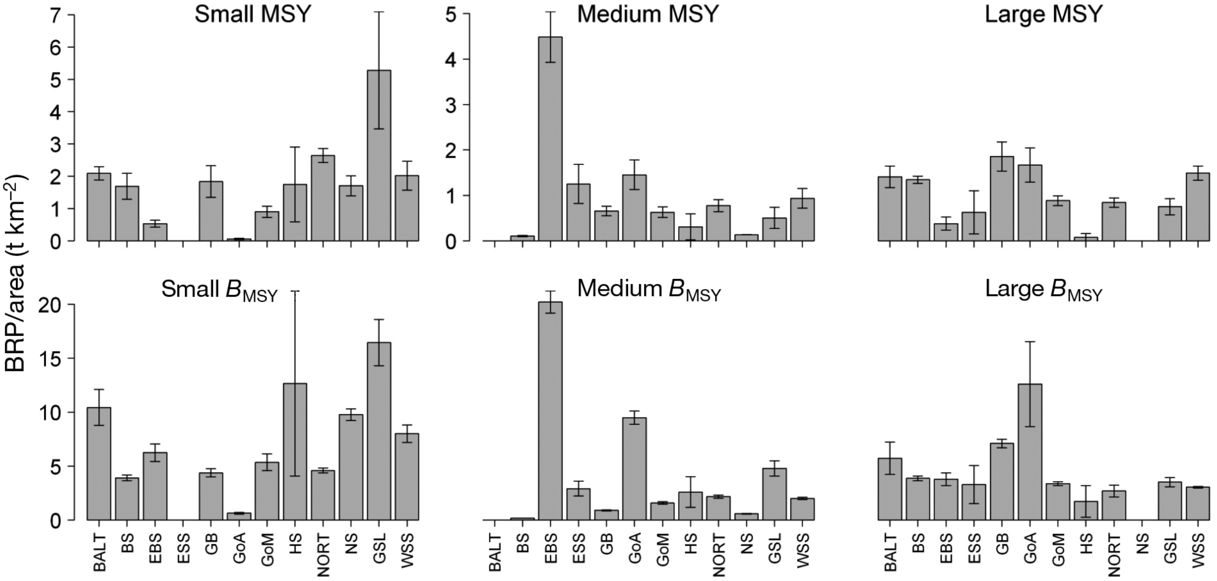

Fig. 5. Area-corrected maximum sustainable yield (MSY) and biomass at maximum sustainable yield (B_{MSY}) derived from the process error model for the size class aggregation type by ecosystems. See Table 1 for definition of ecosystem abbreviations

ern Bering Sea and southern Gulf of St. Lawrence were the most productive (Figs. 4 & 5). For both systems, the most productive aggregate group within the feeding guild aggregation type was the planktivore aggregate group (Fig. 4). However, for the size aggregation, production was higher within the 'medium' size aggregate group for eastern Bering Sea and not the 'small' aggregate group (Fig. 5).

Despite physical differences among the ecosystems, estimated BRPs appear to be independent of ecosystem size. Specifically, the Barents Sea, which was the largest ecosystem at ~748 000 km^2, had BRPs that were generally intermediate to other systems. Whereas the relatively small ecosystem, Georges Bank, had high demersal area-corrected MSY, which may be related to its shallow average depth and rel-

Table 3. Measures of central tendencies for estimated biological reference points obtained for the aggregate groups. Values were derived using the process model. Ecosystems without data for an aggregate group were excluded from calculations

Aggregate group	Biological reference point									
	MSY$_{\text{mean}}$	MSY$_{\text{median}}$	MSY$_{\text{SD}}$	MSY$_{\text{range}}$	MSY$_{\text{CV}}$	$B_{\text{MSY}_{\text{mean}}}$	$B_{\text{MSY}_{\text{median}}}$	$B_{\text{MSY}_{\text{SD}}}$	$B_{\text{MSY}_{\text{range}}}$	$B_{\text{MSY}_{\text{CV}}}$
Pelagic	2.13	1.76	1.34	0.97–5.46	62.9	8.68	9.80	4.57	2.36–16.31	52.7
Demersal	1.34	1.17	0.83	0.45–3.32	62.2	6.48	5.45	3.04	3.49–13.16	46.9
Planktivore	2.12	1.82	1.48	0.20–5.73	70.1	8.21	8.93	5.04	0.71–16.33	61.3
Benthivore	0.63	0.56	0.30	0.22–1.11	48.0	2.98	1.66	2.87	0.85–9.79	96.2
Zoopivore	0.46	0.29	0.45	0.01–1.01	98.9	1.33	1.23	1.05	0.04–3.18	79.3
Piscivore	0.85	0.74	0.42	0.23–1.68	48.8	3.96	3.34	2.49	1.67–9.67	62.9
Small	1.71	1.73	1.40	0.01–5.28	81.9	6.88	5.81	4.83	0.01–16.46	70.2
Medium	1.02	0.66	1.22	0.11–4.48	119.7	4.10	2.06	5.57	0.18–19.17	135.8
Large	1.03	0.88	0.56	0.08–1.86	54.7	4.38	3.34	2.87	1.65–11.96	65.5

Table 4. Results of 2-factor ANOVAs for MSY and B_{MSY}. The 2 factors were ecosystem and aggregate group (see Table 1). ***Factor significant at $p < 0.001$

	df	SS	MS	F-value	Pr(>F)
MSY					
Ecosystem	11	34.59	3.144	5.040	8.04×10^{7}***
Agg. group	8	37.63	4.704	7.540	1.22×10^{8}***
Residuals	176	109.79	0.624		
$\boldsymbol{B}_{\textbf{MSY}}$					
Ecosystem	11	653.3	59.39	5.689	1.20×10^{6}***
Agg. group	8	433.0	54.12	5.184	3.33×10^{5}***
Residuals	78	814.3	10.44		

atively high primary production (O'Reilly & Zetlin 1998). There did not appear to be a trend in BRPs with regard to ocean basin or latitude (data not shown).

DISCUSSION

We have shown that, with a few exceptions, estimated aggregate group BRPs are relatively invariant among ecosystems when data are aggregated to reflect habitat, trophodynamic or allometric affinities. While aggregate production varied across aggregation types and ecosystems, MSY never exceeded 6 t km^{-2} and was generally less than 3 t km^{-2}. The comparative ecosystem approach is important for revealing commonalities and differences across ecosystems. Yet, to date, the bulk of scientific literature on ecosystems is composed of 'within ecosystem' comparisons, which focus on comparing different sections of various time series (Murawski et al. 2010). 'Within ecosystem' comparisons are helpful in determining covariation among changes in species production dynamics and regime shifts within particular ecosystems but do not often identify broader, overarching ecosystem patterns and functions. Our study revealed insights from a broader intersystem comparison (Murawski et al. 2010) within the temperate northern hemisphere ecosystems. Although not replicates in traditional statistical parlance, all of our ecosystems are similar in that they are highly productive and have sustained long-term fisheries removals (Fu et al. 2012). Through applying surplus production models to several types of functional aggregations, we can draw some generalities that are applicable to a wide range of ecosystems.

Previous studies have demonstrated that developing estimates of aggregate ecosystem MSY is a more conservative management approach than summing estimates from multiple single-species models (Pope 1975, Brown et al. 1976, May et al. 1979, Collie & Gislason 2001, Walters et al. 2005, Mueter & Megrey 2006, Sparholt & Cook 2010) This occurs because within any given aggregation, it is assumed that as individual species compete with one another resources become limited and each species cannot be maintained at carrying capacity simultaneously (Gamble & Link 2009). In addition, the functional aggregate group is less annually variable than individual species as perturbations in population dynamics are smoothed. Moreover, Bundy et al. (2012) show that aggregating at the full system level is even more conservative (1 to 5 t km^{-2}) than aggregating at the functional group level, as presented here.

There was no apparent pattern in aggregate productivity with respect to ocean basin, region or component species. For many different aggregation types the southern Gulf of St. Lawrence and the eastern Bering Sea were the most productive ecosystems. The southern Gulf of St. Lawrence was located within the Atlantic basin at the mid-range of our study geographically while the eastern Bering Sea was the most northerly of the Pacific basin ecosystems examined. The high production from both can be attributed to the pelagic and planktivore aggregate groups. But there were differences in the most productive size class aggregation, with the southern Gulf of St. Lawrence dominated by the 'small' size class and the eastern Bering Sea dominated by the 'medium' size class. Both the southern Gulf of St. Lawrence and eastern Bering Sea are relatively shallow with seasonal ice cover; however, the southern Gulf of St. Lawrence is an inland sea containing a mixture of estuarine and marine, as well as subtropical to subarctic species (Fu et al. 2012).

We found that aggregations typically associated with 'forage fish' (pelagic, planktivore and 'small') were consistently more productive than other aggregation groups. 'Forage fish' play a key ecological role within marine ecosystems, transferring energy from primary production to upper trophic levels (Pikitch et al. 2012). When dealing with single species management, BRPs may be overestimated with respect to MSY or underestimated with respect to B_{MSY} without explicitly accounting for this higher natural mortality (Tyrrell et al. 2011). However, as noted previously, by aggregating species we indirectly account for these interactions while simultaneously dampening single species variability; thus, aggregate 'forage' BRPs may be a useful alternative. It seems reasonable that special attention should be afforded these aggregate 'forage' groups as trophic pressures may increase as predator stock sizes continue to rebuild (Overholtz et al. 2008, Smith et al. 2011).

To utilize information from comparative studies, outputs should be familiar to managers. Therefore, we provide BRP estimates derived from aggregates rather than single species. In fisheries science, BRPs are benchmarks from which to assess the status of fish stocks. In single-species assessment, they are usually based on fishing mortality or biomass levels. As we transition to EBFM, the concept of reference points will need to be expanded to include other ecological indicators and multivariate indices (Link 2005). However, a first step is to apply more familiar BRPs, such as MSY and B_{MSY}, in a context broader than single species such as the aggregate reference points presented here. While we assume that LMR managers could interpret other metrics, the familiarity with more traditional BRPs may aid in the transition to other EBFM reference points. In addition to familiarity, the value of aggregated metrics can be high. A major criticism of MSY is its appropriateness as a management goal (Punt & Smith 2001). This is based on the static nature of MSY, which ignores natural fluctuations in species abundance. By aggregating species into similar life-history categories some of this natural fluctuation may be dampened. This could lead to more robust yet conservative estimates of productivity.

Conceivable uses of such aggregated metrics warrant consideration. We could envision them being adopted in the following way. First, aggregate BRPs should be used as overall caps to fishery removals with respect to aggregate groups. This proposed usage conforms to the recent paradigm of using MSY as a limit rather than a target and has had some precedence in some ecosystems (e.g. Witherell et al. 2000). Aggregated metrics can also balance yield and biodiversity objectives (Worm et al. 2009, Gaichas et al. this volume). Species within aggregate groups should generally have similar life histories; however, some are more productive than others. To optimize biodiversity objectives, removals should be distributed within the aggregation with some consideration of individual species productivity. This way, lower productive stocks will be safeguarded against overfishing (Mueter & Megrey 2006). This also creates a bridge between single species assessments and multispecies assessment that can better inform managers of potential risks of particular management decisions (Mace 2001).

As fishery management transitions towards an ecosystem approach, comparative studies like this one will provide useful insights. Comparative studies allow for ad hoc replication between similar ecosystems. The aggregation schemes we employed were based on various criteria, but there does not appear to be a difference in using habitat, feeding guild or size class. Future choices regarding the best aggregation to use for developing decision support tools will certainly need to be based on individual ecosystem history and species composition as well as the management question being addressed, but we assert that the general patterns we observed should be informative for such selections. The logical next step would be to move to the final level of comparative hierarchy outline by Murawski et al. (2010). That would be a global comparison between dissimilar ecosystems. By comparing the contrast between ecosystems from temperate marine ecosystems to coral reef ecosystems or even terrestrial ecosystems we can begin to answer the broadest of ecosystem questions related to biodiversity, variability and productivity (Murawski et al. 2010). This work represents a useful step to that end and ultimately a global synthesis of the determinants of fisheries production.

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Contribution to the Theme Section 'Comparative analysis of marine fisheries production'

Comparative analysis of cod and herring production dynamics across 13 northern hemisphere marine ecosystems

Kirstin K. Holsman[1,*], Timothy Essington[2], Thomas J. Miller[3], Mariano Koen-Alonso[4], William J. Stockhausen[5]

[1]Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, Washington 98195-5672, USA
[2]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington 98195-5020, USA
[3]Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, Maryland 20688, USA
[4]Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, St John's, Newfoundland and Labrador A1C 5X1, Canada
[5]Alaska Fisheries Science Center, NOAA Fisheries, Seattle, Washington 98115, USA

ABSTRACT: We conducted a comparative ecosystem analysis to understand environmental and biological drivers of production dynamics of 2 common species groups, cod (*Gadus morhua* and *G. macrocephalus*) and herring (*Clupea harengus* and *C. pallasii*), across 13 large marine ecosystems. For all 4 species, we fit a hierarchy of nested surplus production models with terms for trophodynamic and biophysical covariates; models were then compared using an information-theoretic framework. Across ecosystems, models including terms for biophysical covariates exhibited stronger fits to the data and were often included in the top set of selected models. However, the numerical effects of covariates differed among systems and species. For example, surplus production in several ecosystems was significantly affected by sea surface temperature, but to differing degrees (i.e. direction and magnitude of effect). Similarly, surplus production of cod was positively associated with herring biomass in 4 of the ecosystems examined, whereas negative trophodynamic interactions alluded to complex cultivation-depensation food-web dynamics in 5 other systems. Importantly, no single covariate emerged as the most important predictor of surplus production nor were biological reference points from models with covariates always more conservative than those without covariates. This suggests that inclusion of trophodynamic and biophysical covariates in simple production models has the potential to increase model fit, but the relative benefit will be stronger for systems and species where trophodynamic and biophysical processes are tightly coupled to species productivity.

KEY WORDS: Cod · Herring · Surplus production · Fisheries management · Trophic dynamics · Biological reference points · Environmental factors · Maximum sustainable yield · MSY

INTRODUCTION

Ecosystem-based approaches have been promoted as a way to improve fisheries assessment and management (Pikitch et al. 2004, US Commission on Ocean Policy 2004, Link 2010). There are multiple facets and goals of the ecosystem-based approach, but a central feature is a holistic perspective on fisheries productivity that considers multiple controls beyond fishing mortality and stock size (Walters & Martell 2004, Hollowed et al. 2011). One potential benefit of this approach is improved estimates of both biological reference points (Overholtz et al. 2008, Tyrrell et al. 2011) and of population trajectories under various future management and climatic scenarios. For example, consideration of trophodynamic interactions in both stock assessments and harvest policies might improve assessment accuracy and

*Email: kirstin.holsman@noaa.gov

identify trade-offs that emerge between fisheries that target multiple species in a food web (Link 2010, Constable 2011, Smith et al. 2011).

Although the importance of biophysical and trophodynamic drivers of fisheries production dynamics are widely acknowledged (e.g. Mantua et al. 1997, Lehodey et al. 2006, Baum & Worm 2009), identifying and ranking the relative influence of these drivers on production rates is challenging. Often covariates of fisheries production dynamics are determined through a correlation analysis of data from multiple time series. Yet, survey and biophysical time-series data are frequently autocorrelated, so that spurious relationships between production dynamics and environmental variables are not uncommon. For example, Leggett et al. (1984) analyzed data from 1966 to 1978 for capelin *Mallotus villosus* and found a strong correlation between recruitment, sea surface temperature, and the frequency of onshore winds during larval emergence from spawning beaches. Yet, when Carscadden et al. (2000) updated the original analysis with additional years of data, temperature was no longer a useful predictor of recruitment. These authors speculated that the original correlation was spurious rather than causative. In a broad review of such relationships, Myers (1998) noted that recruitment correlations become particularly unreliable when time series are short relative to generation times. Other authors have since demonstrated additional challenges inherent in using correlative approaches to evaluate processes that may act synergistically to regulate production dynamics (Hunt et al. 2002, Hunt & McKinnell 2006).

The comparative approach has been identified as a promising tool to provide ecosystem-scale scientific advice for fisheries (Megrey et al. 2009, Murawski et al. 2009). We suggest that the comparative approach is also helpful in assessing the importance of ecological covariates in predicting production of fisheries stocks. By assessing covariates of fisheries production across multiple ecosystems that have unique histories of environmental forcing and food web dynamics, it may be possible to identify covariates that consistently predict production levels and thereby diminish the likelihood of drawing spurious correlations. Indeed, Myers (1998) recommended a comparative approach in his review of correlative studies of environmental controls of recruitment. More generally, such analyses offer the potential to distinguish covariates that regulate production in many different ecosystems as opposed to the system-specific effect of individual covariates. Additionally, a comparative approach can also reveal how mean levels of productivity vary across ecosystems and thereby detect controls of productivity that might be concealed in analysis of data from a single ecosystem (Perry & Schweigert 2008).

As a part of a larger collaborative project to compare the dynamics of marine ecosystems (see Gaichas et al. 2012, this Theme Section), we assembled time series data on biomasses and harvest of multiple species in 13 different northern temperate ecosystems (see Fig. 2 in Link et al. 2012, this Theme Section). The overall goal of the project was to quantify the relative importance of biophysical (environmental), trophodynamic and exploitative processes on production. To maximize the strength of the comparative approach, we apply a simple production model to population and harvest biomass data for cod and herring species, which were present in most of the 13 northern ecosystems. These 2 species groups have traditionally supported culturally and economically important fisheries (Kurlansky 1997) and have also long been the focus of efforts to relate population dynamics to environmental conditions (e.g. Hjort 1914, Sinclair & Tremblay 1984). As a result, there are ample data sources from a diverse array of marine fishery ecosystems on which to base comparative analyses. The surplus production modeling framework was chosen because the notion of surplus production is fundamental to both single species and ecosystem-based approaches (Schnute & Richards 2002, Walters et al. 2008). Moreover, despite their simplicity, surplus production models can outperform more complicated age-structured models (NRC 1998). Here we use a surplus production modeling framework to ask: (1) how do average surplus production levels relate to ecosystem scale properties such as temperature, (2) do particular biophysical or trophodynamic variables consistently predict production dynamics across ecosystems, and (3) are biological reference points (e.g. maximum sustainable yield [MSY]) for each species group similar across ecosystems?

MATERIALS AND METHODS

We evaluated patterns in biomass and annual surplus production for Atlantic and Pacific cod (*Gadus morhua* and *G. macrocephalus*, respectively) and Atlantic and Pacific herring (*Clupea harengus* and *C. pallasii*, respectively) from 13 high-latitude ecosystems that varied in size and ecosystem structure (Table 1). Although we recognize that there are specific differences between the species pairs, we argue that each occupy similar niches in the individual

Table 1. Ecosystem abbreviation and area, and the number (*n*) and range of years of cod and herring biomassdata included in each ecosystem- and species-specific analysis

Ecosystem	Abbreviation	Area (10^3 km^2)	Cod		Herring		Data source
			n	Years	*n*	Years	
Baltic Sea	BALT	211.1	34	1974–2007	34	1974–2007	Stock assessment
Barents Sea	BS	525.3	63	1946–2008	59	1950–2008	Stock assessment
Eastern Bering Sea	EBS	430.8	32	1977–2008	29	1978–2006	Stock assessment
Eastern Scotian Shelf	ESS	113.7	38	1970–2007			q-corrected biomass
Georges Bank	GB	42.2	44	1963–2006	41	1967–2007	q-corrected biomass
Gulf of Alaska	GoA	238.4	32	1977–2008	29	1980–2008	Minimum swept area
Gulf of Maine	GoM	76.5	44	1963–2006	41	1967–2007	q-corrected biomass
Hecate Strait	HS	23.5	25	1984–2008	59	1951–2009	q-corrected biomass
Newfoundland and Labrador	NL	388.2	27	1981–2007			Minimum swept area
North Sea	NORT	609.7	44	1963–2006	44	1963–2006	Stock assessment
Norwegian Sea	NS	728.3			59	1950–2008	Stock assessment
Southern Gulf of St. Lawrence	sGoSL	74.1	38	1971–2008	38	1971–2008	q-corrected biomass
Western Scotian Shelf	WSS	73.3	38	1970–2007	38	1970–2007	q-corrected biomass

ecosystems in which they are found; both species of herring are important forage fish prey for a myriad of predators, including cod, which are in turn a dominant component of the predatory groundfish guild in each ecosystem.

Sources of population biomass (either survey-based or stock assessment-based estimates) and annual catches are provided by Bundy et al. (2012, this Theme Section). Overall, data time series ranged from 1946 to 2009, although time-ranges for specific ecosystems varied based on available data for each system. Annual biomass and catch of cod or herring from surveys or assessments were standardized to tons per square kilometer of each ecosystem prior to analysis by dividing by ecosystem area. We note that estimates of ecosystem area are not necessarily indicative of habitable area, particularly for herring that are more coastal (e.g. the entire eastern Bering Sea is not inhabited by Pacific herring).

We used an annual surplus production modeling approach to evaluate drivers of stock productivity. This choice was based on the recognition that environmental and trophodynamic effects are most directly manifest in stock productivity because this metric integrates effects on growth, mortality and recruitment. Moreover, the surplus production approach allowed us to conduct comparative analysis across ecosystems using a common framework and currency. The annual surplus production (ASP_t) of a species in year t was calculated as:

$$\mathrm{ASP}_t = B_{t+1} - B_t + C_t \qquad (1)$$

where C_t is annual catch and B_t and B_{t+1} are the mean biomass estimates in years t and $t + 1$, respectively. In some systems, biomass estimates from surveys contained one or more positive outliers, typically caused by a single survey tow containing unusually high catches. These high catch events most likely reflect differences in catchability or species aggregation rather than true variation in annual production. Preliminary analyses indicated that the inclusion of anomalously large biomass estimates led to unrealistic rates of increase in population biomass from time t to $t + 1$ and subsequently produced extraordinarily high, then low, ASP values when estimated survey biomass returned to levels that preceded the outlier. We therefore smoothed biomass time series to account for this observation error by using a Kalman filter (i.e. local level structural time-series model, StructTS() function in R; R Development Core Team 2010). This approach implemented an autoregressive integrated moving average (ARIMA[0,1,1]) model and appeared to have little effect in most systems (particularly for biomass estimated from stock assessments) but was able to reduce noise and eliminate anomalous biomass estimates for several ecosystems and species (Fig. 1).

To identify covariates that best predict inter-annual variation in ASP for each species from each ecosystem, we statistically fit multiple models, each containing different combinations of covariates, and used multi-model inference to identify the weight of evidence in support of each covariate (Burnham & Anderson 2002). In particular, we fit a null model where ASP varied randomly around a mean value (i.e. no relationship to biomass) and a Schaefer surplus production model (Hilborn & Walters 1992) where ASP exhibited a parabolic relationship with biomass

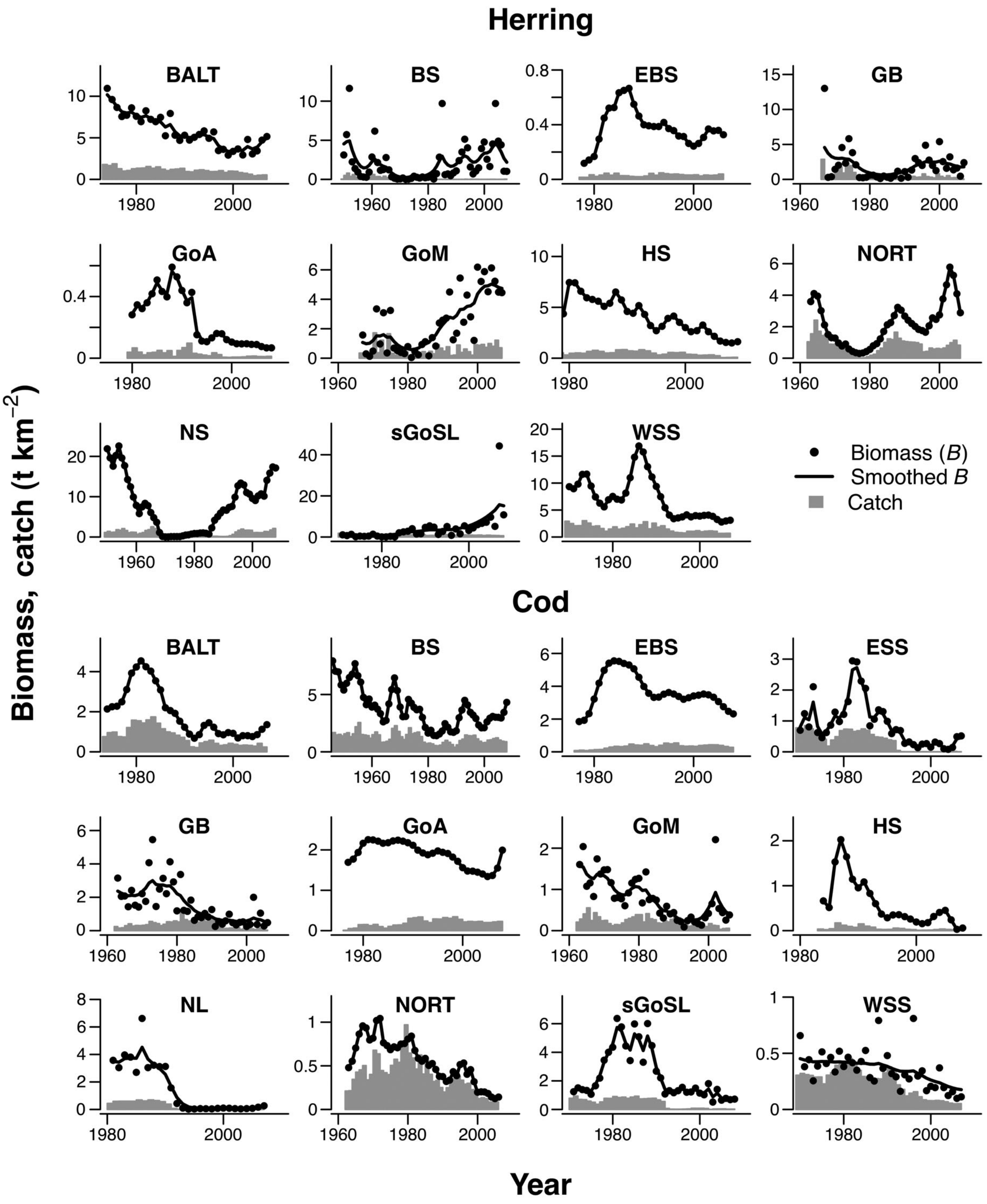

Fig. 1. Regional time series of observed biomass, Kalman-filtered (smoothed) biomass, and observed harvest (catch) for cod and herring in different ecosystems. See Table 1 for ecosystem abbreviations

according to parameters r (maximum annual per-biomass rate of population increase) and K (equilibrium population biomass in the absence of fishing). To this simple production model we added a number of biological and environmental covariates (m) that modified annual surplus production additively such that:

$$\text{A}\hat{\text{S}}\text{P}_t = rB_t\left(1-\frac{B_t}{K}\right)+\sum_{i=1}^{m}\gamma_i X_{i,t}+\varepsilon_t \qquad (2)$$

where $X_{i,t}$ is the Z-score standardized value of covariate i in year t, γ_i describes the effect of covariate i, and ε_t is an independently and normally distributed random variable with variance σ ($\sim N[0,\sigma^2]$).

We selected covariates that indexed important trophodynamic or ecosystem processes and were broadly available for most of the systems in our study (see Fu et al. 2012, this Theme Section). Our selected biophysical covariates included mean sea surface temperature (T) and wind speed (V) as well as 2 atmospheric indices of marine productivity depending on ocean basin: the Pacific Decadal Oscillation (PDO) for Pacific ecosystems and the North Atlantic Oscillation index (NAO) for Atlantic systems. We hypothesized that ASP may vary as a function of prey and/or predator abundance, so we also included herring biomass as prey in the models for cod (lagged by 1 yr to reflect subsequent production), and cod biomass within the same year as an index of predation in herring models. In addition to the aforementioned models with normally distributed errors, we additionally fit both the null (i.e. random variation around the mean) and simple production model (i.e. no covariates) using autocorrelated residuals (i.e. $\varepsilon_t = \varphi \cdot \varepsilon_{t-1} + v_t$) where φ represents the degree of temporal autocorrelation and v_t is an independently and normally distributed random variable (i.e. $v_t \sim N\,[0,\sigma^2]$).

We fit all models to the data by minimizing the negative log-likelihood using the optim() or lm() functions of the R statistical system (R Development Core Team 2010; www.r-project.org); a penalized likelihood was used to constrain K (and subsequently B_{MSY}) within reasonable bounds (i.e. $0 < K < 40$) for models that failed to converge on biologically realistic parameter estimates (e.g. Collie & DeLong 1999). We then ranked candidate models using Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham & Anderson 2002). We expect that most species will exhibit some degree of autocorrelation in errors of surplus production. However, because our objective is to use a comparative approach to evaluate the relative effect of including environmental covariates on emergent biological reference points from surplus production models (rather than find the best fitting model for each system *per se*), we choose to only include models with independent errors in model averaged parameter estimates. We recognize that for systems where cod or herring exhibit a high degree of autocorrelation, these may not be the top selected models. For all models with independent, normally distributed errors (i.e. not autocorrelated), we used the Akaike weight (W_i) of each model (i) to find a 95% confidence set of models (i.e. the subset of top-ranked models whose Akaike weights together comprise 95% of the total). Variable weights ($W_{+(j)}$), which measure the explanatory power of each predictor variable (j), were calculated by summing the normalized Akaike weights (W_i') of all models in the 95% subset in which that variable appeared. We also calculated model averaged estimates ($\hat{\hat{\beta}}_j$) for each parameter across all models by summing the product of the normalized model Akaike weights and parameter coefficient values ($\hat{\beta}_{i,j}$) for each model across all models (R) in the 95% subset (Burnham & Anderson 2002) such that:

$$\hat{\hat{\beta}}_j = \sum_{i=1}^{R} W_i' \,\hat{\beta}_{i,j} \text{ where } W_i' = \frac{W_i}{\sum_{i=1}^{R} W_i} \tag{3}$$

The weighted unconditional variance estimator for the same model averaged parameter is then given by:

$$\operatorname{var}\left(\hat{\hat{\beta}}_j\right) = \left[\sum_{i=1}^{R} W_i' \sqrt{\operatorname{var}\left(\hat{\beta}_{i,j} \mid g_i\right) + \left(\hat{\beta}_{i,j} - \hat{\hat{\beta}}_j\right)^2}\,\right]^2 \tag{4}$$

where $\hat{\hat{\beta}}_j$ is the averaged parameter estimate from Eq. (3) and $\operatorname{var}(\hat{\hat{\beta}}_{i,j} \mid g_i)$ is the variance in $\hat{\hat{\beta}}_j$ conditional on model g_i. We similarly calculated the model-averaged mean response and unconditional variance of the response variable by replacing β in Eqs. (3) & (4) with estimated surplus production (ASP_i) from each model in the 95% subset. The unconditional variance was used to construct 95% confidence intervals around the model-averaged mean response assuming that the variable was normally distributed. Lastly, we calculated MSY and B_{MSY} reference points for ecosystem- and species-specific models using model averaged parameter values for r and K as:

$$\text{MSY} = \frac{r \cdot K}{4} \tag{5}$$

$$B_{\text{MSY}} = \frac{K}{2} \tag{6}$$

RESULTS

Biomass and catch time series displayed considerable variability within and across ecosystems for each species (Fig. 1). In general, herring biomass was higher and more variable than cod biomass; across ecosystems, coefficients of variation (i.e. standard deviation/mean; CV) for herring biomass before Kalman filtering averaged 80.9% whereas cod CVs were 63.5%. Similarly, overall regional mean herring biomass across years ranged from 0.02 to 22.58 t km^{-2}, while average cod biomass ranged from 0.03 to 7.94 t km^{-2}. In 5 of the 13 ecosystems we examined (BALT, EBS, GoA, HS, and WSS; see Table 1 for abbreviations), herring and cod exhibited similar temporal trends in biomass (mean Pearson's correlation coefficient of 0.76), whereas in the remaining ecosystems, patterns of cod and herring biomass were decoupled, or in the case of GoM and NORT, negatively correlated (correlation coefficients of –0.52 and –0.70, respectively; Fig. 1).

ASP dynamics within ecosystems were also more variable for herring than cod (mean CV values of 5.6 and 2.8, respectively), and exhibited a wider range of average levels across ecosystems (ranges of –1.47 to 5.69 and –0.56 to 2.56 t km^{-2}, for herring and cod, respectively; Fig. 2). Pacific cod exhibited lower mean surplus production rates (0.2 ± 0.1 t km^{-2}) than Atlantic cod in the ecosystems we examined (0.44 ± 0.11 t km^{-2}), but there were no clear differences in ASP for herring from Atlantic or Pacific ecosystems (0.79 ± 0.15 and 0.37 ± 0.34 t km^{-2}, respectively).

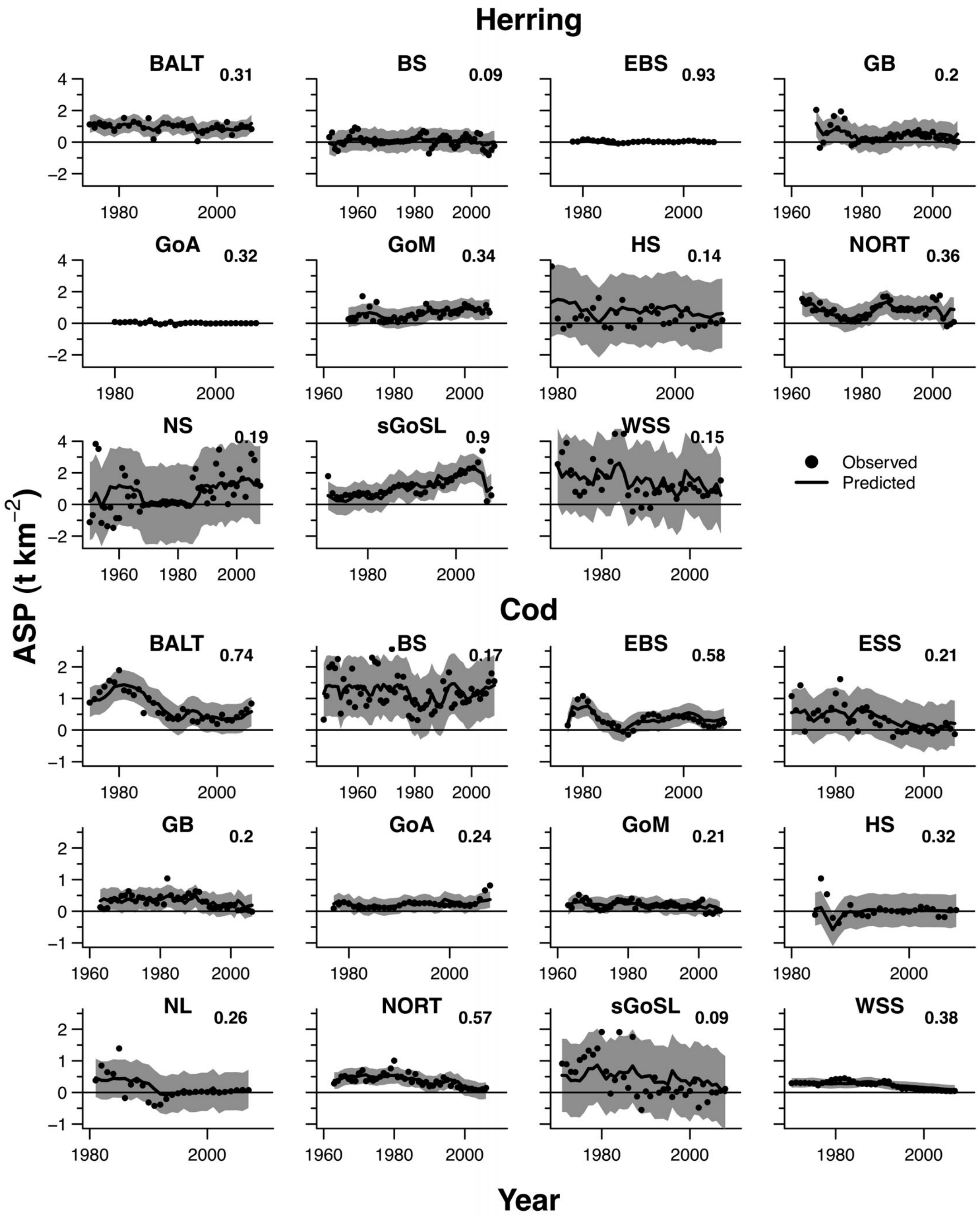

Fig. 2. Observed annual surplus production values (ASP; points) for herring and cod from each ecosystem. Solid lines: model averaged predicted values from top AIC$_c$ selected models. Shading: 95% confidence intervals; numerical values: R^2 values for model fits. See Table 1 for ecosystem abbreviations

We were able to achieve credible fits to Schaefer production models for 12 of the 13 ecosystems for herring, and 9 of 13 ecosystems for cod; GB herring, and NL and WSS cod production dynamics were not well described by the Schaefer production model (Fig. 3). Furthermore, parameter estimates for EBS cod surplus production should be considered cautiously as the estimate for *K* was near the upper limit set by the penalized likelihood (i.e. ~40). Lastly, although the estimate of *K* for cod from BALT was substantially below the upper limit, it is still well outside the range of the data and should also be considered cautiously.

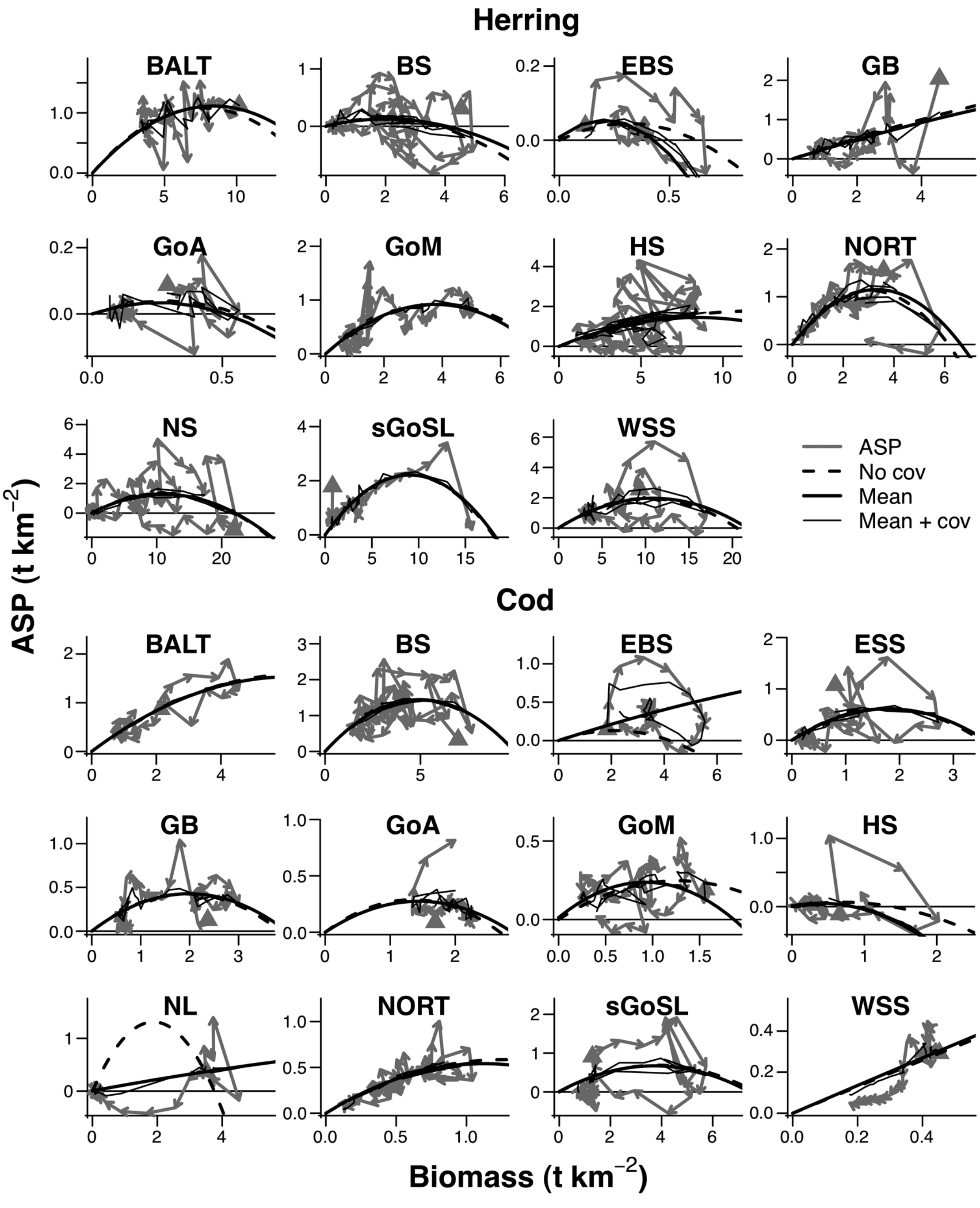

Fig. 3. Observed annual surplus production (ASP) and biomass (t km^{-2}) of herring and cod species from each ecosystem (gray arrows; 'ASP'); ▲: first year in each time series. Predicted ASP values from averaged parameter estimates of top AICc selected models (thin black lines; 'Mean + cov'), estimates of ASP curves from models without covariates (dashed 'No cov.'), and ASP curves from covariate models under mean environmental conditions (thick black lines; 'Mean') are also shown. See Table 1 for ecosystem abbreviations

Although, temporal autocorrelation in surplus production was strong for both species from most ecosystems (φ > 0.2; Table 2), ecological covariates appeared to explain a large portion of the observed autocorrelation; in approximately 40% of the ecosystems we analyzed, AIC_c selected one or more models with ecological covariates above the simple Schaefer model with autocorrelation (Table 3). That said, we did not find overwhelming support for one specific model with covariates; for most ecosystems there were multiple models that equally explained surplus production for cod or herring species (Table 3). Model-averaged parameter weights and coefficient values indicated that temperature was an important predictor of ASP dynamics, especially for herring (i.e. values were often non-zero; Tables 2 & 4), but the direction of the effect was species- and system-dependent (Fig. 4). For herring, positive anomalies in sea surface temperature were positively correlated with surplus production in WSS, NS, GoM and HS ecosystems, whereas herring production was significantly reduced during warm conditions in NORT and BS (Fig. 4). For cod, positive anomalies in annual sea-surface temperatures were associated with marginal declines in ASP in most ecosystems; this was most notable in GoA and GoM (Fig. 4). Average parameter weights and coefficient values for terms representing variability in wind and atmospheric indices indicated that both were important predictors of ASP dynamics (i.e. values were often non-zero; Table 4 & Fig. 4, respectively), yet these factors had mixed effects on herring and cod production, and confidence intervals of mean parameter estimates frequently overlapped zero (Table 2).

We found some evidence of bottom-up or facilitative processes between herring and cod. In roughly a third of the ecosystems we examined, mean parameter weights for the effect of herring (lagged by 1 yr)

Table 2. Model-averaged parameter values for (A) herring and (B) cod from each ecosystem (excluding models with autocorrelation). Note that values have not been standardized to mean biomass for each species from each ecosystem. Parentheses: unconditional standard error for each average parameter value. **Bold:** significant parameter values (i.e. estimate interval does not overlap zero). *Italics*: ecosystems where surplus models converged on the upper limit for *K* (40) and that should be considered cautiously. *B*: biomass; MSY: maximum sustainable yield; T: sea surface temperature; PDO/NAO: Pacific Decadal Oscillation or North Atlantic Oscillation index, given as applicable; cod: biomass of cod; $herring_{t-1}$: biomass of herring in the previous year; φ: degree of temporal autocorrelation; *r*: maximum annual per-biomass rate of population increase; *K*: equilibrium population biomass in the absence of fishing; NA: data not available. See Table 1 for ecosystem abbreviations

(A) Herring

Ecosystem	B_{MSY}	MSY	T	Wind speed	PDO/NAO	Cod	φ	*r*	*K*
BALT	**8.39 (3.59)**	**1.11 (0.07)**	**0.11 (0.06)**	NA	**0.09 (0.05)**	0.04 (0.04)	0.04 (0.08)	**0.26 (0.04)**	**16.78 (7.18)**
BS	**2.01 (1.76)**	**0.12 (0.06)**	**−0.08 (0.04)**	−0.02 (0.02)	0.02 (0.02)	−0.02 (0.02)	**0.41 (0.08)**	**0.12 (0.07)**	**4.02 (3.52)**
EBS	0.21 (0.23)	**0.05 (0.03)**	0	0	0	**0.03 (0.02)**	**0.29 (0.08)**	**0.48 (0.26)**	0.42 (0.46)
GB	***20.0 (1.00)***	***2.56 (1.14)***	*−0.04 (0.04)*	*0 (0.01)*	***0.11 (0.06)***	*0.04 (0.04)*	***0.20 (0.08)***	*0.26 (2.28)*	***40.0 (2.00)***
GoA	**0.26 (0.21)**	**0.03 (0.01)**	0	**−0.02 (0.01)**	0	**0.03 (0.01)**	0.08 (0.11)	**0.23 (0.10)**	**0.52 (0.42)**
GoM	**3.75 (2.04)**	**0.92 (0.07)**	**0.05 (0.04)**	0 (0.01)	0.01 (0.02)	0.03 (0.03)	**0.09 (0.07)**	**0.49 (0.07)**	**7.5 (4.08)**
HS	**8.44 (3.35)**	**1.44 (0.19)**	0.04 (0.05)	0.05 (0.06)	**−0.19 (0.13)**	**−0.24 (0.14)**	**0.28 (0.07)**	**0.34 (0.11)**	**16.88 (6.70)**
NORT	**3.32 (1.87)**	**1.15 (0.07)**	**−0.12 (0.06)**	NA	0 (0.02)	0.02 (0.03)	**0.44 (0.08)**	**0.69 (0.07)**	**6.64 (3.74)**
NS	**11.05 (8.28)**	**1.28 (0.23)**	**0.16 (0.12)**	−0.06 (0.07)	0.05 (0.06)	NA	**0.25 (0.07)**	**0.23 (0.06)**	**22.1 (16.56)**
sGoSL	**9.04 (5.89)**	**2.21 (0.11)**	0.01 (0.02)	0.04 (0.04)	**−0.17 (0.07)**	0.01 (0.02)	**0.31 (0.08)**	**0.49 (0.04)**	**18.08 (11.78)**
WSS	**10.86 (5.84)**	**1.97 (0.22)**	**0.41 (0.20)**	**0.15 (0.12)**	−0.04 (0.06)	**0.18 (0.15)**	**0.43 (0.09)**	**0.36 (0.08)**	**21.72 (11.68)**

(B) Cod

Ecosystem	B_{MSY}	MSY	T	Wind speed	PDO/NAO	$Herring_{t-1}$	φ	*r*	*K*
BALT	**6.15 (1.74)**	**1.53 (0.09)**	0 (0.01)	NA	−0.01 (0.02)	0.02 (0.02)	**0.41 (0.07)**	**0.5 (0.1)**	**12.3 (3.48)**
BS	**4.97 (2.60)**	**1.44 (0.07)**	0.02 (0.02)	0.03 (0.03)	0 (0.01)	0.03 (0.03)	**0.15 (0.06)**	**0.58 (0.05)**	**9.94 (5.20)**
EBS	***20.0 (1.00)***	***1.12 (1.08)***	*−0.01 (0.01)*	*0 (0.01)*	*0.01 (0.01)*	***−0.29 (0.03)***	***0.87 (0.23)***	*0.11 (2.16)*	***40.0 (2.00)***
ESS	**1.8 (0.98)**	**0.61 (0.07)**	−0.03 (0.03)	0.02 (0.03)	−0.03 (0.03)	NA	**0.24 (0.07)**	**0.68 (0.14)**	**3.60 (1.96)**
GB	**1.99 (1.19)**	**0.43 (0.04)**	0 (0.01)	**−0.05 (0.02)**	**0.04 (0.02)**	−0.01 (0.01)	**0.26 (0.07)**	**0.43 (0.07)**	**3.98 (2.38)**
GoA	**1.44 (1.00)**	**0.27 (0.06)**	**−0.05 (0.02)**	−0.01 (0.01)	−0.01 (0.01)	−0.02 (0.02)	**0.99 (0.60)**	**0.38 (0.12)**	**2.88 (2.00)**
GoM	**0.92 (0.59)**	**0.23 (0.04)**	−0.05 (0.02)	0	0 (0.01)	−0.01 (0.01)	**0.28 (0.07)**	**0.50 (0.14)**	**1.84 (1.18)**
HS	**0.39 (0.64)**	0.04 (0.06)	−0.02 (0.02)	0 (0.01)	0.01 (0.01)	0.03 (0.03)	**0.21 (0.13)**	**0.21 (0.19)**	0.78 (1.28)
NL	***19.2 (3.29)***	*1.10 (2.28)*	*0.01 (0.01)*	*0.06 (0.04)*	*−0.02 (0.02)*	*NA*	***0.21 (0.09)***	*0.11 (1.39)*	***38.4 (6.58)***
NORT	**1.13 (0.39)**	**0.54 (0.03)**	−0.02 (0.02)	NA	0 (0.01)	−0.02 (0.02)	**0.31 (0.07)**	**0.96 (0.15)**	**2.26 (0.78)**
sGoSL	**3.71 (2.29)**	**0.66 (0.14)**	−0.03 (0.04)	0.02 (0.03)	−0.1 (0.07)	−0.02 (0.03)	**0.23 (0.09)**	**0.36 (0.12)**	**7.42 (4.58)**
WSS	***19.86 (1.46)***	***6.76 (1.47)***	*0*	*0*	*0*	***0.03 (0.01)***	***0.71 (0.1)***	*0.68 (2.01)*	***39.72 (2.92)***

Table 3. Model rank based on AIC$_c$ weights for models from each ecosystem (excluding models with autocorrelation). Parentheses: AIC$_c$ weights (W'_i) standardized by the sum of AIC$_c$ weights of all models included in the model comparison (i.e. models with independent errors); **bold:** models with standardized cumulative AIC$_c$ weights ≤0.95. Surplus production models — null: random variation around the mean, 0: no covariates, AC null and AC 0: models with auto-correlated errors. Covariates included in each model: sea surface temperature (T), wind (V), PDO/NAO index (A), and cod or herring$_{t-1}$ biomass (S). See Table 1 for ecosystem abbreviations

(A) Herring

Rank	BALT	BS	EBS	GB	GoA	GoM	HS	NORT	NS	sGoSL	WSS
1	**T,A (0.31)**	**AC 0**	**AC null**	**AC 0**	**V,S (0.29)**	**T (0.21)**	**AC 0**	**AC 0**	**AC 0**	**A (0.31)**	**AC null**
2	**T,A,S (0.2)**	**AC null**	**AC 0**	**A (0.18)**	**V,A,S (0.2)**	**0 (0.14)**	**AC null**	**AC null**	**AC null**	**V,A (0.19)**	**AC 0**
3	**A (0.19)**	**T (0.16)**	**S (0.25)**	**T,A (0.15)**	**V (0.12)**	**S (0.1)**	**S (0.16)**	**T (0.45)**	**T (0.25)**	**T,A (0.11)**	**T,V,S (0.19)**
4	**T,S (0.13)**	**T,S (0.11)**	**null (0.21)**	**A,S (0.13)**	**T,V,S (0.09)**	**T,S (0.09)**	**A,S (0.16)**	**T,S (0.16)**	**0 (0.19)**	**A,S (0.1)**	**T,S (0.14)**
5	**T (0.09)**	**T,V (0.1)**	**0 (0.1)**	**T,A,S (0.1)**	**V,A (0.08)**	**A,S (0.07)**	**A (0.11)**	**T,A (0.13)**	**T,V (0.13)**	**V,A,S (0.05)**	**T (0.14)**
6	**A,S (0.05)**	**T,A (0.1)**	**V,S (0.09)**	**0 (0.08)**	**T,V,A,S (0.03)**	**T,A (0.07)**	**V,A,S (0.1)**	**0 (0.08)**	**T,A (0.12)**	**T,V,A (0.05)**	**T,V (0.1)**
7	null (0.02)	**T,V,S (0.07)**	**T,S (0.07)**	**S (0.06)**	**S (0.03)**	**T,V (0.06)**	**T,A,S (0.08)**	**S (0.07)**	**A (0.1)**	**0 (0.04)**	**T,A (0.08)**
8	0 (0.01)	**0 (0.07)**	**A,S (0.06)**	**T (0.06)**	**T,V (0.03)**	**A (0.06)**	**V,S (0.08)**	**T,A,S (0.05)**	**V (0.1)**	**V (0.03)**	**0 (0.06)**
9	AC null	**T,V,A (0.06)**	**T (0.04)**	**V,A (0.05)**	**A,S (0.03)**	**V (0.04)**	**T,S (0.06)**	**A (0.04)**	**T,V,A (0.06)**	**T,A,S (0.03)**	**V (0.05)**
10	S (0)	**null (0.06)**	**V (0.03)**	**T,S (0.04)**	**T,S (0.02)**	**T,A,S (0.04)**	**T,A (0.05)**	A,S (0.02)	**V,A (0.05)**	**AC 0**	**T,A,S (0.05)**
11	AC 0	**V (0.05)**	**A (0.03)**	**V,A,S (0.04)**	**T,V,A (0.02)**	**V,S (0.03)**	**T,V,A,S (0.05)**	null (0)	null (0.01)	**T (0.02)**	**T,V,A,S (0.04)**
12		**T,A,S (0.05)**	**T,V,S (0.02)**	**T,V,A (0.03)**	0 (0.01)	**T,V,S (0.02)**	**V,A (0.04)**			**T,V,A,S (0.01)**	**T,V,A (0.04)**
13		**T,V,A,S (0.03)**	V,A,S (0.02)	**T,V,A,S (0.02)**	A (0.01)	**V,A,S (0.02)**	**0 (0.03)**			S (0.01)	**V,S (0.02)**
14		**S (0.03)**	T,A,S (0.02)	**V (0.02)**	null (0.01)	T,V,A (0.02)	**T,V,S (0.03)**			T,V (0.01)	**A (0.02)**
15		**V,S (0.03)**	T,V (0.01)	**AC null**	T,A,S (0.01)	V,A (0.02)	**T,V,A (0.02)**			V,S (0.01)	**S (0.02)**
16		**A (0.02)**	T,A (0.01)	V,S (0.02)	T (0)	AC 0	T (0.01)			T,S (0.01)	null (0.02)
17		V,A (0.02)	V,A (0.01)	T,V (0.02)	AC null	T,V,A,S (0.01)	V (0.01)			T,V,S (0)	V,A (0.01)
18		A,S (0.01)	T,V,A,S (0)	T,V,S (0.01)	T,A (0)	null (0)	null (0.01)			AC null	A,S (0.01)
19		V,A,S (0.01)	T,V,A (0)	null (0)	AC 0	AC null	T,V (0)			null (0)	V,A,S (0.01)

(B) Cod

Rank	BALT	BS	EBS	ESS	GB	GoA	GoM	HS	NL	NORT	sGoSL	WSS
1	**0 (0.35)**	**0 (0.18)**	**AC null**	**A (0.19)**	**AC 0**	**AC null**	**AC null**	**AC null**	**AC 0**	**S (0.28)**	**AC null**	**AC 0**
2	**A (0.18)**	**S (0.14)**	**AC 0**	**0 (0.18)**	**V,A (0.2)**	**AC 0**	**AC 0**	**null (0.34)**	**V (0.28)**	**T (0.19)**	**AC 0**	**AC null**
3	**S (0.17)**	**V (0.13)**	**S (0.47)**	**T (0.17)**	**AC null**	**T (0.2)**	**T (0.29)**	**0 (0.14)**	**0 (0.22)**	**T,S (0.13)**	**A (0.19)**	**S (0.42)**
4	**AC 0**	**T (0.1)**	**A,S (0.14)**	**V (0.13)**	**V,A,S (0.14)**	**T,S (0.17)**	**T,S (0.23)**	**T (0.1)**	**AC null**	**0 (0.12)**	**0 (0.13)**	**A,S (0.12)**
5	**T (0.1)**	**V,S (0.08)**	**T,S (0.14)**	**T,V (0.11)**	**V (0.12)**	**T,V (0.13)**	**T,A (0.09)**	**S (0.09)**	**V,A (0.14)**	**T,A (0.11)**	**T,A (0.11)**	**T,S (0.11)**
6	**A,S (0.08)**	**A (0.06)**	**V,S (0.12)**	**T,A (0.09)**	**A (0.1)**	**T,V,S (0.07)**	**T,V (0.08)**	**T,S (0.07)**	**A (0.12)**	**A,S (0.08)**	**A,S (0.08)**	**V,S (0.11)**
7	**T,A (0.05)**	**T,V (0.06)**	**T,A,S (0.06)**	**V,A (0.08)**	**V,S (0.08)**	**T,A (0.07)**	**T,V,S (0.06)**	**AC 0**	**T (0.09)**	**T,A,S (0.05)**	**V,A (0.08)**	**0 (0.07)**
8	T,S (0.05)	**AC 0**	**T,V,S (0.04)**	AC 0	**T,V,A (0.06)**	**T,A,S (0.06)**	**T,A,S (0.06)**	**A (0.05)**	**T,V (0.06)**	A (0.04)	**V (0.07)**	**A (0.03)**
9	T,A,S (0.03)	**T,S (0.05)**	V,A,S (0.03)	AC null	**A,S (0.05)**	**A,S (0.06)**	**null (0.06)**	**T,A (0.04)**	**null (0.04)**	AC 0	**T (0.07)**	**V,A,S (0.03)**
10	AC null	**A,S (0.05)**	T,V,A,S (0.01)	T,V,A (0.04)	**T,V (0.05)**	**T,V,A (0.05)**	**S (0.04)**	**V (0.04)**	T,A (0.04)	AC null	**S (0.06)**	**V (0.03)**
11	null (0)	**V,A (0.04)**	null (0)	null (0)	**T,V,A,S (0.04)**	**A (0.04)**	**T,V,A (0.02)**	A,S (0.03)	T,V,A (0.02)	null (0)	**T,V,A (0.04)**	**T,A,S (0.03)**
12		**T,A (0.03)**	0 (0)		**T,V,S (0.04)**	**S (0.03)**	**0 (0.02)**	T,A,S (0.02)			**T,A,S (0.03)**	**T,V,S (0.02)**
13		**T,V,S (0.03)**	T (0)		**0 (0.03)**	**T,V,A,S (0.03)**	**T,V,A,S (0.02)**	T,V (0.02)			**T,V (0.03)**	T (0.02)
14		**V,A,S (0.02)**	V (0)		**T,A (0.03)**	**0 (0.02)**	V,S (0.01)	V,S (0.02)			**V,A,S (0.02)**	T,A (0.01)
15		T,V,A (0.02)	A (0)		**T,A,S (0.02)**	**V,A,S (0.02)**	A,S (0.01)	T,V,S (0.01)			**null (0.02)**	V,A (0.01)
16		AC null	T,V (0)		S (0.01)	**V,A (0.02)**	A (0.01)	V,A (0.01)			**V,S (0.02)**	T,V (0.01)
17		T,A,S (0.02)	T,A (0)		T (0.01)	null (0.01)	V (0.01)	T,V,A (0.01)			T,S (0.02)	T,V,A (0)
18		T,V,A,S (0.01)	V,A (0)		T,S (0.01)	V,S (0.01)	V,A,S (0)	V,A,S (0.01)			T,V,A,S (0.01)	T,V,A,S (0)
19		null (0)	T,V,A (0)		null (0)	V (0.01)	V,A (0)	T,V,A,S (0)			T,V,S (0.01)	null (0)

Table 4. Average surplus production parameter AIC_c weights for (A) herring and (B) cod. **Bold:** overall regional means. *Italics:* ecosystems where surplus models converged on the upper limit for K (40) and should be considered cautiously. Wind = wind speed. See Table 1 for ecosystem abbreviations and Table 2 for column heading abbreviations

(A) Herring

Ecosystem	r	K	T	Wind	PDO/NAO	Cod
BALT	1.00	1.00	0.76	0.00	0.77	0.39
BS	0.93	0.93	0.72	0.37	0.28	0.34
EBS	0.78	0.78	0.16	0.18	0.14	0.56
GB	*1.00*	*1.00*	*0.41*	*0.17*	*0.76*	*0.41*
GoA	1.00	1.00	0.21	0.91	0.38	0.73
GoM	1.00	1.00	0.51	0.18	0.27	0.39
HS	1.00	1.00	0.29	0.32	0.63	0.73
NORT	1.00	1.00	0.80	0.00	0.22	0.29
NS	1.00	1.00	0.56	0.34	0.33	0.00
sGoSL	1.00	1.00	0.24	0.36	0.90	0.20
WSS	1.00	1.00	0.81	0.46	0.24	0.48
Mean	**0.97**	**0.97**	**0.5**	**0.3**	**0.45**	**0.41**

(B) Cod

Ecosystem	r	K	T	Wind	PDO/NAO	Herring$_{t-1}$
BALT	1.00	1.00	0.19	0.00	0.32	0.31
BS	1.00	1.00	0.28	0.37	0.21	0.38
EBS	*1.00*	*1.00*	*0.25*	*0.16*	*0.19*	*1.00*
ESS	1.00	1.00	0.38	0.34	0.39	0.00
GB	1.00	1.00	0.24	0.77	0.66	0.38
GoA	1.00	1.00	0.80	0.32	0.35	0.46
GoM	0.94	0.94	0.88	0.19	0.19	0.42
HS	0.65	0.65	0.26	0.08	0.14	0.24
NL	*0.96*	*0.96*	*0.19*	*0.49*	*0.29*	*0.00*
NORT	1.00	1.00	0.50	0.00	0.25	0.55
sGoSL	0.98	0.98	0.29	0.27	0.58	0.23
WSS	*1.00*	*1.00*	*0.19*	*0.19*	*0.21*	*0.85*
Mean	**0.96**	**0.96**	**0.37**	**0.26**	**0.32**	**0.4**

on cod, or cod on herring (in the same year), were greater than 0.5, indicating models with terms for trophodynamic covariates comprised more than 50% of the cumulative AIC_c model weights from each ecosystem (Table 4). In BALT, BS, and HS, increased biomass of herring was associated with slight increases in cod ASP the following year, whereas in EBS, GB, GoM, and sGoSL, and NORT, cod ASP was negatively correlated with herring biomass in the previous year (Fig. 4). However, in most ecosystems, parameter estimates indicate a weak effect of herring biomass in a previous year on cod ASP, since model averaged parameter intervals often overlapped zero (except for EBS and WSS, which should be considered cautiously; Table 2). In contrast, cod biomass was an important predictor of herring surplus production in the same year, especially in EBS, GoA, HS and WSS (Table 2), but somewhat unexpectedly was positivity correlated with ASP in most systems except HS and BS (Fig. 4).

Across ecosystems, there were associations between mean MSY corrected for biomass and biophysical attributes. Mean estimated MSY values for herring were largest in the warmest systems in our study, but colder systems on average exhibited slightly higher estimates of MSY for cod (Fig. 5a). Mean MSY estimates for both species were negatively correlated with mean wind speed across systems, although the pattern was considerably stronger for herring than for cod (Fig. 5b). Finally, mean MSY estimates were differently correlated with the average biomass of predator or prey species; estimated herring MSY values were lower in systems with high mean cod biomass, whereas estimated cod MSY values were higher in systems with higher mean herring biomass (Fig. 5c,d).

Model-averaged estimates of biological reference points varied across ecosystems and species. MSY for both species were always less than 2.5 t km^{-2}, with estimates generally higher for herring than for cod (mean of 0.9 and 0.4 t km^{-2}, respectively). MSY for herring from EBS, BS, and GoA had low values of MSY (0.03 to 0.07 t km^{-2}) as compared to the remaining ecosystems where MSY estimates were an order of magnitude larger (0.92 to 2.2 t km^{-2}), although differences were much smaller when values were standardized by mean ecosystem biomass. MSY and B_{MSY} of cod ranged between 0.2 and 1.5 t km^{-2} and 0.5 and 6.2 t km^{-2}, respectively, and were highest for BALT and lowest for HS (Fig. 6). Similarly, B_{MSY} was lowest for EBS, BS, and GoA (1.4 to 2.2 t km^{-2}) and highest for sGoSL, and generally ranged between 3.3 and 10.9 t km^{-2}. Maximum population growth rate (r) ranged between 0.12 and 0.96 and was relatively constant across ecosystems and species (mean = 0.44 ± 0.05; Fig. 6).

Estimated MSY was robust to changes in model formulation; including physical or trophic covariates in surplus production models either had little effect on MSY or resulted in lower estimates of MSY than those of models without covariates (Fig. 6). This may be due to the mitigating effects of r, which were more sensitive to inclusion of covariates and exhibited regional and species-specific estimates of r (i.e. both positive and negative deviations from no-covariate models; Fig 6). Lastly, surplus production models with biophysical or trophic covariates had different effects on estimated $B_{MSY.}$ Inclusion of physical covariates sometimes resulted in less conservative, slightly higher estimates of B_{MSY} than models without covariates. In contrast, surplus production models containing trophic covariates generally resulted in lower or unchanged estimates of B_{MSY} values as compared to models without covariates (Fig. 6).

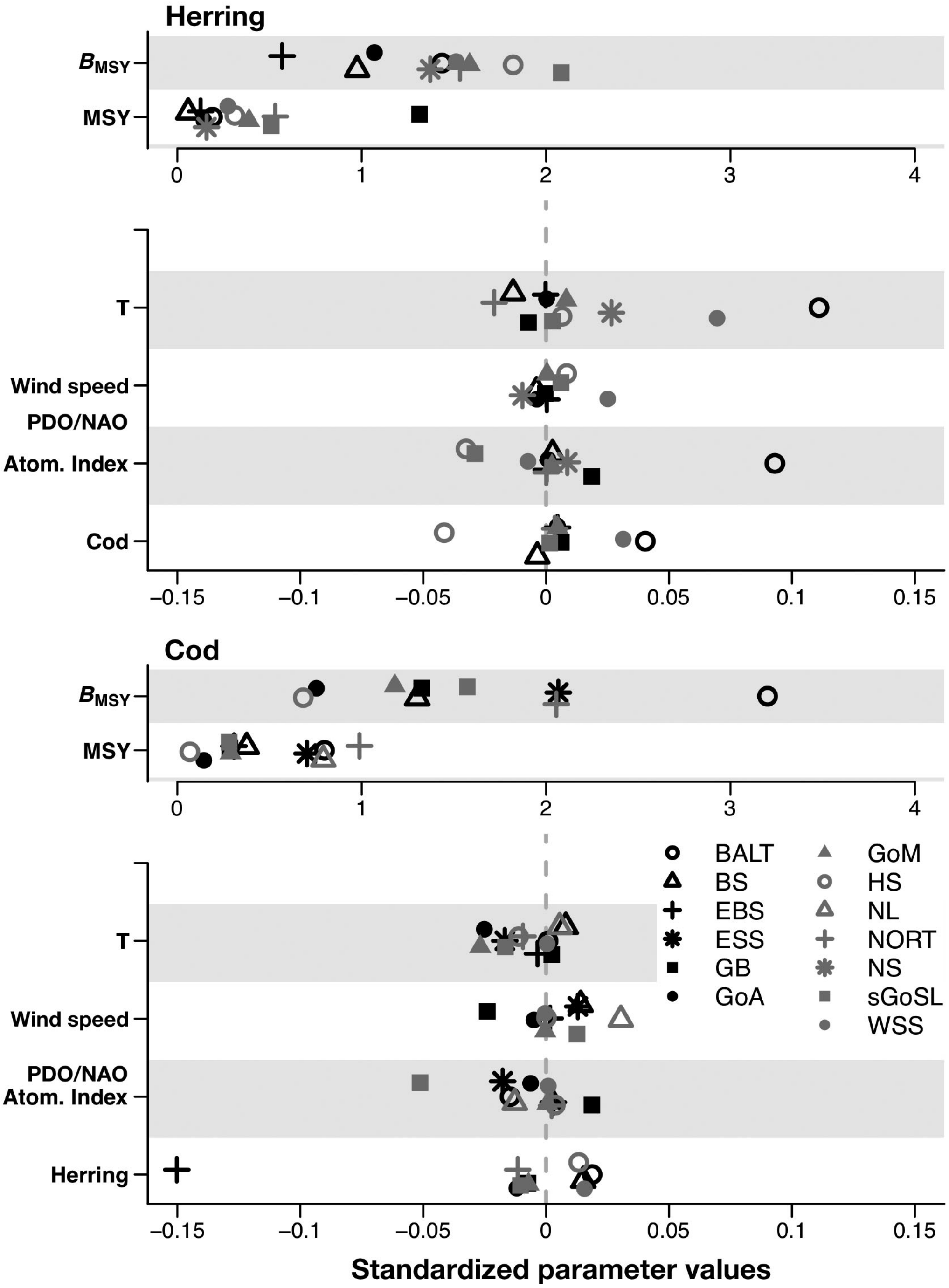

Fig. 4. Ecosystem-specific mean parameter estimates from top AIC_c selected models for herring and cod. Data are staggered for visual purposes and standardized to mean biomass for each species from each ecosystem. See Tables 1 & 2 for abbreviations

DISCUSSION

We conducted a cross-ecosystem comparative analyses to (1) identify whether inter-annual production dynamics are consistently predicted by particular biophysical variables, (2) relate mean production levels to ecosystem attributes, and (3) derive and compare biological reference points. We suggest 2 findings of our analyses are of note. First, biophysical and trophodynamic models commonly improved model fits: production models with biophysical and trophodynamic covariates were often preferred over simple models in most ecosystems. Especially for herring, inclusion of covariates partially accounted for

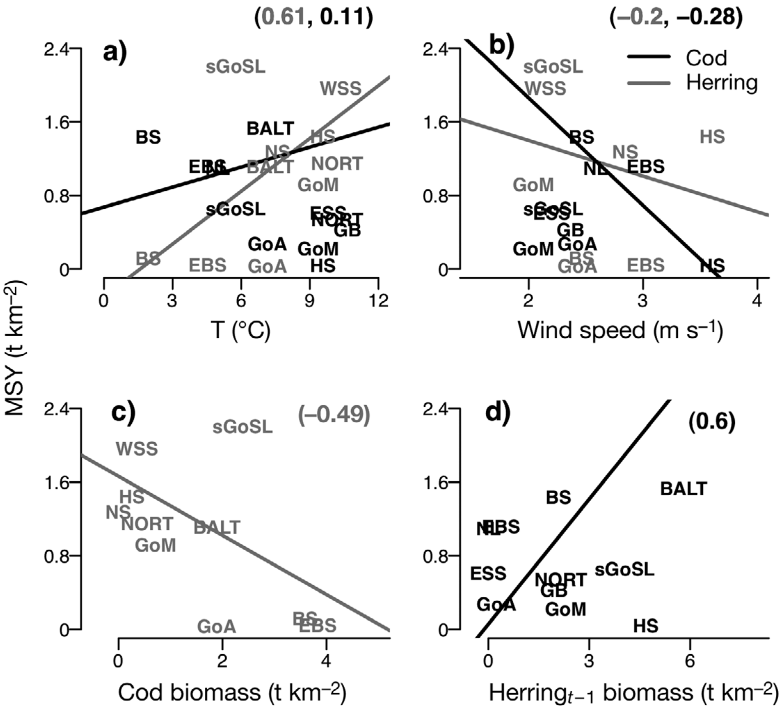

Fig. 5. Maximum sustainable yield (MSY) of cod (black) or herring (gray) species from each ecosystem as a function of mean environmental and biological parameters: (a) sea-surface temperature (T), (b) wind speed, (c) herring predator (cod biomass), and (d) cod prey (herring biomass). Values in brackets: adjusted R^2 values of the lines (grey: herring, black: cod). See Table 1 for ecosystem abbreviations

annual variation in auto-correlated errors that typified ASP. Yet, despite considerable inter-annual variability in ASP, no biophysical variables were consistently important in predicting production dynamics across ecosystems. Often individual parameters had different and even opposite effects on predicted ASP for either species from various ecosystems.

Second, inclusion of covariates into production models had species- and ecosystem-specific effects on resultant biological reference points (i.e. MSY and B_{MSY}) that reflect regional influences of biophysical or trophodynamic processes on species production. Although B_{MSY} and r estimates varied between models with and without covariates, estimates of MSY remained relatively unchanged. This is similar to previous studies that found MSY to be robust to changes in bottom-up drivers while biological reference points including MSY were lower if predation was accounted for in production models (i.e. Collie & Gislason 2001, Tyrrell et al. 2011). In contrast, inclusion of covariates did not universally result in more conservative estimates of r or B_{MSY}, nor did they always differ from parameters estimated from models without biophysical covariates. That said, when differences were observed in models for either species, trophic covariates generally lowered B_{MSY}, whereas physical covariates slightly raised B_{MSY} from the baseline estimated from models with no covariates. Differences in biological reference point estimates generally were larger when surplus production rates were highly correlated with biophysical covariates. Thus, inclusion of covariates should influence estimates of MSY and B_{MSY} accordingly for species in regions where production is highly responsive and tightly coupled to measured ecosystem processes.

Surplus production models are simple, computationally efficient methods to derive key population dynamic parameters from time series of population biomass indices (Schnute & Richards 2002). Our surplus production model fits were greatly improved by application of a Kalman filter to the input data prior to production modeling to smooth out observation error in relative abundance. Although not a common practice in many stock assessments, our analyses suggest that prior data smoothing can stabilize resultant estimates. Similarly, Walters & Hilborn (2005) used a simple smoother of relative abundance to stabilize estimates of recruitment and also recommend their use in assessment more generally. However, such filtering is not a panacea. For example, filtering the herring biomass data for GB may have removed contrast in biomass and ASP needed to parameterize the model. Kalman-filtered biomass and surplus production values for GB are restricted to the domain of the ascending limb of the production function, which is consistent with observations that the stock was heavily depressed during much of the time series we analyzed (Melvin & Stephenson 2007). Yet, specific additional outliers need to be removed (requiring additional information beyond the scope of this study), or further recovery of the stock is needed in order to fit to the parabolic production curve of the Schaefer model. Conversely, non-stationarity in GB ecosystem processes driving surplus production may render divergent biological reference points for historical and contemporary abundances, a feature that simple production models with equilibrium assumptions are unable to capture (Walters et al. 2008). Similarly, lack of contrast and non-stationarity precluded our ability to fit production models to 4 of 13 cod stocks (i.e. WSS, NL and EBS, and to a lesser degree BALT). In particular, the data time series of population production from EBS

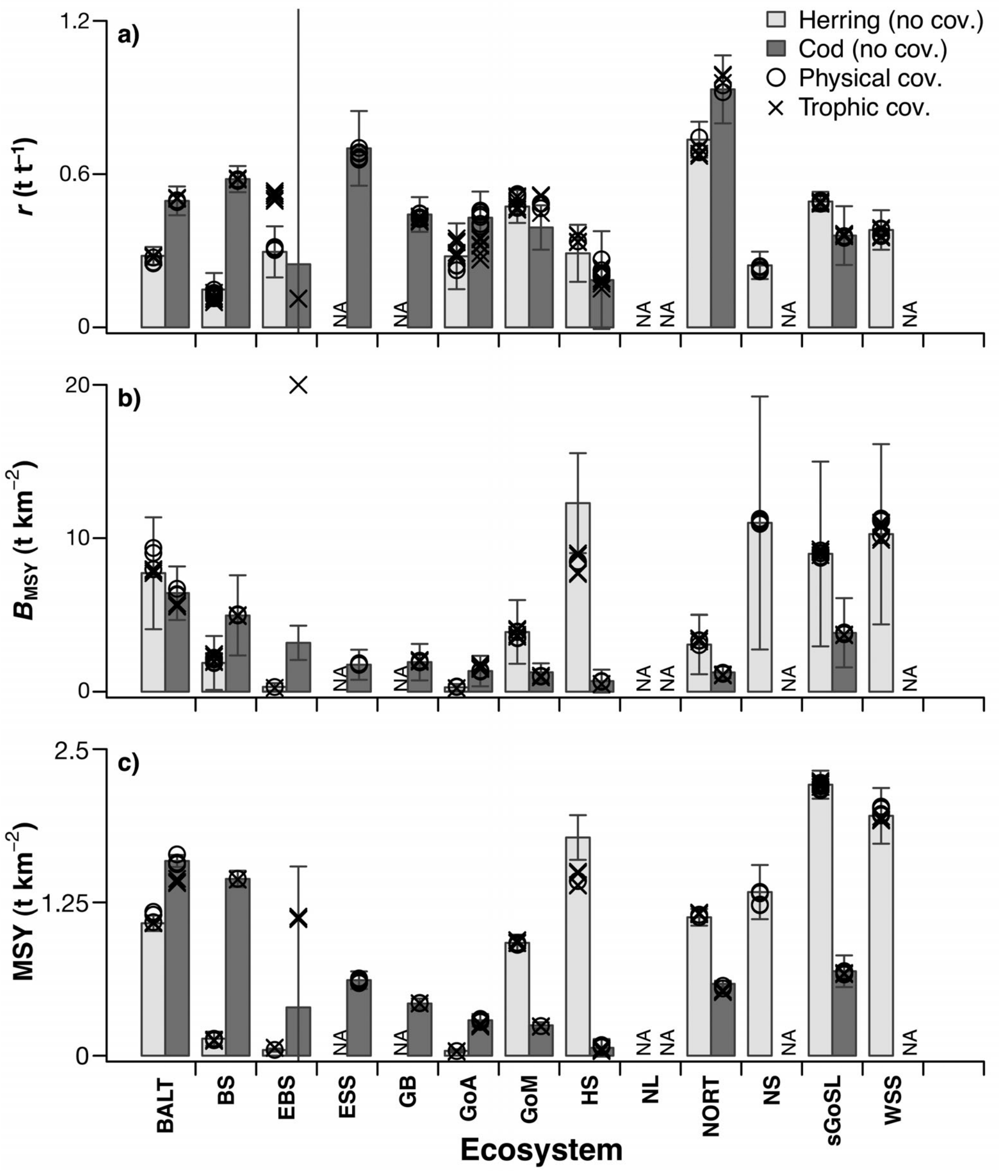

Fig. 6. Estimated values for maximum sustainable yield (MSY), biomass at MSY (B_{MSY}), and population growth rate (r) for herring (light gray) and cod (dark gray) species from 13 focal ecosystems. Shaded bars: estimated values from models without covariates (±1 SE), symbols: individual model values from the top AIC$_c$ selected models with physical (O) and/or trophic covariates (×). NA: data not available. See Table 1 for ecosystem abbreviations

and NL were indicative of non-stationary production, leading to clockwise cycles of production and biomass that are not well explained by the Schaefer production model with stationary model parameters (Walters et al. 2008).

Even within the same ocean basin, variation in PDO and NAO indices are often associated with regional and species-specific changes in ecosystem structure. For example, positive PDO values are often correlated with below average ocean conditions (e.g. increased predation risk, decreased upwelling, reduced food supply; Emmett et al. 2006) in the northern California current and above average conditions for salmon in Alaska (Mantua et al. 1997). We also found species- and ecosystem-specific associations between ASP and atmospheric indices. Specifically, production dynamics of herring were more frequently coupled with atmospheric indices of ecosystem production than those of cod; slight changes in PDO or NAO indices were associated with measurable changes in ASP of herring species from BALT, HS and sGoSL, but only appreciably impacted estimated ASP of cod from GB (i.e. GB was the only ecosystem where average parameter confidence limits for NAO did not overlap zero). Similarly, biophysical covariates, particularly sea surface temperature and wind indices were more influential in models for herring species than cod species, as evidenced by mean parameter values and weights. In part, this may result from divergent life-history traits; herring are highly fecund and shorter-lived than cod and experience fluctuations in biomass that can vary by orders of magnitude with changes in environmental conditions (Nash & Dickey-Collas 2005). In contrast, cod production integrates long-term trends in regional conditions and may lag one to many years behind ecosystem changes (e.g. Brodziak & O'Brien 2005).

Our results also support efforts to include trophic interactions in surplus production models (i.e. Collie & DeLong 1999, Gamble & Link 2009); for most ecosystems, models with covariates for cod or herring biomass ranked highly with AIC_c, although the direction of species covariate effects was sometimes unexpected. We anticipated that cod production would be positively correlated with herring production since herring are often found in the diets of adult cod (Link & Garrison 2002). Yet, while cod production was lower when herring biomass was also depressed in some ecosystems (i.e. BALT, BS), in others, particularly EBS, cod production was negatively correlated with herring production in the previous year. This may result from disparate juvenile cod and adult herring survival responses to environmental conditions, juvenile cod competition with herring for mutual prey resources, increased mortality from aggregation of mutual predators, or even direct predation mortality (Fauchald 2010).

Systems with strong negative correlations may also represent cultivation-depensation processes (Walters & Kitchell 2001). According to this hypothesis, dominant predator fishes (i.e. cod) prey on forage fish species (i.e. herring), which in turn compete with larval and juvenile age classes of the predator, indirectly increasing recruitment success in subsequent years. If harvest reduces predator biomass below some critical threshold, depensation may occur as forage fish populations are released from predatory control and increasingly prey upon or compete with juvenile predators for mutual resources. We find some evidence of cultivation-depensation in 3 systems in particular (NORT, GoM, and sGoSL) and possibly GB and EBS. In these systems, herring biomass and ASP increased over time, coincident to low cod biomass and ASP that persisted even after harvest pressure on that species was reduced or eliminated. Additional analyses are needed to evaluate mechanisms driving this potentially important relationship.

The 13 systems we examined spanned a wide range of ecosystem properties from 2 ocean basins. MSY estimates did not differ by ocean basin, nor were they related to area, average depth or annual average primary production. However, MSY estimates (corrected for mean biomass for each species from each ecosystem) were related to average sea surface temperature for a number of systems, even though parameter values were not large. This suggests that large-scale climatic events (i.e. regime shifts, climate change) that induce significant warming of shallow surface waters will also be associated with changes in production of these 2 species. Our results suggest generally that herring production in these ecosystems should increase as ecosystems warm, whereas cod production should decline. Additionally, one might expect that as biophysical conditions change, populations may shift their distributions to track centers of production (Nye et al. 2009), potentially affecting spatial patterns of abundance and estimates of surplus production.

Although we found consistent evidence for the importance of including biophysical and trophodynamic covariates in production models, their inclusion did not appear to result in a consistent effect on resultant biological reference points. This finding has implications for management advice. Increasingly, analysts are asked to provide estimates of the uncertainty associated with biological reference points. Typically, biophysical and trophodynamic considerations are viewed as factors that increase observation error in input data. Our results suggest the contrary, namely that biophysical and trophodynamic covariates can be important sources of process error, and that failure to incorporate their effects can lead to underestimates of the uncertainty in biological reference points.

In summary, we found that inclusion of ecological covariates can strengthen the fit of common production models to surplus production data and help capture some of the dynamic error that is associated with highly correlated production rates observed in some ecosystems. Yet, despite similarities across the systems we examined, no single covariate was universally selected by AIC and the relative influence of an ecological covariate was system dependent, even when parameters were corrected for variability in biomass. This suggests that the potential benefit of including ecological covariates in surplus production models is species- and system-dependent, and highlights the importance of selecting biophysical and trophodynamic covariates for a region and species that have strong mechanistic underpinnings and reflect true variation in production rates.

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Contribution to the Theme Section 'Comparative analysis of marine fisheries production'

Aggregate surplus production models for demersal fishery resources of the Gulf of Maine

M. J. Fogarty[1,*], W. J. Overholtz[1,2], J. S. Link[1]

[1]Northeast Fisheries Science Center, National Marine Fisheries Service, 166 Water St., Woods Hole, Massachusetts 02543, USA

[2]*Present address:* 193 Percival Rd., Falmouth, Massachusetts 02356, USA

ABSTRACT: We developed surplus production models for 12 demersal fish species in the Gulf of Maine at the single-species and aggregate-species levels. Summed single-species production model reference points were higher than estimates from the aggregate surplus production model. The equilibrium yield (maximum sustainable yield, MSY) and biomass at MSY (B_{MSY}) levels for the summed single-species production model reference points exceeded the aggregate model results by 28.0 and 27.5%, respectively. Biological interactions such as predation and competition are potential reasons for differences between the aggregate and summed results. Not accounting for biological interactions may result in overly optimistic predictions of long-term sustainable yield and unrealistically high estimates of B_{MSY}. We found high concordance between single-species production model reference points and results from a range of other estimation methods employed in assessment of these species, suggesting that the results from the aggregate production model analyses are not artifacts related to model type. Tests for the effect of environmental variables, including the Atlantic Multidecadal Oscillation (AMO) index, the winter North Atlantic Oscillation (NAO) index, and the Extended Reconstructed Sea Surface Temperature (ERSST) series suggested possible effects of the NAO at a lag of 0 and the ERSST at a lag of 2 yr based on cross-correlation analyses. However, further tests proved inconclusive when the covariates were introduced into an extended surplus production model. Given the potential shifts in productivity that can accompany climate change, this issue should be periodically re-evaluated, and, where appropriate, a more dynamic approach to setting reference points should be pursued.

KEY WORDS: Ecosystem-based fishery management · Reference points · Aggregate multispecies model · Environmental effects

INTRODUCTION

The Gulf of Maine is a semi-enclosed continental shelf sea delimited on its seaward boundary by Georges Bank and on its landward margins by bordering sections of the US states of Massachusetts, New Hampshire, and Maine and the Canadian provinces of New Brunswick and Nova Scotia (Fig. 1). The system is characterized by an extremely complex topography, reflecting its recent glacial history. Three major deep basins and over 20 smaller basins occur within the Gulf. Two ledge-bank systems within the Gulf, Stellwagen Bank and Jeffries Ledge, are historically important fishing grounds. Stellwagen Bank is now a designated National Marine Sanctuary. The rich mosaic of sediment types associated with these features results in high habitat diversity in the system. The deep Northeast Channel (Fig. 1) provides a major pathway for inflow of nutrient-rich continental slope water into the Gulf. These physical characteristics collectively contribute to a diverse and productive fauna.

*Email: michael.fogarty@noaa.gov

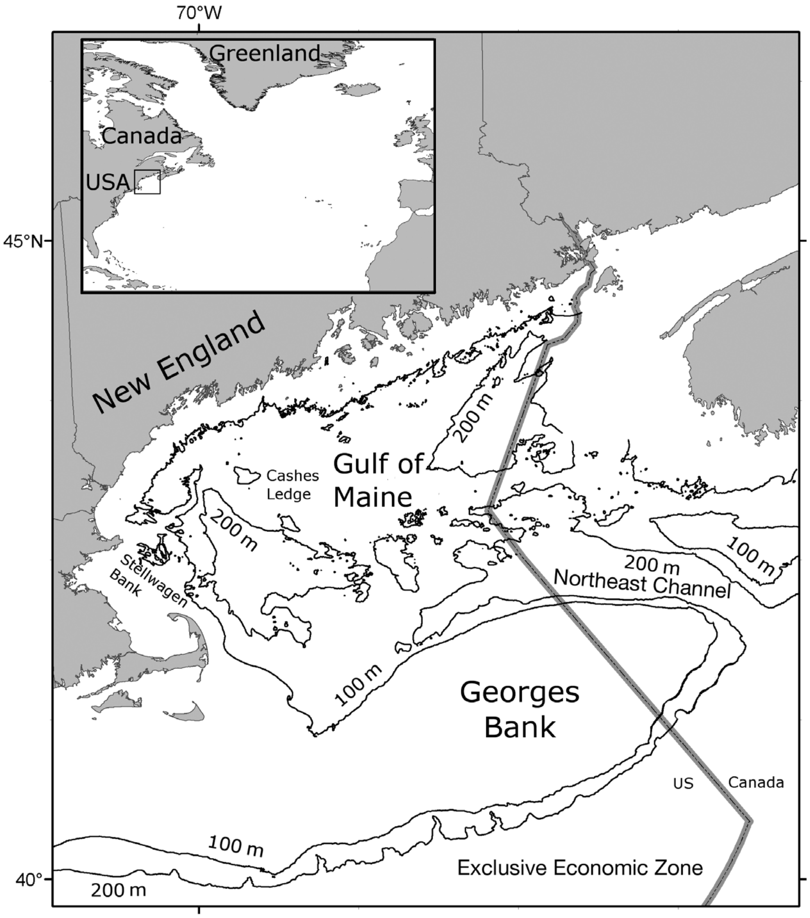

Fig. 1. Gulf of Maine, showing major basin systems, the position of the Northeast Channel, and the location of Georges Bank. The inset shows the location of the Gulf of Maine (boxed area) in the Northwest Atlantic

Fisheries within the Gulf, capitalizing on this productivity, were among the earliest maritime industries established following European settlement in the region over 400 yr ago (Lear 1998, Bolster 2008). For example, fisheries on Stellwagen Bank can be traced to the turn of the 17th century (Rosenberg & Claesson 2008), and fishing remains a major industry in the Gulf. The lobster fishery in particular is among the most valuable in the nation. The ecological structure of the Gulf of Maine has been altered radically by centuries of fishing and other human activities (Apollonio 2002). The decimation of populations of large whales, the sequential depletion of fish populations such as sturgeon (*Acipenser* spp.) and halibut *Hippoglossus hippoglossus* that have not recovered, and the impacts on diadromous species through obstruction of river systems have fundamentally changed the structure and productivity patterns in the Gulf.

We assessed the recent dynamics of an economically important assemblage of 12 demersal fish species in the Gulf of Maine using aggregate-species production models. These species are taken together in a mixed-species trawl fishery. Our objective was to capitalize on the greater stability and predictability of aggregate system properties using simple and robust models to estimate community-level biological reference points and to compare these results with comparable single-species model results. The aggregate-species models implicitly account for interspecific interactions among species in the assemblage. They can also readily accommodate environmental and climate forcing in an analytically tractable setting (Mueter & Megrey 2006). Brown et al. (1976) provided one of the earliest demonstrations of the value of this general approach. For the Northeast US Continental Shelf Large Marine Ecosystem (NES LME) as a whole, an aggregate multispecies model provided more conservative biological reference points (total system maximum sustainable yield, MSY) relative to the sum of single-species MSY estimates (Brown et al. 1976). Ralston & Polovina (1982) showed that aggregate-species production models can outperform comparable models focused on higher levels of taxonomic resolution in the Hawaiian longline fishery. Sparholt & Cook (2009) recently applied an aggregate production model approach to 5 Northeast Atlantic fish stocks and concluded that suitable biological reference points could be derived for this species complex in a combined-species analysis.

Tradeoffs inevitably arise in the balance of mechanistic detail and parameter uncertainty in models of multispecies systems. Aggregate production models provide one potentially effective approach to coping with the issues that emerge with increasing model complexity (Sugihara 1984). These simple models nonetheless must be carefully evaluated and the potential for adverse effects on low productivity stocks assessed (Gaichas et al. 2012). Vulnerable species (so-called weak-link stocks) will require special consideration in any management regime, and it will be particularly important to include appropriate safeguards in systems based on aggregate production dynamics.

METHODS

Catches and abundance estimates were assembled for 12 economically important demersal fish stocks in Gulf of Maine (GOM) for the period 1964 to 2007 (Table 1). Species selected for analysis comprise dominant components of the GOM otter trawl fishery (Lucey & Fogarty in press). Landings data were compiled for each species from the Northeast Fisheries Science Center (NEFSC) commercial fishery statistics data base. We used NEFSC autumn research survey estimates (stratified mean catch in kg tow^{-1}) for the GOM, adjusted for catchability to the survey gear (Brodziak et al. 2004) and the area swept by the trawl, to generate total biomass estimates (see also Link et al. 2006). Approximately 75 stations are occupied in the GOM in each survey, and the modal coefficient of the estimates for the species included in this analysis is 30%. Biomass estimates for each stock were summed to produce an aggregate estimate for the 12-species complex.

These aggregate estimates of biomass and landings were then used as primary inputs in a quadratic surplus production model. The basic approach followed the methods described by Jacobson et al. (2002) and Mueter & Megrey (2006). We based our analysis on a discrete-time version of the simple logistic production model:

$$B_{t+1} = B_t + (\alpha - \beta\bar{B}_t)\cdot\bar{B}_t - C_t + \varepsilon_t \qquad (1)$$

where α is the intrinsic rate of increase, β is a density-dependent term, α, $\beta > 0$, B_t is the aggregate annual biomass at time t, and ε_t is a normally distributed random variable with mean 0 and constant variance. Following Mueter & Megrey (2006), $\bar{B}_t = [B_{t+1} + B_t]/2$. By definition, the annual surplus production in year t (ASP$_t$) is the change in biomass from year t to year t+1 plus the catch in year t (e.g. Quinn & Deriso 1999).

Table 1. Demersal teleost species included in the Gulf of Maine assemblage considered in this analysis

Species	Common name
Gadus morhua	Atlantic cod
Melanogrammus aeglefinus	Haddock
Merluccius bilinearis	Silver hake
Urophycis tenuis	White hake
Urophycis chuss	Red hake
Pollachius virens	Pollock
Limanda ferruginea	Yellowtail flounder
Pseudopleuronectes americanus	Winter flounder
Hippoglossoides platessoides	American plaice
Glyptocephalus cynoglossus	Witch flounder
Lophius americanus	Monkfish
Sebastes fasciatus	Redfish

We can rearrange Eq. (1) to give:

$$\text{ASP}_t = B_{t+1} - B_t + C_t = (\alpha - \beta\bar{B}_t)\cdot\bar{B}_t + \varepsilon_t \qquad (2)$$

The MSY is given by:

$$\text{MSY} = \frac{\alpha^2}{4\beta} \qquad (3)$$

The corresponding proportional fishing mortality at MSY is:

$$F_{\text{MSY}} = \frac{\alpha}{2} \qquad (4)$$

representing the annual proportion of the population removed by harvesting. Finally, the biomass level at MSY is given by:

$$B_{\text{MSY}} = \frac{\alpha}{2\beta} \qquad (5)$$

The parameters α and β were estimated by the method of maximum likelihood using a process-error model. We evaluated variability in the estimates of the biological reference points using a nonparametric bootstrap routine with 1000 replicates to generate probability distributions for each reference point. Because of the time series nature of the data, we employed a moving blocks bootstrap procedure (Efron & Tibshirani 1994). The series was divided into intervals (blocks) of 3 yr, and we randomly selected a selection of these blocks rather than individual observations for each of the 1000 iterations of the bootstrap.

Contrast with single-species models

For comparison, biological reference points were also derived for each of the individual stocks using single-species production models employing the same methods used for the aggregate-species model. We then compared the summed single-species results with those for the base case aggregate model. We also compared the single-species surplus production model results with biological reference points reported in the comprehensive Groundfish Assessment Review Meeting (GARM) report (NEFSC 2008) and additional analyses for hake species. A wide range of model types was used in the GARM analyses, and the selection of reference points differed substantially from the surplus production model analysis. Models and analytical approaches for individual species in the GARM included age- and size-structured models and index-based analyses drawing on survey (and in some cases catch) information. The GARM analyses had a principal focus on maintaining target levels of spawning stock biomass and specifying corresponding fishing mortality rates using spawning-biomass-per-recruit analyses. For index-based assessments, we expanded survey catch-per-tow estimates to total biomass using the area-swept and survey catchability approach described above. Once placed on an absolute scale, these reference points could then be compared with the production model results. Again, because the basis for selecting and estimating reference levels differed markedly from the production model approach, the GARM results are intended only to provide a general point of comparison and to test for concordance and directionality of overall results.

Environmental effects

We examined the potential effect of environmental or climate-related factors on surplus production in this system. The covariates used were the Atlantic Multidecadal Oscillation (AMO) index, the winter (December to February) North Atlantic Oscillation (NAO) index, and the Extended Reconstructed Sea Surface Temperature (ERSST) index for the Northeastern US. Both the NAO and AMO are basin-wide indicators. The AMO index is based on spatial patterns in SST variability after removing the effects of anthropogenic forcing on temperature (Enfield et al. 2001). The NAO is the dominant mode of climate variability over the North Atlantic Basin (Hurrell 1995) and is known to exert important ecosystem effects (Stenseth et al. 2002). The broad-scale ERSST series is based on a comprehensive analysis of long-term temperature records obtained from ships-of-opportunity (Smith & Reynolds 2003, 2004). In each case, we converted the observations to standard normal deviates with 0 mean and unit standard deviation.

To examine candidate lags to be included in the analysis, we first examined the cross-correlation structure (Box & Jenkins 1976) for ASP and each of the environmental covariates. Following identification of candidate environmental variables and lags, we incorporated these metrics in an extended production model:

$$\mathrm{ASP}_t = (\alpha - \beta \bar{B}_t)\,\bar{B}_t \mathrm{e}^{\sum_{j=1}^{m} \delta_j X_{j,t-\tau}} + \mathrm{e}_t \qquad (6)$$

where δ_j is a coefficient for the effect of the jth covariate, $X_{j,t\text{-}\tau}$ is the value of covariate j at lag τ , and all other terms are defined as before. All candidate models were compared using the Akaike Information Criterion (AIC; Akaike 1992) to test whether the fit with environmental covariates performed better than the base case (Eq. 2). We used the corrected $\mathrm{AIC_c}$ to adjust for sample size effects:

$$\mathrm{AIC_c} = -2\log_\mathrm{e}(L) + \frac{2K(K+1)}{n-K-1} \qquad (7)$$

where L is the likelihood estimate, K is the number of parameters estimated, and n is the number of observations (Burnham & Anderson 1998).

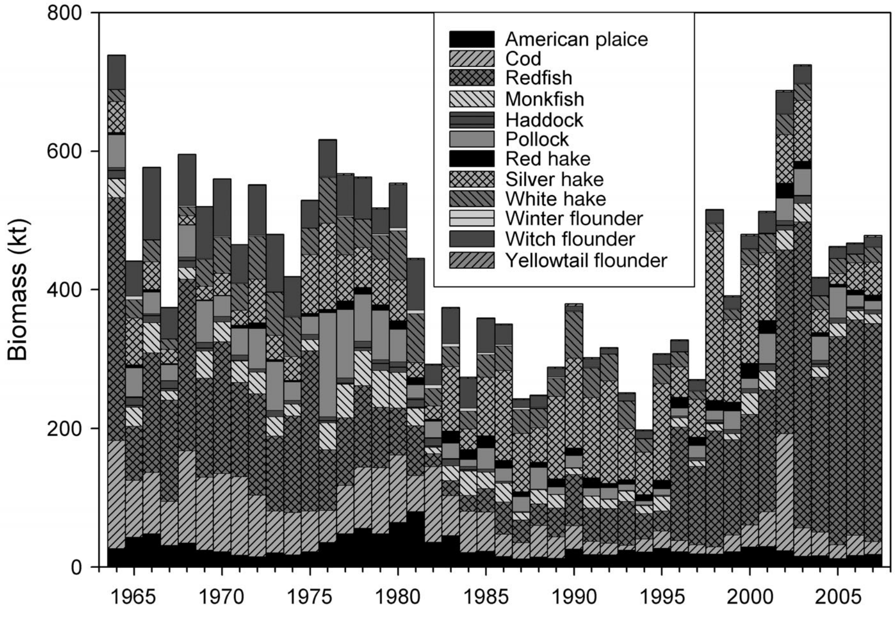

Fig. 2. Biomass (kt) of selected demersal fish species for the Gulf of Maine during 1964 to 2007

RESULTS

Aggregate biomass of the 12-species complex declined through the mid-1990s but has since increased, nearly recovering to the levels at the start of the survey time series (Fig. 2). Substantial changes in relative species composition are again evident throughout the series with important changes in the abundance of key species such as cod, haddock, and redfish. The coefficient of variation of the aggregate biomass series (30.5%) was substantially lower than that of the individual species, which ranged from 50.0 to 87.6% (mean 64.8%). The greater relative precision of the combined series is a potential advantage of dealing with aggregate data.

Total aggregate catch of the demersal species complex declined steadily during 1964 to 2007. The relative species composition of the catch has varied considerably over time (Fig. 3). In particular, red hake was dominant in the first decade of the series. Sharp declines in red hake catch in this initial period accounted for the overall drop in the total catch from just under 250 kt in 1964 to a low of ~20 kt in 2007 (Fig. 3). The coefficient of variation of the individual catch series was again higher than for the aggregate series but less markedly so than for the biomass series (mean 84.52% compared with 70.67%) and the range of the coefficients of variation (CVs) for the individual catch series was quite broad (45.13 to 171.95%). We note that the CV in the catch series is affected by management actions, and these have changed over the time period covered in this analysis.

The summed landings and biomass series were used to generate estimates of annual surplus production for the assemblage (Fig. 4). ASP has fluctuated in the GOM over the entire period, with several periods of negative surplus production reflecting periods of non-sustainable harvesting (Fig. 4).

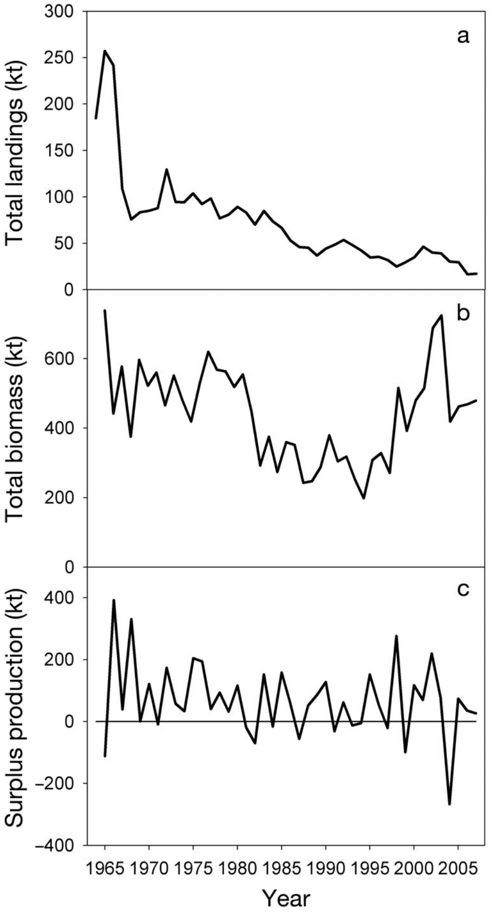

Fig. 4. (a) Total landings (kt), (b) biomass (kt), and (c) annual surplus production (kt) of 12 demersal fish species in the Gulf of Maine used in this analysis

Contrast with single-species models

The point estimate of the MSY for the 12-species assemblage was 74 kt and the B_{MSY} was 510 kt (Table 2). The corresponding F_{MSY} was 0.16 (Table 2). Bootstrap probability distributions for each reference point are provided in Fig. 5; the B_{MSY} distribution was strongly skewed with a long tail. The summed MSY estimate for the individual surplus production models (94.5 kt) was ~28% higher than for the aggregate model. The summed B_{MSY} estimate (650 kt) exceeded the aggregate model results by 27.5%. The variability in the reference point determinations for both the aggregate and summed single-species results complicates detailed comparison and testing. Strong negative covariances between the parameter estimates for MSY and B_{MSY} introduces additional uncertainty because the covariance terms themselves enter the overall variance for these reference points as negative terms

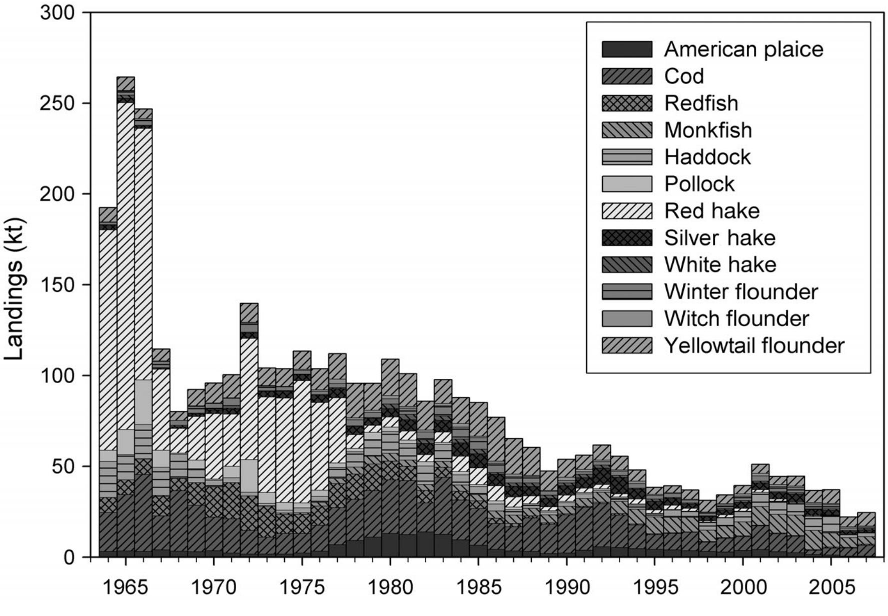

Fig. 3. Landings (kt) of selected demersal fish species for the Gulf of Maine during 1964 to 2007

Table 2. Biological reference points derived from simple production models and Groundfish Assessment Review Meeting (GARM) assessment results (NEFSC 2008). MSY: maximum sustainable yield, F_{MSY}: fishing mortality at MSY, B_{MSY}: biomass at MSY

Species	Production model reference points		
	F_{MSY}	MSY (kt)	B_{MSY} (kt)
Cod	0.27	18.842	69.329
Haddock	0.17	0.862	5.065
Silver hake	0.45	31.551	69.886
White hake	0.13	5.115	38.905
Red hake	0.44	3.687	8.437
Pollock	0.23	13.987	58.986
Yellowtail flounder	0.60	1.341	2.216
Winter flounder	0.36	2.557	7.040
American plaice	0.06	3.296	54.986
Witch flounder	0.02	3.045	15.237
Monkfish	0.15	4.367	27.977
Redfish	0.04	5.830	154.72
Sum		94.497	650.030
Aggregate model	0.16	73.846	509.746

The estimated F_{MSY} levels for individual species ranged from 0.02 to 0.60 (Table 2), reflecting both real differences in life history characteristics and the effects of noisy data at the single-species level. The single-species estimate for yellowtail flounder at $F_{\mathrm{MSY}} = 0.6$ is unreasonably high, and the estimates for silver and red hake are also very high (Table 2). The estimate of F_{MSY} for the aggregate model case (0.16) was lower than two thirds of the estimates for individual species (Fig. 6), suggesting its general utility as a conservative reference point. However, any attempt to manage using an aggregate target F strategy would need to consider that some fraction of species included in the analysis would require special consideration to ensure that they were not overexploited and driven to low biomass levels because of low productivity. The use of supplemental management measures designed to reduce fishing mortality on these vulnerable stocks through gear modifications, spatial protection, and other mechanisms would be required. We note that this issue is no more problematical for the aggregate analysis than for single-species analyses for mixed-species fisheries confronting the weak stock constraint.

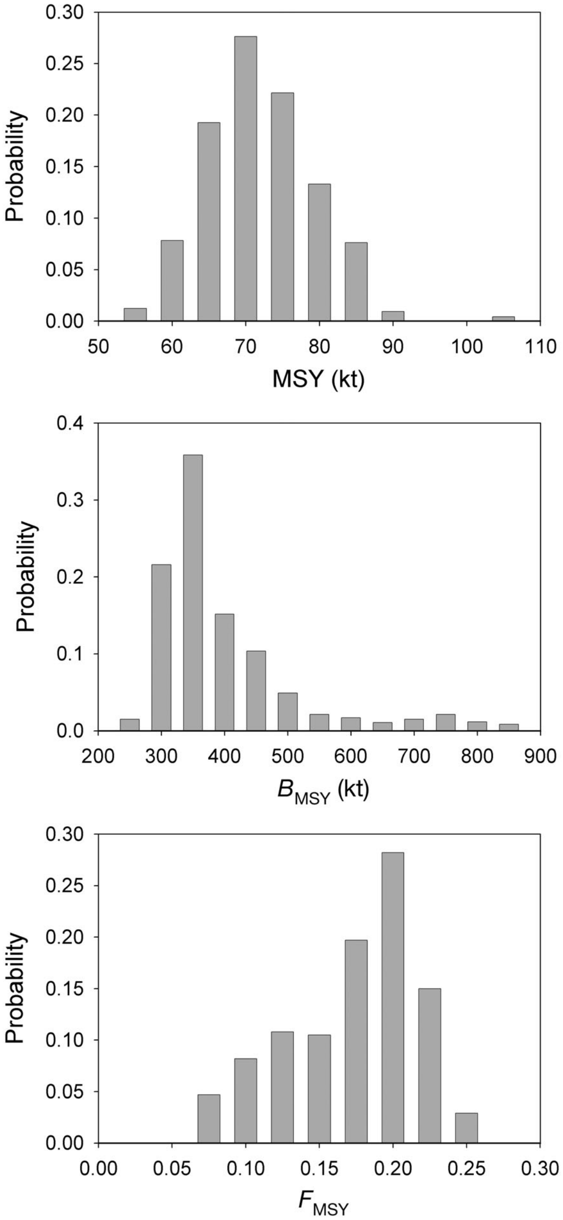

Fig. 5. Empirical probability distribution of biological reference points based on aggregate surplus production models using 1000 nonparametric bootstrap replicates for each reference point type

A comparison of derived reference points for single species production models relative to the results from the GARM and hake analyses indicate a strong concordance in results (Fig. 7). The Spearman rank order correlation for the 12 species was 0.86 for the MSY estimates and 0.81 for B_{MSY}. Although the basis for reference point determination differs markedly in the production model approach and the various methods employed in the GARM, the general picture that emerges is consistent for the individual species involved in both cases (Fig. 7). The greatest divergence occurs for the B_{MSY} estimate for redfish, which is substantially higher in the GARM analyses. The summed estimate for the 12 species is quite similar for the single-species production model and the GARM results for both MSY and B_{MSY} (triangles in Fig. 7).

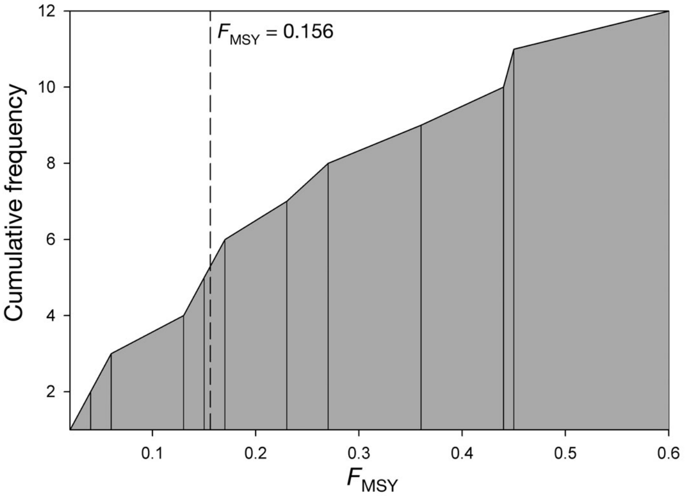

Fig. 6. Cumulative frequency distribution of fishing mortality at maximum sustainable yield (F_{MSY}) levels for single-species production model results for the 12-species system. Solid vertical lines indicate the values for individual species results. The dashed vertical line indicates the position of the aggregate species F_{MSY} value

Environmental effects

The AMO index has steadily increased over the last 3 decades (Fig. 8). The first decade of the standardized NAO series was dominated by negative anomalies, followed by a preponderance of positive anomalies punctuated by some sharp reversals in the mid-1990s (Fig. 8). The ERSST series reflects generally low temperature values in the 1960s and generally high values in the last decade (Fig. 8). An examination of the cross-correlations between ASP and each of the 3 environmental variables indicated potential effects of NAO at a lag of 0 and for ERSST at a lag of 2 yr (Fig. 9). We included these terms both together and individually in extended production models to test for environmental effects. The change in AIC_c scores (Δ AIC_c) was low in all cases (Table 3), suggesting that further consideration of these environmental terms was not warranted at this time. Generally, a decrease in the AIC scores greater than 2 is required to be considered meaningful (Burnham & Anderson 1998), and our results did not meet this threshold.

DISCUSSION

Substantial progress is now being made in developing and implementing approaches for marine ecosystem-based fishery management (e.g. Link 2010, Belgrano & Fowler 2011, Christensen & Maclean 2011). A diverse set of modeling tools is being used to guide management options as shown in these recent compilations. For the Northeast US Continental Shelf, a long tradition of multispecies and ecosystem modeling efforts has been used to explore aspects of the dynamics of the system in response to exploitation. Along a continuum from simple to complex model structures, these include aggregate-species surplus production models (Brown et al. 1976), multispecies production models (Sissenwine et al. 1982, Gamble & Link 2009), donor-controlled multispecies models (Overholtz & Tyler 1986), recipient-controlled

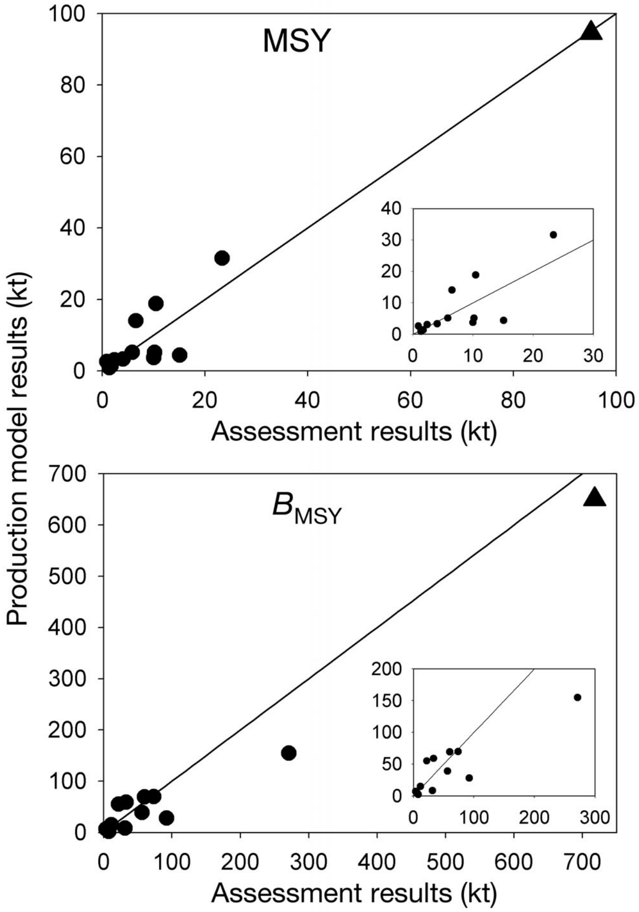

Fig. 7. Relationship between maximum sustainable yield (MSY) and biomass at MSY (B_{MSY}) estimates based on Groundfish Assessment Review Meeting (GARM) and hake assessment results (NEFSC 2008) and single-species production model results. The 1:1 line is indicated, and (▲) represents the summed estimates for each modeling approach. The insets at the lower right of each panel show only the individual species results and not the total. Statistical comparisons (Spearman rank-order correlations) were done only on the individual species results

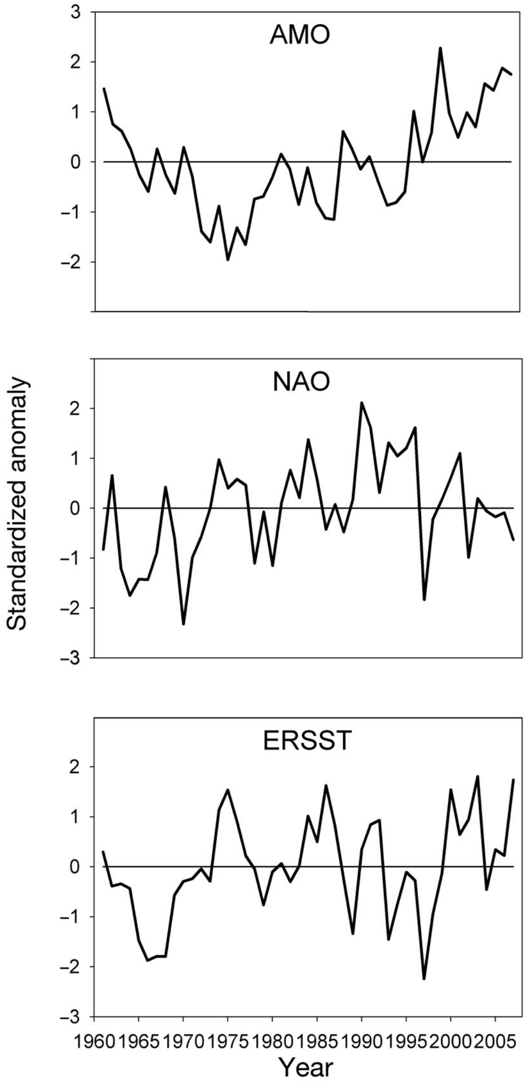

Fig. 8. Environmental and climate-related time series considered in development of the extended production model approach. All variables are expressed as standard normal deviates for the time series represented. AMO: Atlantic multidecadal oscillation. NAO: North Atlantic oscillation. ERSST: Extended reconstructed sea surface temperature

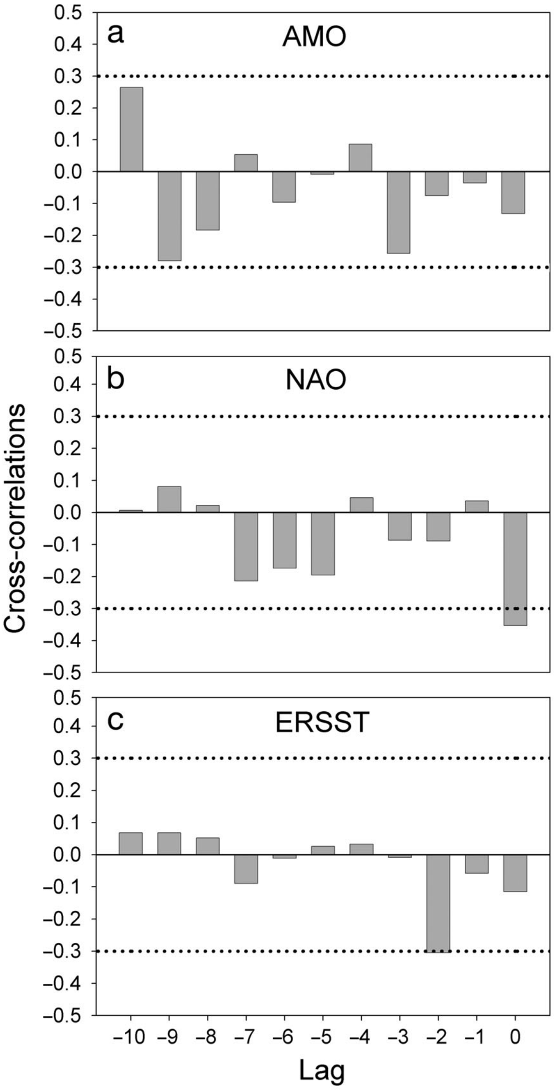

Fig. 9. Cross-correlations between aggregate annual surplus production and (a) the Atlantic Multidecadal Oscillation (AMO), (b) North Atlantic Oscillation (NAO), and (c) Extended Reconstructed Sea Surface Temperature (ERSST). Dashed lines show upper and lower 95% confidence intervals

box models (Overholtz & Link 2009), multispecies delay-difference models (Fogarty et al. 1991, Collie & DeLong 1999), energy budget and network models (Cohen et al. 1982, Sissenwine et al. 1984, Steele et al. 2007, Link et al. 2008a,b), full age- or size-structured consumption models (Overholtz et al. 1991, 1999), and a coupled physical-ecological-fishery model (ATLANTIS; Link et al. 2011). For a full overview of ecological models developed for this system, see Link et al. (2012). The broad array of modeling approaches applied can be effective in testing for consistency in inferences concerning system dynamics and the likely utility of alternative management strategies.

Aggregate surplus production models were used as part of an overall management strategy for the Northeast US Continental Shelf by the International Commission for Northwest Atlantic Fisheries nearly 40 yr ago, representing one of the earliest formal applications of an ecosystem approach to fisheries management. Our updated application of simple multispecies models based on aggregate catch and biomass points to the need for conservative ecological reference points that reduce the risk of over-exploitation at the

Table 3. Change in corrected Akaike Information Criterion (AIC_c) scores for extended production models including environmental covariates relative to the base case model of no covariates. NAO: North Atlantic Oscillation, ERSST: Extended Reconstructed Sea Surface Temperature

Covariates included	Total no. parameters	ΔAIC_c
NAO_0, $ERSST_2$	5	−1.01
NAO_0	4	1.01
$ERSST_2$	4	0.004

system level. Our comparison of aggregate surplus production models and single-species analyses indicate that both the aggregate MSY and B_{MSY} levels are lower for the simple multispecies model, a conclusion consistent with previous analyses. The single-species MSY and B_{MSY} reference point are ~30% higher than the aggregate model findings, suggesting that the former may result in more risk-prone decisions. Brown et al. (1976) found differences of a similar magnitude in their early development of an aggregate production model (see also Mayo et al. 1992 and Mueter & Megrey 2006). Walters et al. (2005) reported differences in management measures derived from single-species and multispecies or ecosystem models that can lead to higher risk when ecological interactions are ignored. Recently, Steele et al. (2011) contrasted single-species results and 2 ecosystem models for Georges Bank species and indicated that all species cannot be simultaneously at high production levels. Not accounting for biological interactions or environmental variability may result in overly optimistic predictions of long-term sustainable yield and unrealistically high estimates of B_{MSY}. An aggregate approach can mitigate such concerns.

The demersal fish assemblage considered here comprises species that are caught together as members of a distinct operational fishery (Lucey & Fogarty in press), are part of recognized ecological assemblages defined in space and time (Garrison 2001), and are connected through trophic interactions (Smith & Link 2010). Linkages through predation are particularly strong among the hakes and several of the gadid species (notably cod, pollock, and white hake). In several cases, reciprocal predation patterns are evident among these species. Other components of the assemblage are connected as members of trophic guilds defined on the basis of diet composition. For example, the gadoids mentioned above along with monkfish are part of a piscivore guild while several of the flatfish species are members of a defined benthivore guild (Garrison & Link 2000). These interconnections reinforce the importance of considering the assemblage as part of a dynamic system subject to technical and biological interactions. That such a system has different properties than those of the individual species comprising it is not unexpected.

Simulation testing of the performance of full multispecies models (Worm et al. 2009) and aggregate production models (Gaichas et al. 2012) clearly indicate that the vulnerability of weak-link stocks must be carefully considered prior to the application of any aggregate reference points. It is possible to devise precautionary harvesting policies that result in minimum loss in yield using conservative exploitation rates to protect vulnerable species (Worm et al. 2009, Gaichas et al. 2012). Gear modifications or the use of protected areas may also be necessary to safeguard highly vulnerable species.

Estimation of biological reference points for aggregate species assemblages can be used to set upper constraints or caps on removals from the system. It has long been recognized that due to biological or technological interactions, an aggregate quota may be more appropriate for managing species assemblages (May 1975, Pope 1975, 1979, Brown et al. 1976, Fukuda 1976, Mayo et al. 1992, Witherell et al. 2000). If fishing effort is relatively high, incidental catches are important, and species overlap, then consideration of total yield from the complex of available species is appropriate (Garrod 1973). This approach will still require specifying individual target exploitation patterns for the species comprising the assemblage, both to protect vulnerable species as noted above and to prevent targeted overfishing of the more valuable species. In the context of the single-species and aggregate-species models considered here, this can be readily accomplished by apportioning the aggregate-level MSY levels to the species level by proportionally adjusting the single-species targets downward. Under this approach, the sum of the adjusted individual species targets would be constrained not to exceed the aggregate level. Other approaches can of course be considered for allocating the total catch among species. Solutions that maximize yield or profit from the assemblage subject to constraints that prevent the assemblage total from being exceeded, while also preventing unacceptable declines in individual species, can be constructed and may be preferable.

We note that while we have focused on selected teleost species in this analysis to allow a general comparison with existing groundfish assessments, these species also interact directly with other parts of the system, notably with small elasmobranches (dogfish and skates), pelagic fishes, and invertebrates (particularly crustaceans and mollusks) through trophic and, in some cases, technical interactions. The development of a full ecosystem-based fishery management strategy for the GOM will require consideration of this broader set of interactions. Such an approach can be developed as a direct extension of the methods employed here or by considering models that can address interactions among different subgroups (e.g. Fogarty & Brodziak 1994, Collie & DeLong 1999) in a multispecies analysis with intermediate levels of aggregation.

Although our analysis of a particular set of environmental or climate-related effects does not warrant inclusion in extended production models at this time, it is clear that we should view overall production in the system as a dynamic process that should be carefully monitored and periodically re-evaluated. There is ample evidence of large-scale changes in physical forcing in this system (Ecosystem Assessment Program 2009), and these changes are manifest in shifts in distribution patterns of marine organisms (Nye et al. 2009, Lucey & Nye 2010). If overall declines in productivity become evident, the multispecies reference points would have to be adjusted accordingly to reduce the risk of overfishing. This would allow fish stocks to maintain some potential for responding to further environmental change (Hilborn et al. 2003, Stram & Evans 2009).

Perceived constraints on the application of multispecies and ecosystem models to support ecosystem-based fishery management continue to be expressed (e.g. Hilborn 2011). These concerns are largely centered on the data requirements for complex ecological models. While many multispecies and ecosystem models do in fact require information on diet composition, feeding interactions, and other factors that can be difficult and expensive to obtain, our results show the potential utility of quite simple multispecies models in which the interaction terms are implicit rather than explicit. In principle, these methods could provide an avenue for estimation of ecological/multispecies reference points in data-limited situations. They can hold advantages even in data-rich situations where greater stability and predictability of aggregate system dynamics are found. For example, despite significant compositional changes, system-level properties including catch, total biomass, and aggregate size composition in the NES LME have been much more stable than the individual components (Hennemuth 1979, Murawski & Idoine 1992, Fogarty & Murawski 1998, Auster & Link 2009). These characteristics appear to reflect compensatory processes related to a sequence of species replacements under the constraint of overall energy limitations in the system. These characteristics contribute to the greater overall stability and predictability at the system level. Renewed evaluation and potential broader application of simple aggregate production models appear to be warranted to meet the challenge of coping with complexity in ecosystem-based management.

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Contribution to the Theme Section 'Comparative analysis of marine fisheries production'

Using an aggregate production simulation model with ecological interactions to explore effects of fishing and climate on a fish community

Robert J. Gamble*, Jason S. Link

National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, Massachusetts 02543, USA

ABSTRACT: Ecosystem-based fishery management requires operating models that are capable of evaluating the effects of a triad of drivers (exploitation, ecological interactions, and the physical environment) on fish populations. We present a simple operating model, AGG-PROD, that takes into account these drivers. AGG-PROD aggregates species into functional groups and applies exploitation rates to these groups, while accounting for the interactions between these groups and the environment. We loosely modeled the Northeast US Large Marine Ecosystem fish community, exploring a range of harvest, ecological interactions (competition and predation), and climate effects scenarios. We examined the independent effects of each of the triad of drivers at their base levels on the 3 main functional groups. We then explored the effects of targeted harvest on specific functional groups as well as different levels of total system harvest, both with and without climate effects. Our results indicate that the triad of drivers can lead to unanticipated, indirect effects on groups of species, and that all 3 should be taken into account by an operating model in a Management Strategy Evaluation context. Harvest tends to affect groups with a slower overall growth rate the most, while groups affected by strong ecological interactions often exhibit strong competitive or predatory release when other groups are reduced in biomass. Climate effects reduce primarily the biomass of groundfishes in our model, indicating the need for more conservative exploitation under future climate projections.

KEY WORDS: Ecosystem-based fishery management · Production model · Ecological interactions · Climate · Exploitation · Northeast United States Large Marine Ecosystem · Management strategy evaluation · Triad of drivers

INTRODUCTION

Ecosystem-based fisheries management (EBFM) has called for broader consideration of the factors which impact on the dynamics of living marine resources (LMR) (NMFS 1999, Link 2002a,b, 2010, Pikitch et al. 2004). One of the common themes in these calls for EBFM is the need to consider a triad of drivers (see Fig. 1 in Link et al. 2012, this Theme Section) that influence fish populations: (1) fisheries exploitation, (2) physico-chemical factors (especially climate), and (3) ecological interactions among species (Link et al. 2010a). Fisheries exploitation is long understood to have direct effects on marine ecosystems through direct removals of exploited stocks (Pauly & Christensen 1995, Worm et al. 2009), and inducing indirect effects on other species in the ecosystem via predatory (Sissenwine 1984, Bax 1991, 1998, Christensen 1996, Link 2002a) or competitive release (Link 2002a). Overfishing also leads to ecosystem level effects such as eutrophication, outbreaks of disease in the trophic levels beneath the overfished species, and species introductions (Jackson et al. 2001). Ecological interactions and related trophodynamic processes, such as predation or competition as referred to above, are also recognized as potentially

*Email: robert.gamble@noaa.gov

dominant drivers (Frank et al. 2005, Daskalov et al. 2007, Tyrrell et al. 2011). Physico-chemical drivers are important in that fisheries production is linked to primary production (Ware & Thomson 2005, Chassot et al. 2010), early life history survivorship is at least partially, if not mainly, dictated by biophysical conditions (Beaugrand et al. 2003, Platt et al. 2003), and climate change can affect marine populations (Anderson & Piatt 1999, Chavez et al. 2003, Nye et al. 2009). While each of these drivers can have important effects on an ecosystem, they are not routinely considered simultaneously (cf. Lucey & Nye 2010, Fulton et al. 2011). Thus there is a need for models that can explicitly explore the effects of this triad of drivers on an ecosystem simultaneously.

Another key element of EBFM is to determine the maximum sustainable yield (MSY) in an ecosystem (Link 2010). Doing so is important, as each ecosystem has known limitations to productivity (Pauly & Christensen 1995), with the amount of fish harvested ultimately limited by primary production (Ryther 1969, Ware & Thomson 2005). There are methods of estimating MSY for an ecosystem. These methods effectively account for a broader set of consideration (e.g. species interactions, climate) than methods for calculating single species MSY, and thus can give quite different results than a simple summation of all species production for a given ecosystem (Au 1973, May 1975, Pope 1975, 1979, Brown et al. 1976, Fukuda 1976, May et al. 1979, Walters et al. 2005, NEFSC 2008, Tyrrell et al. 2011).

The combination of, and interactions between, these drivers suggests the need to utilize a Management Strategy Evaluation (MSE; Smith et al. 1999, Sainsbury et al. 2000). MSEs have a core operating model capable of evaluating this triad of drivers under a variety of scenarios. Executing such an MSE should take the relative effects of these drivers into consideration and be able to provide outputs related to achieving a system-level MSY, as well as exploring tradeoffs among the species and drivers inherent to an ecosystem.

While there are many classes of extant ecosystem models that could serve as MSE operating models, there is an important class of models between the simpler, stock-focused models that are typical in stock assessments (or that incorporate other factors such as Extended Single-species Assessment Models, ESAMs) and the full ecosystem models such as GADGET, APECOSM, InVitro, or ATLANTIS. Aggregate Surplus Production (ASP) models are part of this intermediate class of models (Hollowed et al. 2000, Plagányi 2007, Townsend et al. 2008, Link et al. 2010b). These models require the same basic inputs as standard stock assessment models or ESAMs, but are aggregated across species at a higher level of biological hierarchy. ASPs estimate biological reference points (BRPs) commonly used in LMR management (such as MSY), but for an aggregate group of species. ASP models can also simulate the effects of ecological interactions, harvest, and climate, making them a valuable tool generally for EBFM and specifically within an MSE context as an operating model (Link et al. 2010c).

Such ASP models have a number of advantages. They fall into the simpler range of the complexity continuum of models. Models of low to intermediate complexity often have higher forecast skill than more complex models (Costanza & Sklar 1985, Walters 1986, Fulton et al. 2003, Adkison 2009, Hannah et al. 2010). Additionally, surplus production models can outperform age-structured models in providing more robust characterizations of fish population dynamics (Ludwig & Walters 1985, 1989, Hilborn & Walters 1992). For instance, Ludwig & Walters (1985) generated data from a model with 2 age classes (pre-recruitment and catchable adults) with random recruitment (Deriso 1980). When they fit parameters from both the original age-structured model and a simple surplus production model to the generated data, the surplus production model performed just as well or better than the original model. Additionally, ASPs rely on relatively common and easy to collect data (biomass or abundance estimates and fisheries landings) and thus are of use even in many data-limited ecosystems (Graham 1935, Pitcher & Hart 1982, Smith 1994). ASP models can incorporate stochasticity, trophic interactions, and environmental and climate forcing relatively simply and easily (Clark et al. 2003, Rose 2004, Jacobson et al. 2005, Keyl & Wolff 2008). ASP models capitalize on the stability of aggregate groupings that, although dynamic, are nevertheless less variable than those commonly observed for their component species (Duplisea & Blanchard 2005, Auster & Link 2009). Finally, ASPs produce outputs that are widely used in fisheries management and do not require additional familiarization for managers.

Although several assumptions need to be met for use of ASP models (e.g. comparable life histories and vital rates among species within an aggregate group), these models have the ability to provide synthetic information useful for implementing EBFM. The main strengths of this approach are its relative simplicity, minimal assumptions, requirement of readily available data, and relative portability of the approach for ease of use on different data sets. The drawbacks are those usually associated with production models (e.g. missing internal stage or age related dynamics, and ignoring different life history characteristics of individual species within an aggregation, which is explored more thoroughly in Gaichas et al. 2012, this Theme Section).

Here we describe a particular ASP model, AGG-PROD, which is an aggregated application of MS-PROD (Gamble & Link 2009) used to model functional groups of species. The objectives in doing so are to explore the aggregate properties and outputs from modeling such groups, and contrast various scenarios that could be used in an MSE context among the triad of drivers that influence LMR dynamics. Our focus here is to explore how aggregate BRPs change under differing scenarios.

METHODS

Model description

We used an application of AGG-PROD to examine the effects of different harvest, climate, and ecological scenarios on aggregated groups of fish loosely parameterized to reflect the Northeast US Large Marine Ecosystem (NEUS LME). This model is a variation of an MS-PROD, a multi-species surplus production model described previously (Gamble & Link 2009), where instead of individual species, aggregated, functional groups were considered. AGG-PROD is identical to MS-PROD, except that due to lack of a species focus, the within-group competition terms are removed. The model formulation is:

$$\frac{\mathrm{d}B_I}{\mathrm{d}t} = r_I B_I \left(1 - \frac{B_I}{K_I} - \frac{\sum_{1}^{G} \beta_{IG} B_G}{(K_\sigma - K_G)} \right) - B_I \sum_{1}^{P} \alpha_{IP} B_P - h_I B_I \qquad (1)$$

where B_I is the biomass of an aggregated group of species or stocks (I), r_I is the growth rate of group I, K_I is the carrying capacity of group I, h_I is the harvest rate (a proxy for fishing mortality, defined as the instantaneous removal rate) on group I, G is a group other than I with corresponding B and K, β_{IG} is the competition interaction coefficient between groups I and G, K_σ is the system carrying capacity, P is a group which preys on group I with a corresponding B, and α_{IP} is the predation interaction coefficient between groups I and P.

This model framework is based on the general form of extended Schaefer-types of models (e.g. Prager 1994, Collie & DeLong 1999. Mueter & Megrey 2006, Gamble & Link 2009) and has been employed for all fished species in over 10 northern hemisphere ecosystems (Bundy et al. 2012, this Theme Section, Lucey et al. 2012, Theme Section). This resultant form here is similar to other fisheries production models applied in the NEUS region (e.g. Spencer & Collie 1996, Collie & DeLong 1999) and elsewhere (e.g. Constable 2001, Mueter & Megrey 2006). Unlike those other approaches, here we are aiming to simulate a system with specified parameters, not fit it to the typical data series, in an MSE context. The other distinction of our approach is that, like Lucey et al. (2012), the main aspects that influence aggregate dynamics are partitioned into their explicit ecological and fishing factors. We also note that values of *K* are fixed and not linked to prey population abundances. Although the latter would be feasible, for this approach we simply address the relative impacts of harvesting, predation, and competition rather than the feedback among predator–prey linkages. We address climate effects via alterations to *r* (see 'Scenarios' below).

We note the following major assumptions of our modeling approach:

(1) Aggregated groups have a carrying capacity that is distinct from the systemic carrying capacity, but such a systemic carrying capacity does exist (e.g. Brown et al. 1976, May et al. 1979, Pauly & Christensen 1995, Pauly et al. 1998, 2002).

(2) Harvest and species interactions (competition and predation) in our model may similarly influence a group's ability to reach its carrying capacity (e.g. May 1975, Pope 1975, 1979, Brown et al. 1976, Fukuda 1976).

(3) Considering only aggregated groups will not reveal whether aggregated fishing mortality levels might cause specific stocks within the group to be overfished, or indeed what the likely result of any set of fishing levels will be on individual stocks (Worm et al. 2009, Gaichas et al. 2012).

(4) There is no age structure in the model, and therefore the effects of stage-specific mortality, growth, and related demographic processes cannot be modeled.

Base model parameterization and simulations

The parameterization for the simulations using AGG-PROD was informed by the parameterization for MS-PROD, which was applied to a simulated fish community that was generally based on the NEUS LME (Gamble & Link 2009). We parameterized the model for 3 groups: groundfishes, small pelagics, and elasmobranchs. We chose these groupings primarily because they correspond to the fishery management plans in the region. While groundfishes could have been further split into gadids, flatfish, and an 'other' groundfish group, we considered the groups chosen to have enough similarity among life history parameters used in the model. Specifically, the species chosen for the groundfish group have growth rates higher than those in the elasmobranch group, and lower than those in the small pelagics group. Additionally, competition (for space and due to diet overlap) is likely greater for the members of the groundfish group than for members of the elasmobranch or small pelagics groups.

The biomasses for each group were calculated by summing the individual biomasses for each stock within the group (NEFSC 2002, 2007, Overholtz et al. 2008). While each stock was not considered individually, the component stocks present in each group are shown in Table 1. Growth rates (*r*) for each group were calculated based on a biomass-weighted average of the individual *r* values from the MS-PROD formulation. The individual *r* values were calculated by doubling estimates of fishing mortality at maximum sustainable yield (F_{MSY}) for groundfishes, pelagics, and elasmobranchs (Applegate et al. 1998, Quinn & Deriso 1999, Hilborn & Walters 1992, NEFSC 2002, 2007, Overholtz et al. 2008). System fish carrying capacity (*K*) was set to ~7 700 000 mt as the sum of the group *K* values for groundfishes (~2 800 000 mt), small pelagics (~2 600 000 mt), and elasmobranchs (~2 300 000 mt). These *K* values were estimated as twice B_{MSY} for individual stocks within each group and then summed (by definition; Applegate et al. 1998, Quinn & Deriso 1999, Hilborn & Walters 1992, NEFSC 2002, 2007, Overholtz et al. 2008). Competition coefficients between groups were informed by diet matrices and overlap in habitat. Predation was set only on the pelagics, as informed by stomach content data (Link & Almeida 2000). Spatial overlap was set to 0.6 between all groups based largely upon information of seasonal movements for the pelagic and elasmobranch species derived from fishery independent surveys. These salient parameters used to initialize the base model are given in Table 2.

Table 1. List of stocks within each group in this formulation of AGG-PROD. CC: Cape Cod, GOM: Gulf of Maine, GB: Georges Bank, SNE: Southern New England, MAB: Mid-Atlantic Bight

Group	Stocks
Groundfishes	American plaice
	CC-GOM yellowtail
	GB yellowtail
	GB cod
	GB haddock
	GB winter flounder
	GOM-GB windowpane
	GOM cod
	GOM haddock
	Halibut
	Ocean pout
	Pollock
	Redfish
	SNE-MAB windowpane
	SNE-MAB winter flounder
	SNE-MAB yellowtail
	White hake
	Witch flounder
Small pelagics	Butterfish
	Herring
	Mackerel
Elasmobranchs	Skates
	Spiny dogfish

Fisheries removals (i.e. harvest, *h*) were set as an annual rate of removal for each group. We set these in accordance to the scenarios we ran (see 'Scenarios' below).

We ran the simulations for 30 yr with an annual time step. The model was developed in Visual C++

Table 2. Basic parameterization for the AGG-PROD simulation model. B_{MSY}: biomass at maximum sustainable yield

Parameter	Groundfishes	Elasmobranchs	Pelagics
Growth rate	0.45	0.2	0.6
Initial biomass (mt)	834002	756418	3377800
Carrying capacity (mt)	2849576	2311462	2591956
B_{MSY} (mt)	1424788	1155731	1295978
Competition coefficient no. 1			
Between Group and Groundfishes	0	0.5	0
Between Group and Elasmobranchs	1	0	0.05
Between Group and Pelagics	0	0.1	0
Predatory loss rates			
With Groundfishes	0	0	8.00×10^{-8}
With Elasmobranchs	0	0	2.00×10^{-7}
With Pelagics	0	0	0
Spatial overlap			
With Groundfishes	0.6	0.6	0.6
With Elasmobranchs	0.6	0.6	0.6
With Pelagics	0.6	0.6	0.6
Harvest loss rate	0.1	0.1	0.1
Demersal	1	1	0
Pelagic	0	0	1

and utilizes a calculation engine designed to account for multiple iterations of simultaneous equation (i.e. groups) solving, using a fourth-order Runge-Kutta numerical integration algorithm. (Note: we developed a software package which utilizes a graphical user interface to handle data inputs for model initialization, parameterization, and scenario development, and additionally to handle and process model outputs. This package is available from the authors upon request.) The current version of the model is a simulator that produces deterministic results, with no direct data fitting beyond the data used to inform the initial parameterization.

Scenarios

We ran 3 classes of scenarios to explore the effects of the triad of drivers on aggregate groups (Table 3). Each class of scenarios was run with 2 different sets of parameters for the groundfish group. The first parameter set used the base parameters described previously. The second parameter set decreased the groundfishes growth rate by 10% ($r = 0.405$) to simulate a negative effect on growth due to climate change. Previous work has linked changes in the intrinsic rate of growth or carrying capacity to climate changes (Brander 1995, O'Brien et al. 2000, Attrill & Power 2002, Clark et al. 2003, Gislason et al. 2010). We applied this climate effect on growth rate only to groundfishes. This was due to small pelagics (e.g. Atlantic herring, Atlantic mackerel, and butterfish) having generally larger range distributions, and hence wider optimal thermal regimes, than groundfishes. Additionally, a recent study (Nye et al. 2009) indicated that many individual stocks of groundfishes in the NEUS LME showed a recent range contraction due to climate effects, while pelagic stocks and all but 1 elasmobranch showed range expansions or no change. Specifically, of the 19 species that make up the aggregate groundfish group, 8 showed a northward movement and 2 showed a southward movement (Nye et al. 2009). Additionally, 8 species showed a range contraction and 2 showed a range expansion. These range changes, especially contractions and poleward movements, are indicative of probable accommodation of differential growth rates relative to changing ambient water temperatures, as approximated here by the change in r. The toggling of the climate effect on groundfish growth rates are seen in Table 3 as the 'Climate effects' column, either with base growth parameters (N) or the modified parameter for groundfishes (Y).

Table 3. Settings for each of the 3 scenario classes exploring the effects of the triad of drivers on aggregate groups. (A) Combination scenarios. The 3 drivers were each toggled on and off at a base level to determine the relative effects of each. Harvest rate (h): 'Y' means h set at 0.1; 'N' means h set at 0.0. Ecological interactions: 'Y' means competition and predation were set as parametized in Table 2; 'N' means all competition and predation were set to zero. Climate effects: 'Y' means groundfish growth rate (r) set at 0.405 to simulate climate effects on growth; 'N' means groundfish r set to base value of 0.45 (as per Table 2). (B) Target harvest scenarios. Harvested group: h set at 0.3 for this group, the rest set at $h = 0$. Ecological interactions: always 'Y' as defined in (A). Climate effects: 'Y' = on, 'N' = off, as defined in A. (C) System harvest scenarios. Harvest rate: h set to a specific value. Ecological interactions: always 'Y' as defined in (A). Climate effects: 'Y' = on, 'N' = off, as defined in (A)

(A) Combination scenarios

Scenario	Harvest rate	Ecological interactions	Climate effects
1	N	N	N
2	Y	N	N
3	N	Y	N
4	Y	Y	N
5	N	N	Y
6	Y	N	Y
7	N	Y	Y
8	Y	Y	Y

(B) Targeted harvest scenarios

Scenario	Harvested group ($h = 0.3$)	Ecological interactions	Climate effects
1	Groundfishes	Y	N
2	Elasmobranchs	Y	N
3	Pelagics	Y	N
4	Groundfishes	Y	Y
5	Elasmobranchs	Y	Y
6	Pelagics	Y	Y

(C) System harvest scenarios

Scenario	Harvest rate	Ecological interactions	Climate effects
1	0	Y	N
2	0.01	Y	N
3	0.05	Y	N
4	0.1	Y	N
5	0.2	Y	N
6	0.3	Y	N
7	0.5	Y	N
8	0	Y	Y
9	0.01	Y	Y
10	0.05	Y	Y
11	0.1	Y	Y
12	0.2	Y	Y
13	0.3	Y	Y
14	0.5	Y	Y

The first class of scenarios, the combination scenarios, independently toggled ecological interactions (competition between all groups, and predation on small pelagics), harvest, and climate effects. Ecological interactions were toggled off by removing interaction terms. Harvest scenarios were toggled on ($h = 0.1$) or off ($h = 0$). Climate effects were toggled on ($r = 0.405$ for groundfishes) or off ($r = 0.45$ for groundfishes) for each scenario in this class.

The second class of scenarios, the targeted harvest scenarios, examined targeted harvest rates on a specific group both with ($r = 0.405$ for groundfishes) and without ($r = 0.45$ for groundfishes) climate effects. One of the groups was subjected to a higher harvest rate ($h = 0.3$) while the other 2 were subjected to a base harvest rate ($h = 0.1$).

The third set of scenarios, the system harvest scenarios, examined the effects of increasing harvest rates on the entire system, again with climate effects toggled on ($r = 0.405$ for groundfishes) or off ($r = 0.45$ for groundfishes). All groups simultaneously had their harvest rates set to: 0, 0.01, 0.05, 0.1, 0.2, 0.3, and 0.5.

In all scenarios, it was possible to partition the losses to biomass to each group at each time step for each type of removal (predation, competition, and harvest). The MS-PROD software package, using the Runge-Kutta numerical integration algorithm calculates these removals at each step of the algorithm and they can then be summed to provide the final removal at each time step of the model. Losses or increases due to climate were calculated as the difference between a group's biomass in a scenario which did not include climate effects, and the corresponding non-climate version of a scenario.

RESULTS

In all scenarios, we expressed the results both in terms of biomass (mt) and as a proportion of group B_{MSY} such that a value greater than 1.0 indicated the group was higher than its B_{MSY}, and a value less than 1.0 indicated the group did not reach the group B_{MSY}.

Combination scenarios

For the combination class of scenarios (where we toggled ecological interactions, harvest, and climate effects separately) the main results show some common patterns. In Scenario 1 (interactions off, $h = 0$, groundfish $r = 0.45$), all groups asymptotically approach their carrying capacities (Fig. 1a). Because of this, each group's final biomass is almost equal to its carrying capacity, and therefore almost double the group's B_{MSY} (Table 4).

In Scenario 2 (interactions off, $h = 0.1$, groundfish $r = 0.45$), no groups reached their carrying capacities (Fig. 1b). Elasmobranchs showed a final biomass less than half that in Scenario 1. The other 2 groups also showed a drop in final biomass, but not to the same extent. Only elasmobranchs fell below a B_{final}/B_{MSY} ratio of 1.0 in this scenario (Table 4).

In Scenario 3 (interactions on, $h = 0$, groundfish $r = 0.45$), no groups reached their carrying capacity. Small pelagics showed a final biomass of less than half that in Scenario 1. Elasmobranchs had a higher biomass, and groundfishes had a lower biomass than in Scenario 2 (Fig. 1c), indicating that harvest effects are stronger than interaction effects on elasmobranchs in the simulated ecosystem while interaction effects are likely stronger than harvest effects on groundfish. Additionally, in this scenario there was a switch in ecosystem dominance (in terms of final biomass) between elasmobranchs and groundfishes (compared to the groundfish-dominated Scenarios 1, 2, and 4) Only small pelagics fell below a B_{final}/B_{MSY} ratio of 1.0 in this scenario (Table 4).

In Scenario 4 (interactions on, $h = 0.1$, groundfish $r = 0.45$), no groups reached their carrying capacity. Elasmobranchs showed a final biomass more than two-thirds less than in Scenario 1, while the other 2 groups had a final biomass at or slightly more than in Scenario 3 due to release of groundfishes and pelagics by elasmobranchs (Fig. 1d). Again, only elasmobranchs fell below a B_{final}/B_{MSY} ratio of 1.0 in this scenario (Table 4).

Scenarios 5 to 8 are equivalent to Scenarios 1 to 4, but with climate effects turned on (groundfish $r = 0.405$). In Scenario 5 (interactions off, $h = 0$, groundfish $r = 0.405$), it took longer for the groundfish group to reach its carrying capacity compared to Scenario 1 (same but with groundfish $r = 0.45$) due to climate being modeled as a reduction in growth rate. In Scenario 6 (interactions off, $h = 0.1$, groundfish $r = 0.405$), the groundfish group had a 3.2% lower biomass and a correspondingly lower B_{final}/B_{MSY} ratio when compared to Scenario 2 (same but with groundfish $r = 0.45$), while the other 2 groups were largely unaffected. In Scenario 7 (interactions on, $h = 0.0$, groundfish $r = 0.405$), the B_{final}/B_{MSY} ratios for all groups were the same as in Scenario 3 (same but with groundfish $r = 0.45$). In Scenario 8 (interactions on, $h = 0.1$, groundfish $r = 0.405$), the groundfish group had a 4.5% lower biomass and a correspondingly lower B_{final}/B_{MSY} ratio when compared to Scenario 4 (same but with groundfish $r = 0.45$) (Table 4).

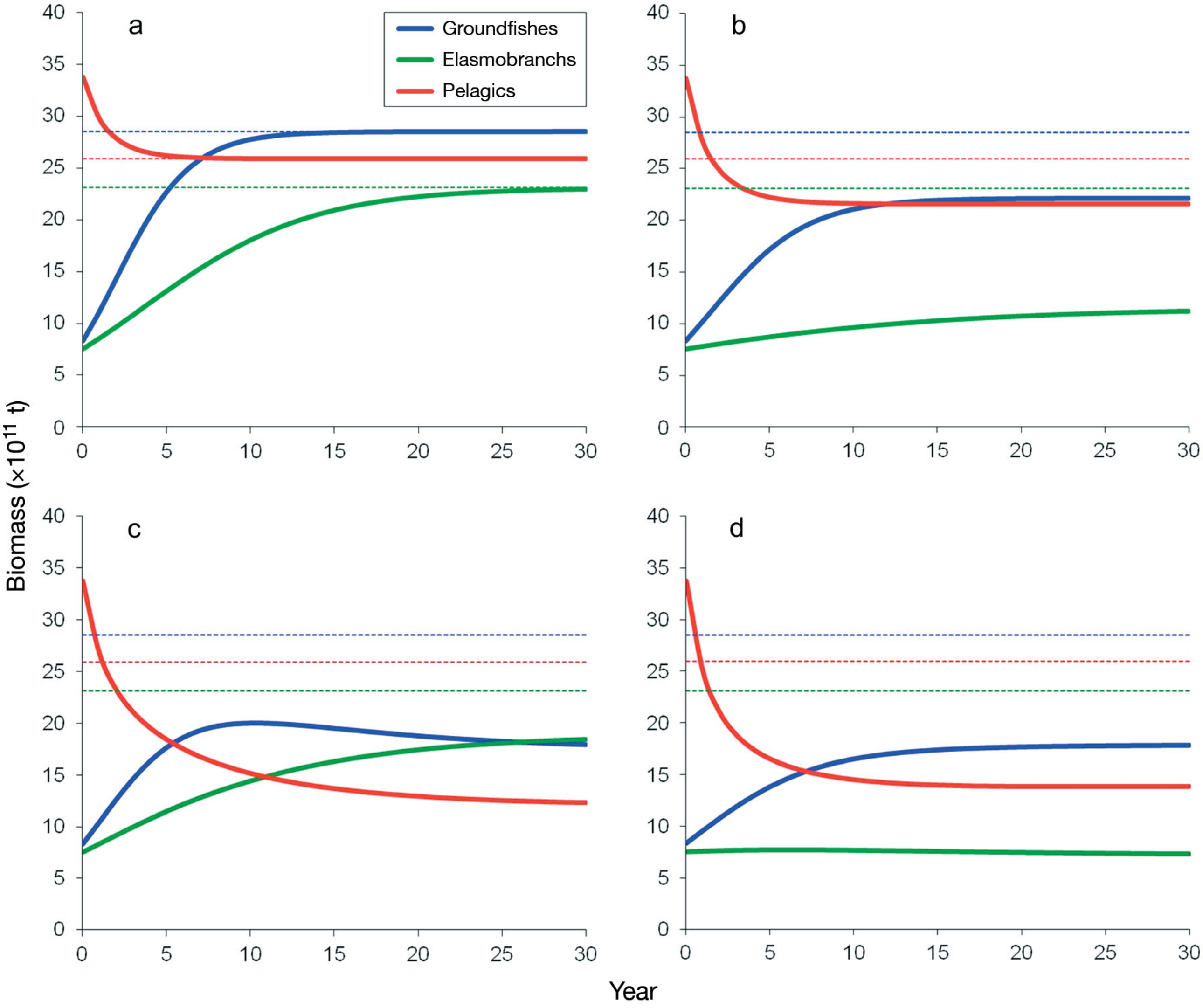

Fig. 1. Results from the combination class of scenarios, showing the effects of independently toggling harvest and interactions: (a) no harvest and no interactions, (b) harvest and no interactions, (c) no harvest but interactions present, (d) harvest and interactions. The dotted lines represent the carrying capacities of each group

Table 4. Summary of combination scenarios of final biomass to biomass at maximum sustainable yield ($B_{\text{final}}/B_{\text{MSY}}$) ratios. In the Harvest, Interactions, and Climate columns, a 'Y' indicates that the corresponding effect on the system is turned on, and a 'N' indicates that the corresponding effect on the system is turned off (see Table 3 for definitions). **Bold** values are <1, indicating that this group did not reach the group B_{MSY}

Scenario	Harvest	Interactions	Climate	Combination $B_{\text{final}}/B_{\text{MSY}}$			
				Groundfishes	Elasmobranchs	Small pelagics	System
1	N	N	N	2.00	1.99	2.00	2.00
2	Y	N	N	1.56	**0.97**	1.67	1.42
3	N	Y	N	1.26	1.60	**0.95**	1.26
4	Y	Y	N	1.25	**0.64**	1.07	1.01
5	N	N	Y	2.00	1.99	2.00	2.00
6	Y	N	Y	1.51	**0.97**	1.67	1.40
7	N	Y	Y	1.26	1.60	**0.95**	1.26
8	Y	Y	Y	1.20	**0.65**	1.08	**0.99**

Generally, the elasmobranch and pelagic groups showed minimal changes in final biomass in the scenarios where climate effects were present (Scenarios 5–8) compared to the non-climate scenarios (Scenarios 1–4). Furthermore, adding the climate effects did not have an impact on final biomasses and therefore the $B_{\text{final}}/B_{\text{MSY}}$ ratio of the groundfish group unless harvest was also occurring. Finally, in all of the combination scenarios except Scenario 8 (interactions on, h = 0.1, groundfish r = 0.405), the total system $B_{\text{final}}/B_{\text{MSY}}$ ratio remained above 1.0, although only barely so in the case of Scenario 4 (interactions on, h = 0, groundfish r = 0.405). In the case of Scenario 8, the total system $B_{\text{final}}/B_{\text{MSY}}$ ratio was 0.99 (Table 4).

The comparative effects of species interactions, climate, and harvest differ among the 3 groups (Fig. 2). When all 3 are present in Scenario 8 (interactions on, h = 0.1, groundfish r = 0.405), groundfishes are affected strongly by harvest, which, in the last year of the run, is responsible for 48 % of the removals of biomass. Of the losses, 30 % come from competition with the other guilds, and 22 % come from the effects of climate (Fig. 2a). Elasmobranchs are most strongly affected by harvest, which is responsible for 73 % of losses to biomass in the final year of the run, while competition is responsible for 27 % (Fig. 2b). Pelagics are the most affected by species interactions of the 3 groups (Fig. 2c), and in the final year of the run most of the losses (62 %) come from predation, 36 % of the losses come from harvest, and the remaining 2 % come from competition.

Targeted harvest scenarios

In the targeted harvest class of scenarios, where interactions were turned on, the harvest rate was set to 0.1 for 2 groups while the third was set to 0.3, and climate effects were toggled off (groundfish r = 0.45), there were 4 main results.

(1) Not surprisingly, the final biomass for each group was lowest when it was assigned the higher harvest rate. This sometimes resulted in shifts in ecosystem structure when compared to the combination scenarios. For example, when combination Scenario 4 (interactions on, h = 0.1, groundfish r = 0.45) was compared to the targeted harvest Scenarios 1 to 3, shifts in pelagic versus demersal dominance of the modeled ecosystem were seen (Fig. 3a–d). Also, in targeted harvest Scenario 1 (interactions on, groundfish h = 0.3, groundfish r = 0.45), final biomass for pelagic fishes was higher than for demersal fishes (Fig. 3b) compared to combination Scenario 4 (Fig. 3a). In targeted harvest Scenario 2 (interactions on, elasmobranch h = 0.3, groundfish r = 0.45) there was less of a difference in pelagic and demersal final biomass (Fig. 3c) than in combination Scenario 4 (Fig. 3a), and in targeted harvest Scenario 3 (interactions on, small pelagic h = 0.3, groundfish r = 0.45), the modeled ecosystem was dominated more by demersal biomass (Fig. 3d) than in combination Scenario 4 (Fig. 3a).

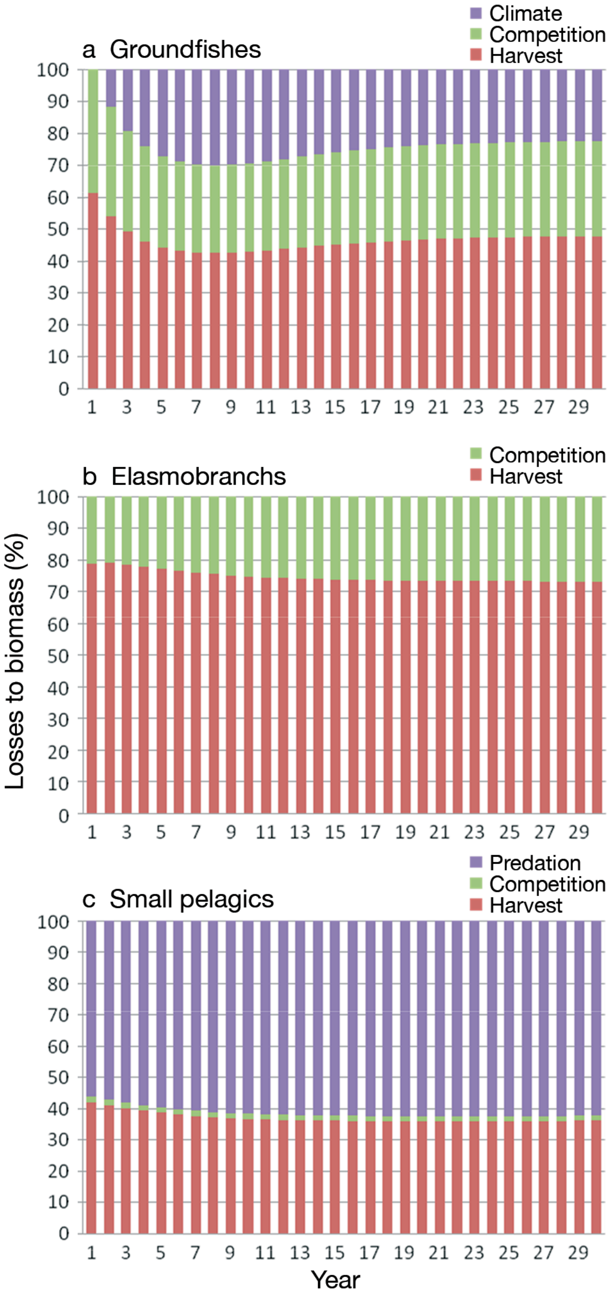

Fig. 2. Proportional losses to biomass in Scenario 8 (h = 0.1; interactions present; climate on—groundfish r = 0.405) in the combination class of scenarios: (a) groundfishes, (b) elasmobranchs, (c) pelagics

These results are primarily due to the increased harvest on a specific group, combined with the trophodynamic interactions (predation and competition) between the groups.

(2) Groundfishes and small pelagics achieved a B_{final}/B_{MSY} ratio greater than 1.0 in all scenarios except when they were targeted at the higher harvest rate (Table 5), while elasmobranchs were below a B_{final}/B_{MSY} ratio of 1.0 in all scenarios. These results are primarily due to the susceptibility of elasmobranchs to harvest relative to the other groups because of their lower growth rate compared to the other 2 groups. The higher harvest rate when applied to groundfishes and small pelagics was enough to lower their respective B_{final}/B_{MSY} ratios below 1.0: groundfishes to a ratio of 0.32 in Scenario 1 (no climate effects) and to 0.21 in Scenario 2 (with climate effects), and pelagics to a ratio of 0.41 in Scenarios 3 (without climate effects) and 6 (with climate effects).

(3) When the targeted harvest was on a group that was parameterized with strong interactions on another group, the second group had a higher final biomass and B_{final}/B_{MSY} ratio than otherwise, due to competitive or predatory release. Small pelagics had the highest final B_{final}/B_{MSY} ratio when elasmobranchs were targeted, due to predatory release. Groundfishes and elasmobranchs had their highest final B_{final}/B_{MSY} ratio in the scenario in which the other group was targeted, due to competitive release (Table 5).

(4) The total system B_{final}/B_{MSY} ratio was higher than 1.0 only when elasmobranchs were preferentially targeted. This resulted because of the combination of predatory release on small pelagics and competitive release on groundfishes (Table 5). This also reflects compensatory dynamics from a systemic perspective.

When climate effects were present (groundfish r = 0.405), the main response was a generally reduced groundfish biomass and B_{final}/B_{MSY} ratio compared to the non-climate scenarios (Table 5). The largest relative change occurred in Scenario 4 (interactions present, groundfish h = 0.3, groundfish r = 0.405), with a 33% decrease in groundfish final biomass and corresponding B_{final}/B_{MSY} ratio compared to Scenario 1 (same but with no climate effects; groundfish r = 0.45).

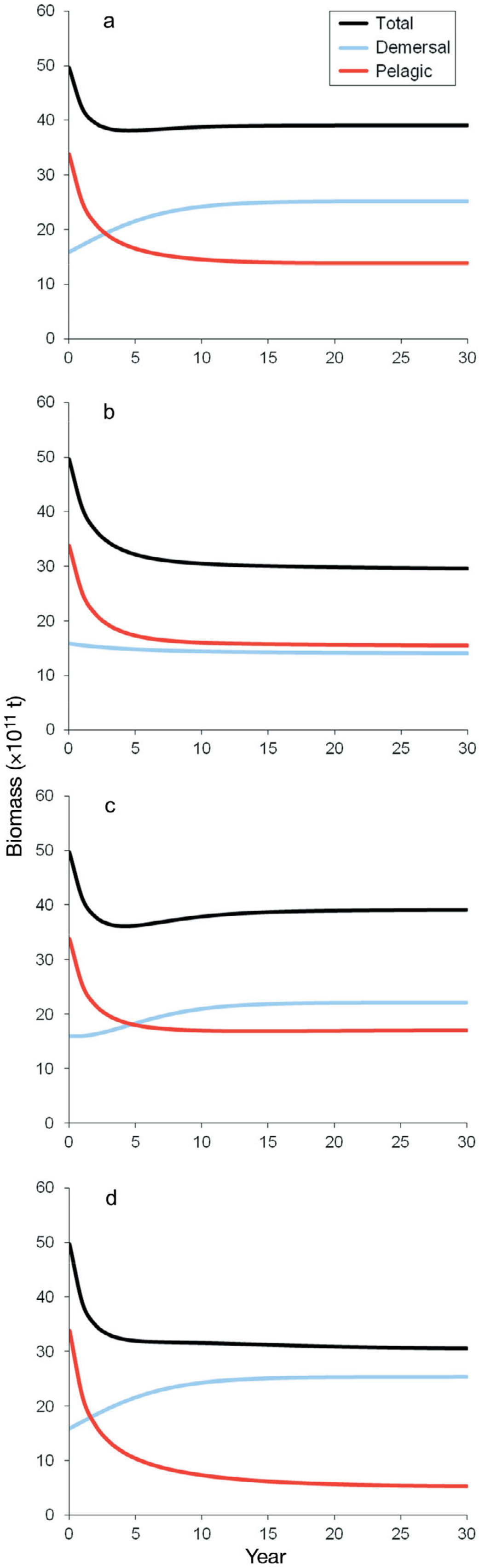

Fig. 3. Effects on the demersal and pelagic fish communities of the targeted harvest class of scenarios with interactions on, but climate effects turned off: (a) triad combinatory Scenario 1 (interactions on, h = 0.1, climate off—groundfish r = 0.45), (b) targeted harvest Scenario 1 (groundfishes targeted at h = 0.3), (c) targeted harvest Scenario 2 (elasmobranchs targeted at h = 0.3), (d) targeted harvest Scenario 3 (pelagics targeted at h = 0.3)

Table 5. Summary of targeted harvest scenarios of final biomass to biomass at maximum sustainable yield ($B_{\text{final}}/B_{\text{MSY}}$) ratios. The targeted group had its harvest rate set to 0.3, while the other 2 groups had their harvest rates set to 0.1. **Bold** values are <1, indicating that this group did not reach the group B_{MSY}

Scenario	Harvested group	Climate	Targeted harvest $B_{\text{final}}/B_{\text{MSY}}$ Groundfishes	Elasmobranchs	Small pelagics	System
1	Groundfishes	N	**0.32**	**0.83**	1.20	**0.76**
2	Elasmobranchs	N	1.55	**0.01**	1.31	1.01
3	Pelagics	N	1.24	**0.66**	**0.41**	**0.79**
4	Groundfishes	Y	**0.21**	**0.85**	1.21	**0.73**
5	Elasmobranchs	Y	1.50	**0.01**	1.32	**0.99**
6	Pelagics	Y	1.19	**0.68**	**0.41**	**0.78**

While harvest had the largest impact on biomass losses of groundfishes for the first half of the model run, climate eventually became the dominant cause of biomass losses. Species interactions stayed relatively consistent in their impacts on groundfish biomass loss over the model run (Fig. 4). Additionally, pelagic and elasmobranch $B_{\text{final}}/B_{\text{MSY}}$ ratios increased in the scenarios where climate was present (Scenarios 4–6; groundfish $r = 0.405$) due to decreased predation and competition effects on the 2 groups, respectively (Table 5).

System harvest scenarios

In the system harvest scenarios where the harvest level for all groups was set to 7 different values (Scenarios 1–7; 0, 0.01, 0.05, 0.1, 0.2, 0.3, 0.5), species interactions were turned on, and climate was toggled off (groundfish $r = 0.45$), each of the 3 groups showed different responses to increasing harvest (Table 6). Elasmobranchs decreased in biomass at each increase in harvest level and fell below a $B_{\text{final}}/B_{\text{MSY}}$ ratio of 1.0 in all scenarios where the system harvest rate was 0.1 or greater (Scenarios 4–7).

Groundfish biomass remained stable when the harvest rate was between 0 and 0.1 (Scenarios 1–4) and only fell below a $B_{\text{final}}/B_{\text{MSY}}$ ratio of 1.0 at a harvest rate of 0.3 or higher (Scenarios 6 and 7). This 'delay' was likely due to competitive release as elasmobranch biomass did drop at the lower harvest rates ($h = 0.01$ to 0.1).

Small pelagic biomass actually increased slightly through the first 4 levels of harvest rates (0–0.1), likely due to predatory release by elasmobranchs. Due to their higher growth rate, they ended with a higher final biomass and $B_{\text{final}}/B_{\text{MSY}}$ ratio than groundfishes at the higher harvest levels (0.3, 0.5). Because of the indirect interaction effects combined with harvest rates, the small pelagics had a $B_{\text{final}}/B_{\text{MSY}}$ ratio above 1.0 at the moderate harvest levels (0.05, 0.1, 0.2) but not at the lower or higher harvest rates (0, 0.01, 0.3, 0.5). Finally, the system $B_{\text{final}}/B_{\text{MSY}}$ ratio fell below 1.0 at a harvest rate of 0.2 or higher (Scenarios 5–7), largely driven by the small pelagic biomasses.

When the effects of climate were added (groundfish $r = 0.405$) in Scenarios 8 to 14, 4 main results occurred (Tables 6 & 7). Groundfishes fell below a $B_{\text{final}}/B_{\text{MSY}}$ ratio of 1.0 at a harvest rate of 0.182, instead of a harvest rate of 0.212 as in the system harvest scenarios without climate effects (Table 6 only shows the scenarios described above; further runs were done to more precisely define the ratio's tipping point). Similarly, the system $B_{\text{final}}/B_{\text{MSY}}$ ratio fell below 1.0 at a harvest rate of 0.098, compared to a harvest rate of 0.104 in the system harvest scenarios without climate effects. The percentage of final biomass compared to the corresponding system harvest scenario without climate effects decreased for groundfish as harvest rates increased (from ~100% at harvest rates of 0 and 0.01 to 35.7% at a harvest rate of 0.5; Table 7). The other groups showed a minor increase in their final biomass and $B_{\text{final}}/B_{\text{MSY}}$ ratio compared to the system harvest scenarios, likely due to competitive release of elasmobranchs and an overall lowering of predation on small pelagics.

Losses to groundfish biomass varied over the range of harvest rates explored when climate effects were present (Fig. 5). At low levels of harvest ($h = 0.01$

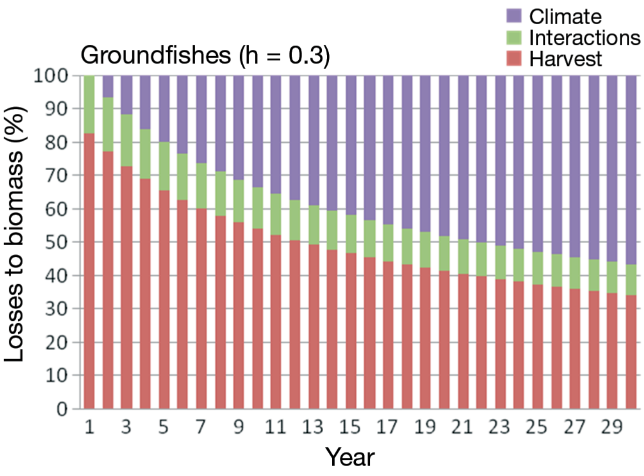

Fig. 4. Proportional losses to biomass of groundfishes according to the targeted harvest of groundfishes ($h = 0.3$) scenario

Table 6. Summary of system harvest scenarios of final biomass to biomass at maximum sustainable yield ($B_{\text{final}}/B_{\text{MSY}}$) ratios. **Bold** values are <1, indicating that this group did not reach the group B_{MSY}

Scenario	Harvested	System harvest $B_{\text{final}}/B_{\text{MSY}}$				
		Climate	Groundfishes	Elasmobranchs	Small pelagics	System
1	0	N	1.26	1.60	**0.95**	1.26
2	0.01	N	1.26	1.49	**0.96**	1.23
3	0.05	N	1.27	1.09	1.02	1.13
4	0.1	N	1.25	**0.64**	1.07	1.01
5	0.2	N	1.04	**0.12**	1.03	**0.76**
6	0.3	N	**0.65**	**0.01**	**0.84**	**0.52**
7	0.5	N	**0.04**	**0.00**	**0.33**	**0.12**
8	0	Y	1.26	1.60	**0.95**	1.26
9	0.01	Y	1.26	1.50	**0.96**	1.23
10	0.05	Y	1.24	1.10	1.02	1.13
11	0.1	Y	1.20	**0.65**	1.08	**0.99**
12	0.2	Y	**0.93**	**0.13**	1.05	**0.73**
13	0.3	Y	**0.49**	**0.01**	**0.88**	**0.48**
14	0.5	Y	**0.01**	**0.00**	**0.34**	**0.12**

and 0.05), losses to biomass for the groundfish group were mostly from interactions with elasmobranchs (Fig. 5a,b). At $h = 0.1$, harvest accounted for a bit less than half of the losses to biomass, with interactions and climate effects approximately equal (Fig. 5c). At $h = 0.2$ and above, elasmobranchs were greatly reduced in biomass, leaving harvest and climate effects as the dominant losses to biomass for groundfishes (Fig. 5d). At $h = 0.3$ and 0.5 (Fig. 5e,f), harvest effects were strongest in the first few years, before climate effects become dominant (about 50% of losses to biomass came from climate at $h = 0.3$ after about Year 17, and greater than 75% of the losses to biomass came from climate at $h = 0.5$ by Year 30).

DISCUSSION

As might be expected, the relative importance among the triad of drivers differed among the 3 functional groups, and under different harvest scenarios.

Table 7. System harvest. Percentage of final biomass when climate effects were turned on compared to turned off

Harvest	Groundfishes	Elasmobranchs	Small pelagics	System
0	100.1	100.0	99.9	100.0
0.01	99.6	100.1	100.0	99.9
0.05	97.8	100.7	100.2	99.4
0.1	95.5	102.0	100.6	98.6
0.2	89.6	105.7	102.1	96.0
0.3	76.6	108.0	103.9	91.5
0.5	35.7	102.5	102.0	94.4

Generally, when harvest occurred, it had the strongest effect on each group, particularly on elasmobranchs due to their low growth rate. Groundfishes were also strongly affected, starting at moderate levels of harvest (h = 0.2 to 0.3), but less so than elasmobranchs—due to the higher growth rate for the groundfish functional group. Additionally, release of competitive effects when elasmobranchs were also fished at the same level tended to keep groundfish—and therefore system—biomass more stable at lower levels of harvest. Finally, small pelagics were least affected by harvest ($h < 0.2$), due to a combination of having the highest growth rate among the 3 groups, and because of the predatory release as groundfish and elasmobranch biomass declined. These results are similar to those seen in previous studies which showed compensatory dynamics in the NEUS LME (Fogarty & Murawski 1998, Auster & Link 2009).

Ecological interactions had the strongest overall effect on small pelagics (predation from both of the other 2 groups), and a moderate effect on groundfish (competition from the elasmobranchs). Elasmobranchs were less strongly affected by competition from groundfish. Climate effects, since they targeted groundfish specifically in our model, primarily resulted in a decrease in groundfish biomass when applied, with a corresponding increase in elasmobranch and, in some scenarios, pelagic biomass, due to competitive and predatory release, respectively. The interplay among these factors, as simulated here, demonstrates that the prominence of any driver can shift given the dynamics and magnitude among the others.

When comparing the effects of the triad of drivers on each group, small pelagics were most strongly affected by ecological interactions, then harvest, and then climate. Elasmobranchs were most strongly affected by harvest, then ecological interactions, and finally climate. Groundfishes, however, appeared to be notably affected by all 3 drivers. Obviously as harvest increased in any class of scenarios, its effect became increasingly dominant, and as long as elasmobranchs remained at relatively high biomass, the corresponding ecological interactions also had a large impact on groundfish biomass losses. Climate tended to also have a stronger effect at higher harvest levels in our scenarios—indicating that climate effects may be more important in heavily exploited

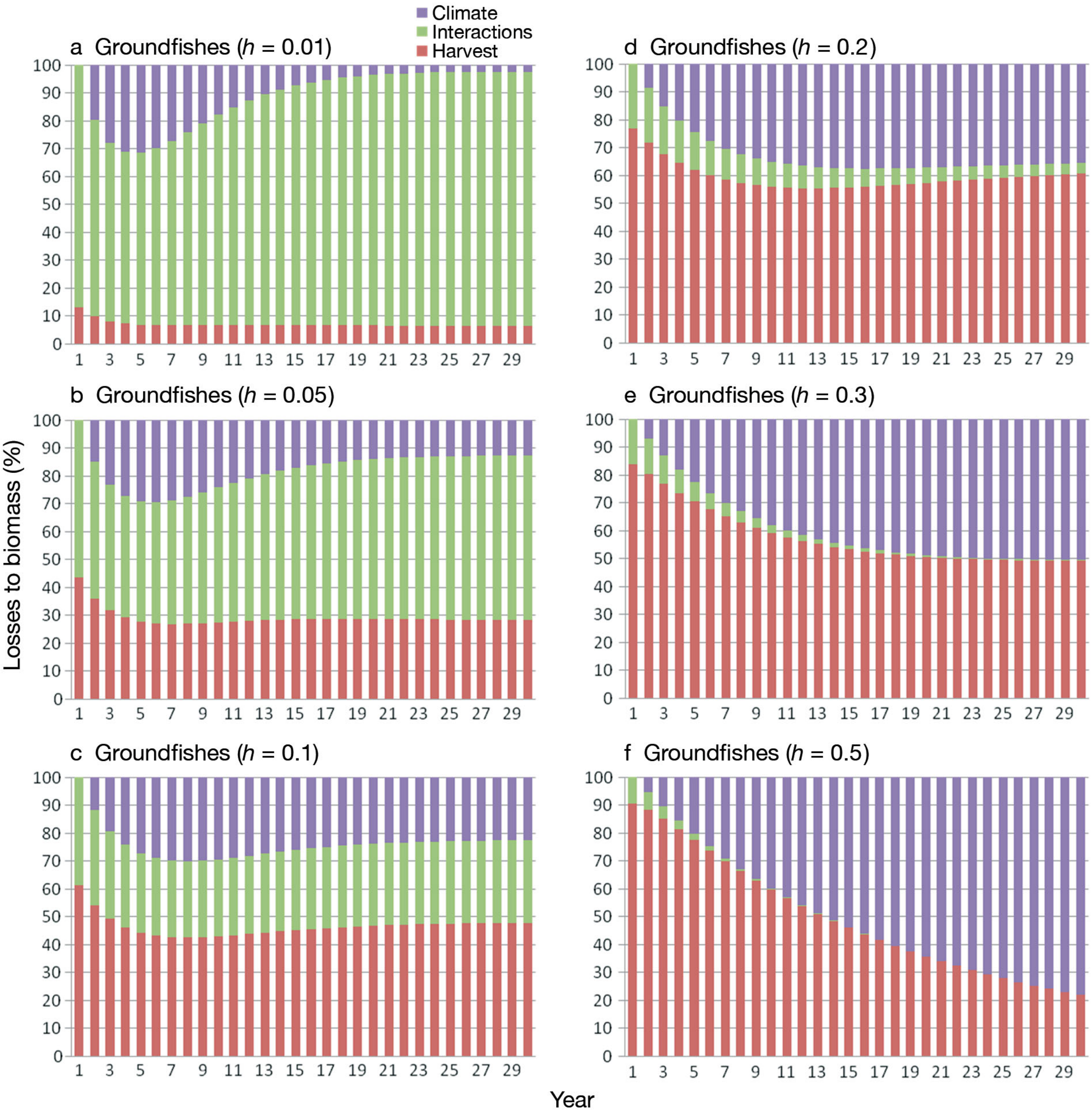

Fig. 5. Proportional losses to biomass of groundfishes caused by the system harvest class of scenarios with climate effects on (groundfish $r = 0.405$) where harvest was set to: (a) 0.01, (b) 0.05, (c) 0.1, (d) 0.2, (e) 0.3, (f) 0.5

ecosystems than in ones with lower levels of exploitation. These results, while simulation only, are confirmed by other empirical and modeling studies (e.g. Mackinson et al. 2008, Blanchard et al. 2010, Coll et al. 2010, Link et al. 2010a, Shin et al. 2010a,b, Tyrrell et al. 2011).

There are some important implications that come from these results. Depending on the life history of the groups, each of the triad of drivers can have very different impacts on each of the groups. Since harvest was the only driver of the 3 that was toggled at different ranges, the relative effects of the triad of drivers in our scenarios is dependent on the level of harvest for each group. It is also important to be careful in choosing the component species of each aggregate group, as a group with widely varying growth rates or other characteristics can create issues of interpretation in the results. While we maintain that it is likely the group as a whole would react with relative stability, the individual species within that group might not do so (see Auster & Link 2009, Gaichas et al. 2012). Other implications from our models relate to harvest levels. For instance, $h > 0.3$ for any group results in the group as a whole having a B_{final}/B_{MSY} ratio less than 1.0, while $h = 0.1$ results in groups with moderate (groundfishes) or high (small pelagics) growth rates having a B_{final}/B_{MSY} ratio above 1.0. The effects of climate further lower the exploitation rate at which this ratio drops below 1.0 for groundfish, indicating that a more precautionary exploitation rate should be considered under climate change. While we do not recommend these as universal basic properties of ecosystems, even for the NEUS LME, we do suggest that this kind of MSE could explore such recommendations, given a properly fitted ASP which incorporates climate and trophodynamic effects. Obviously the choice of parameter values (particularly r) greatly affects the results and the relative importance, but we think that our results generally demonstrate the utility of such an approach.

One of the strengths of our approach is that models like AGG-PROD can elucidate the effects of the triad of drivers on biological reference points (BRPs). While one might qualitatively be able to predict the effects of some of the drivers in isolation on individual groups with no interactions between them, we think that once multiple drivers (climate, interactions, and fishing) are occurring at the same time, a model such as AGG-PROD is very valuable, and needed, in separating their effects on fish populations. Even though we explored only a comparison of final biomass to B_{MSY}, there are some general conclusions we can draw. The most important might be that in the presence of strong impacts from climate or ecological interactions, the effects of setting F to any reference level are difficult to predict. Decreasing the predators through increased harvest can cause forage fish to increase in some cases, but in other cases interactions between predator groups, and differential effects of harvest on them, could result in more complex effects which might be counterintuitive. Climate and environmental effects also have varying impacts on the system, which should be taken into account. Therefore, we propose that if trophodynamic and climate effects are not explicitly included in models which determine BRPs, a more conservative approach should be taken in estimating these BRPs. An important consideration in this approach is that the precision possible in this model for defining BRPs (and the harvest rates corresponding to those BRPs) is likely much greater than could realistically be differentiated in an actual management setting. This will need to be further explored when using these models in a management context beyond a management strategy type of approach.

ASPs like AGG-PROD can be very flexible and valuable tools. For instance, one use is as an operating model in an MSE context. While certain classes of management actions are more difficult to simulate (e.g. spatial management) using ASPs, these models can be easily extended to include ecological interactions and climate effects. In some cases, as we did with groundfish growth rates, a simple modification to a parameter (e.g. r or K) can approximate certain climate effects such as range contraction or population size (Attrill & Power 2002, Nye et al. 2009). Additionally, empirical and modeling studies have shown linkages between growth rates and climate change (Brander 1995, O'Brien et al. 2000, Clark et al. 2003), supporting this approach. Work to further develop this modeling approach will include fitting model parameters to data, sensitivity analyses, and introducing stochasticity representing environmentally driven pressures on the fish populations. Additionally, exploring differential application of harvest rates across the different groups is a logical next step, especially in conjunction with exploring scenarios in a management context of tradeoffs between yield and ecosystem objectives. Ultimately, this model can be used to explore impacts on ecosystem function and yield under multiple strategies (e.g. proportional harvest rates based on productivity of the different stocks versus selective fishing) (Garcia 2011, Rochet et al. 2011).

Aggregating groups as part of a surplus production model has certain benefits. Many important fisheries are multi-species fisheries, such as those which target groundfishes in the NEUS LME, the North Sea, Southeast Australia, and similar temperate shelf systems (ICES 1993, Smith 1994, CEFAS 2001), all of which have management plans that reflect this multispecies targeting. An ASP can easily explore the effects from the triad of drivers on a level that multi-species fisheries operate. Aggregate groups also tend to be more stable than the individual components (Fogarty & Murawski 1998, Auster & Link 2009), so this method can be used initially to determine robust harvest levels to achieve system and aggregate group level BRPs. More complex models which explicitly include multiple species can then be used to examine the implications of those harvest strategies on the individual components of an aggregated group (as was done by Gaichas et al. 2012). This 2-stage approach is also recommended due to the observation that aggregated models may have very different characteristics regarding community stability, resilience, and other behaviors of the components modeled, than one in which the components are disaggregated (Pinnegar et al. 2005).

An ASP model could also be used to provide a precautionary cap on biological reference points determined by a suite of single-species models. Since it has been shown through multi-species and ecosystem modeling exercises (Au 1973, Pope 1979, Collie & Gislason 2001, Walters et al. 2005, Mueter & Megrey 2006, NEFSC 2008) and other analyses (May 1975, Pope 1975, Brown et al. 1976, Fukuda 1976, May et al. 1979, Gislason et al. 2010, Tyrrell et al. 2011) that the sum of single-species MSYs can be quite different than the MSY of the corresponding multispecies group, we suggest that BRPs resulting from an ASP model could be utilized as the maximum total amount that should be removed from the group. A further consideration is that by not directly modeling species interactions in our model, we would expect differences in the estimated BRPs in our approach compared to a model in which those interactions were present explicitly. As an example, not all species in the groundfish group would be affected equally by climate—in fact there might be species which would show increased growth rates. Thus, while we recommend ASPs as useful operating models, they should be applied with an understanding of their limitations as well as their strengths. Particularly we recommend that they be part of a toolbox of models rather than the sole operating model in an MSE.

With EBFM emerging (NMFS 1999, Link 2002a,b, Pikitch et al. 2004, Link 2010), there is a need for tools and methods that can evaluate the triad of drivers in an MSE context (Link et al. 2010b,c), particularly in the context of multi-species fisheries. We think that the utility of ASPs with trophic interactions and climate effects modeled explicitly can be an important element of EBFM by providing aggregate level reference points and as operating models in an MSE context to explore the possible effects of changes in climate and the trophic structure of a fish community. We recommend that they be used with other models, particularly multi-species models which also include the triad of drivers explicitly, to fully explore the dynamics of not only the aggregate groups of interest to a fishery or management, but also the entire system and the individual component species within that system.

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Contribution to the Theme Section 'Comparative analysis of marine fisheries production'

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

Sarah Gaichas[1,7,*], Robert Gamble[2], Michael Fogarty[2], Hugues Benoît[3], Tim Essington[4], Caihong Fu[5], Mariano Koen-Alonso[6], Jason Link[2]

[1]Resource Ecology and Fisheries Management Division, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, Washington 98115, USA
[2]Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, Woods Hole, Massachusetts 02543, USA
[3]Gulf Fisheries Centre, Fisheries and Oceans Canada, Moncton, New Brunswick E1C 9B6, Canada
[4]University of Washington, School of Aquatic & Fishery Sciences, Seattle, Washington 98195-5020, USA
[5]Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, British Columbia V9T 6N7, Canada
[6]Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, St John's, Newfoundland and Labrador A1C 5X1, Canada

[7]*Present address:* Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, Woods Hole, Massachusetts 02543, USA

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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*Email: sarah.gaichas@noaa.gov

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 maximization 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:

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

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:

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

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

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

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

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

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:

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

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:

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

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:

$$\frac{\mathrm{d}B_{\mathrm{T}}}{\mathrm{d}t} = (r_{\mathrm{T}} - \alpha_{\mathrm{T}} B_{\mathrm{T}}) B_{\mathrm{T}} - F_{\mathrm{T}} B_{\mathrm{T}} \qquad (7)$$

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:

$$B_{\mathrm{T}}^{*} = \frac{r_{\mathrm{T}} - F_{\mathrm{T}}}{\alpha_{\mathrm{T}}} \qquad (8)$$

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:

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

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:

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

where

$$\gamma = \frac{r_T - \alpha_T B_0}{\alpha_T B_0} \qquad (11)$$

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:

$$\text{MSY}_T = \frac{r_T^2}{4\alpha_T} \qquad (12)$$

and the fishing mortality rate at MSY is:

$$F_{\text{MSY}} = \frac{r_T}{2} \qquad (13)$$

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-

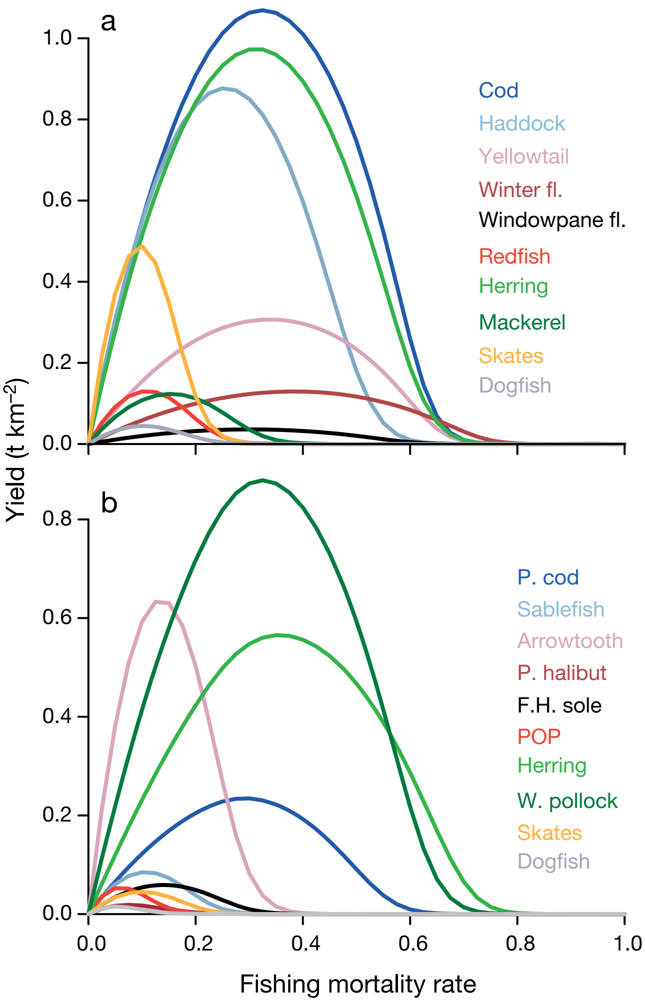

Fig. 1. Yield curves for simulated 10-species interacting fish communities: (a) Georges Bank and (b) Gulf of Alaska; comparable species have similar colors. fl.: flounder; P.: Pacific; F.H.: flathead; W.: walleye

ulated systems, the low productivity of the elasmobranch 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 proportion 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

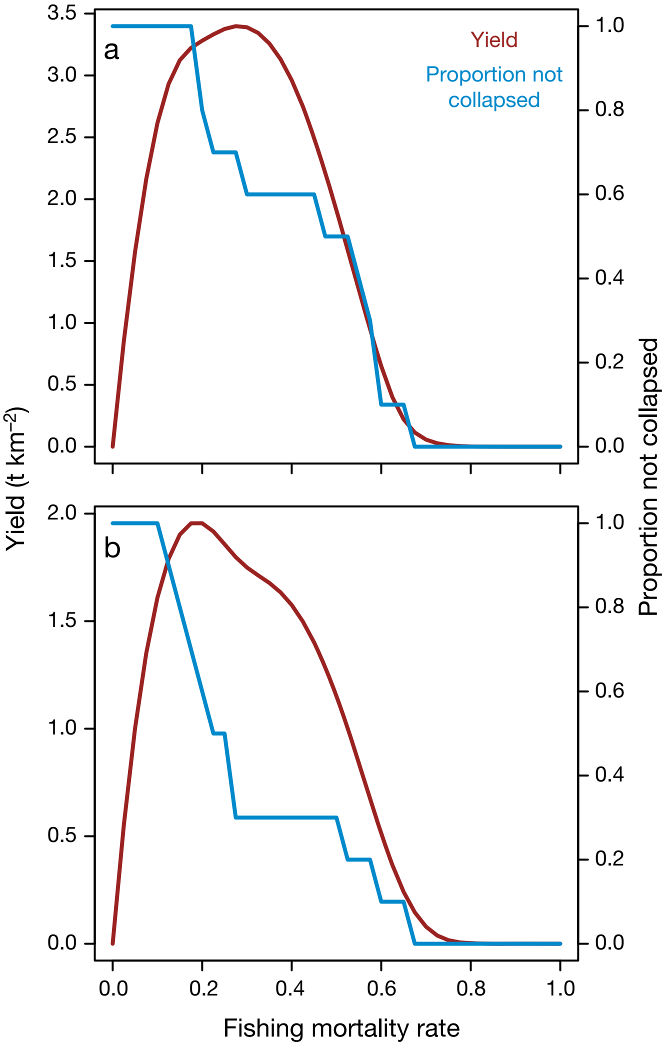

Fig. 2. Full 10-species system aggregate yield and collapse curves (where collapse is defined as biomass <10% of unfished biomass) for (a) Georges Bank and (b) Gulf of Alaska

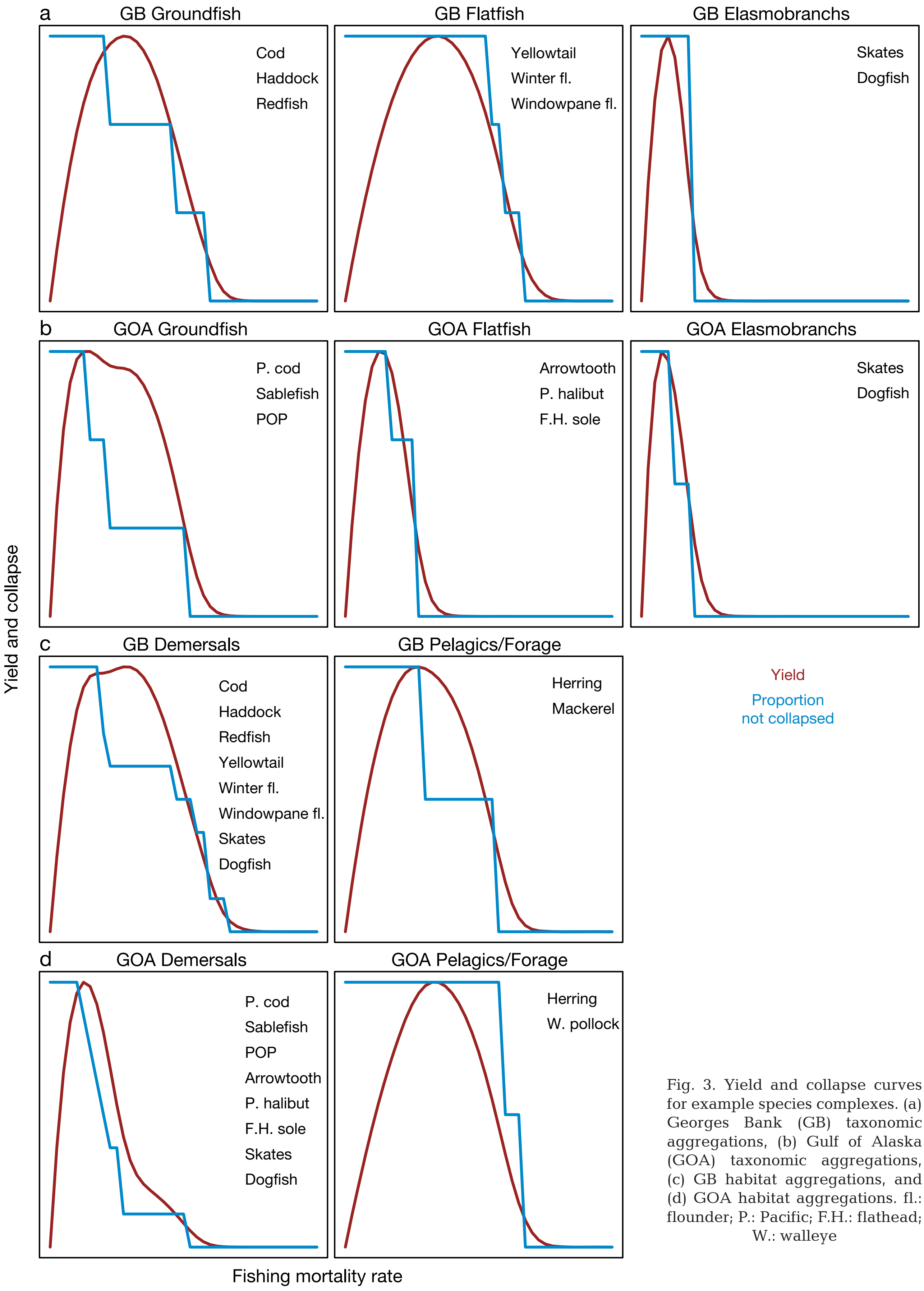

Fig. 3. Yield and collapse curves for example species complexes. (a) Georges Bank (GB) taxonomic aggregations, (b) Gulf of Alaska (GOA) taxonomic aggregations, (c) GB habitat aggregations, and (d) GOA habitat aggregations. fl.: flounder; P.: Pacific; F.H.: flathead; W.: walleye

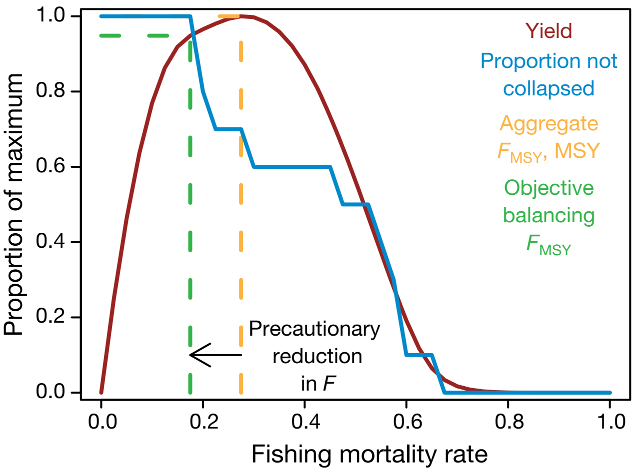

Fig. 4. In multispecies complexes, fishing mortality rate F can be reduced from aggregate F_{MSY} (MSY, maximum sustainable yield) to prevent collapses. For the full 10-species Georges Bank model, nearly 95 % of MSY can be achieved with no species dropping below 10 % of unfished biomass

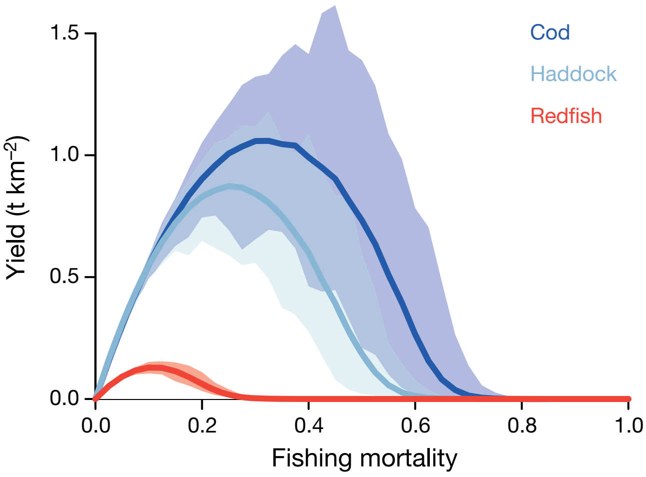

Fig. 5. Average yield curves (lines) with ranges (shading) from 1000 stochastic runs for the Georges Bank groundfish complex

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 planktivores, 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.

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

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 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-

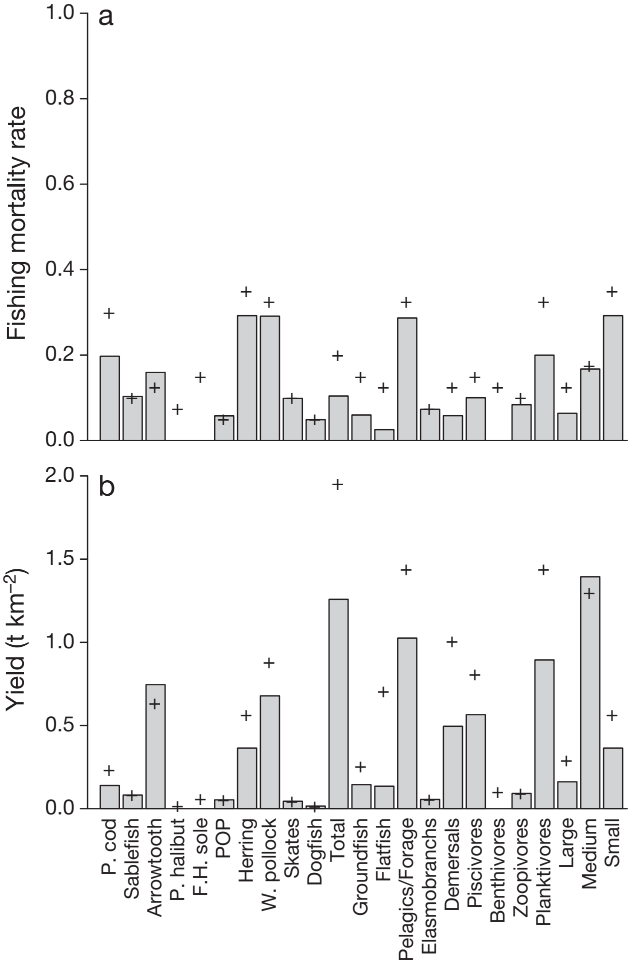

Fig. 6. Estimated (a) fishing mortality rate at maximum sustainable yield (MSY), and (b) MSY from deterministic assessments (bars) for the Gulf of Alaska, with 'true' biological reference points (BRPs) from the simulation model (+). Estimation failed for flathead (F.H.) sole, halibut, and benthivores. P.: Pacific; W.: walleye

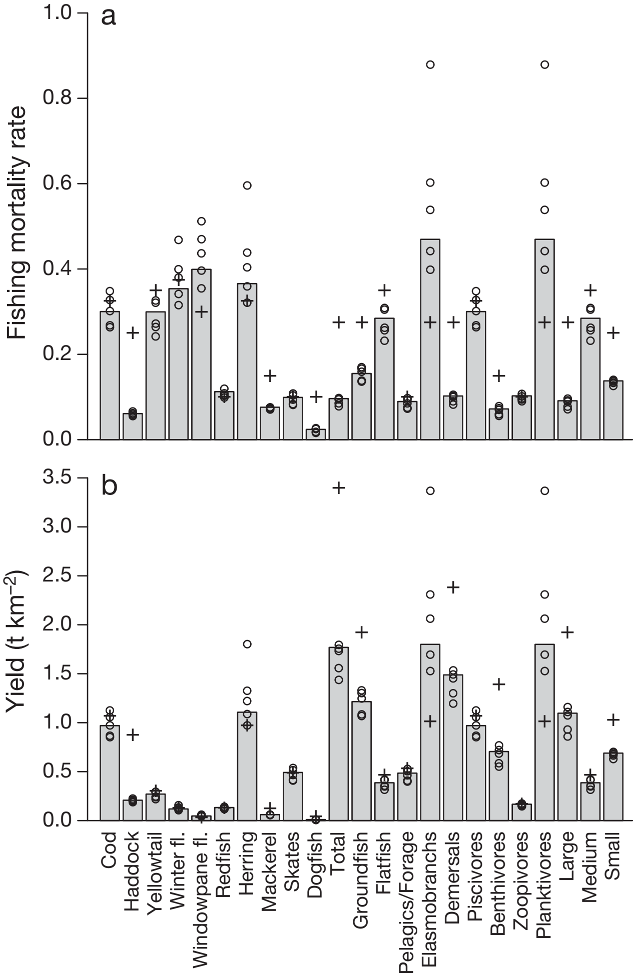

Fig. 7. Assessment-estimated (a) F_{MSY}, and (b) MSY from deterministic (bars) and 5 randomly selected stochastic (open circles) simulations for Georges Bank, with 'true' BRPs from the operating model (+)

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 ecosytem 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.)

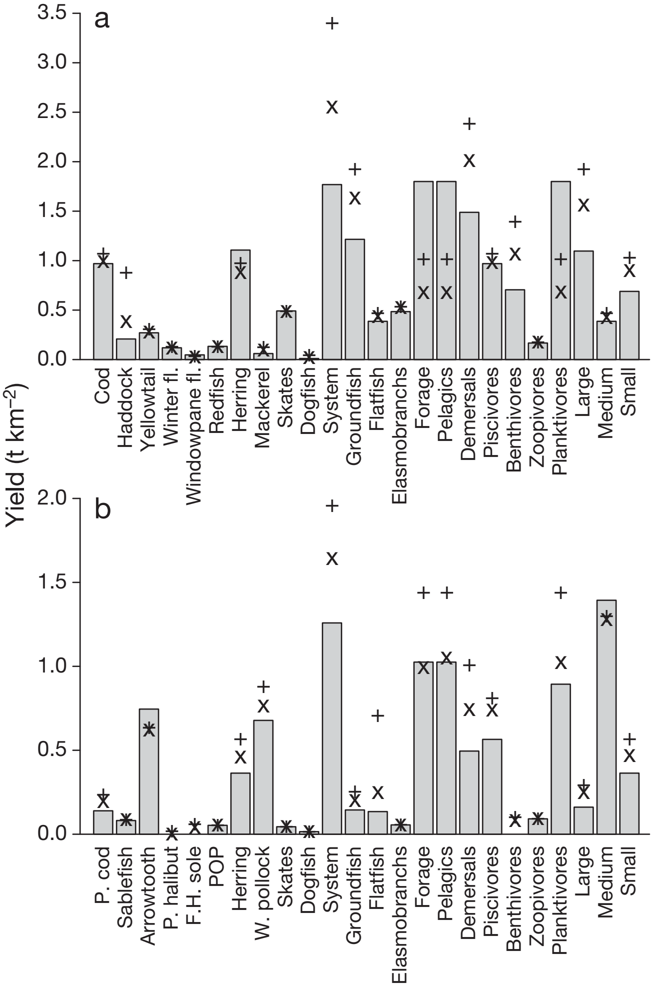

Fig. 8. Comparison of assessment-predicted MSY (bars), true MSY (+), and realized equilibrium yield (X) from 50 yr of fishing at assessment estimated F_{MSY} in (a) Georges Bank and (b) Gulf of Alaska. fl.: flounder; P.: Pacific; F.H.: flathead; W.: walleye

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 stochastic 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 biomass. 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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Contribution to the Theme Section 'Comparative analysis of marine fisheries production'

Synthesizing lessons learned from comparing fisheries production in 13 northern hemisphere ecosystems: emergent fundamental features

Jason S. Link[1,*], Sarah Gaichas[2], Thomas J. Miller[3], Tim Essington[4], Alida Bundy[5], Jennifer Boldt[6], Ken F. Drinkwater[7], Erlend Moksness[8]

[1]National Atmospheric and Oceanic Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, Massachusetts 02543, USA
[2]National Atmospheric and Oceanic Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, Washington 98115, USA
[3]Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, Maryland 20688, USA
[4]School of Fisheries and Aquatic Sciences, University of Washington, Seattle, Washington 98195, USA
[5]Department of Fisheries and Oceans, Bedford Institute of Oceanography, Halifax, Nova Scotia B2Y 4A2, Canada
[6]Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia V9T 6N7, Canada
[7]Institute of Marine Research and Bjerknes Centre for Climate Research, Bergen 5817, Norway
[8]Institute of Marine Research, Flødevigen Marine Research Station, His 4817, Norway

ABSTRACT: Understanding the drivers of the productivity of marine ecosystems continues to be a globally important issue. A vast body of literature identifies 3 main processes that regulate the production dynamics of fisheries: biophysical, exploitative, and trophodynamic. Here, we synthesize results from international workshops in which surplus production models were applied to 13 northern hemisphere ecosystems that support notable fisheries. The results are compared across systems, levels of species aggregation, and drivers. By applying surplus production models at single-species (SS), multi-species (MS), aggregated group, and full-system levels across ecosystems, we find that the different levels of aggregation provide distinct, but complementary, information. Further, it is clear that the triad of drivers contributes to fisheries productivity in each ecosystem, but the key drivers are system-specific. Our results also confirm that full-system yield is less than the sum of SS yields and that some MS and aggregate yields may lead to overharvest of some stocks if species groups are constructed without considering common productivity, inter-species, and environmental interactions. Several fundamental features emerge from this Theme Section including sigmoidal biomass accumulation curves across trophic levels, improvement of model fits by inclusion of environmental or ecological covariates, the inequality of system maximum sustainable yield (MSY) versus aggregated sums and SS sums of MSY, a 1 to 5 t km^{-2} fishery yield rule of thumb, and the finding that tradeoffs among ocean use objectives may not be as harsh as originally thought. These emergent features have the potential to alter our understanding of marine ecosystem dynamics and improve how we manage fisheries production.

KEY WORDS: Ecosystem comparison · Surplus production · Multispecies models · Aggregate biomass estimates · Environmental covariates · Fisheries management · Hierarchical analysis

INTRODUCTION

Ecosystem-based fisheries management (EBFM) has become a dominant paradigm of fisheries science and management, with calls and justifications for EBFM (Link 2002a,b, Garcia et al. 2003, Pikitch et al. 2004) being increasingly replaced by evaluations of and practical suggestions for its implementation (Link 2010, Ellis et al. 2011, Essington & Punt 2011, Hilborn 2011, Rice 2011). It is now clearly recognized that the

*Email: jason.link@noaa.gov

sound management of fisheries requires a consideration of broader factors that influence marine ecosystems. As such, an improved understanding of the drivers of ecosystem dynamics that can influence fisheries resources is required.

Although there are multiple drivers that can influence ecosystem dynamics, we focus here on 3 main processes that affect marine fish productivity: biophysical (environmental), exploitative (fisheries), and trophodynamic (species interactions) factors (Link et al. 2010a). We refer to these as the production 'triad' of drivers because they represent dominant themes of research to understand variation in productivity within and across ecosystems (Fig. 1). Although each is clearly important individually, rarely has the impact of these multiple drivers been assessed simultaneously. The work synthesized here results from several workshops (Link et al. 2010a, Gaichas et al. 2012a, this Theme Section [TS]), all of which used the triad as a central, operating hypothesis questioning how ecosystem dynamics influence fisheries production.

Fisheries production is an important marine 'ecosystem service' worldwide, with economies and social fabrics constructed around that production (Holmlund & Hammer 1999, Allison et al. 2009, Barange et al. 2010, Garcia & Rosenberg 2010, Coulthard et al. 2011, Longhurst 2010). Estimating the productivity of fish populations is an important step in the sound management of fisheries targeting those species. Integrating information on key covariates of production and how production scales across different levels of biological information are therefore key steps toward implementing EBFM. Several studies have already explored those features that can influence fisheries production individually (e.g. Beaugrand et al. 2003, Platt et al. 2003, Koen-Alonso & Yodzis 2005, Lehodey et al. 2006, Chassot et al. 2007, Mueter et al. 2009, Steele et al. 2011). We suggest that extending these approaches to compare the impact of multiple factors simultaneously is one way to improve our understanding of such production.

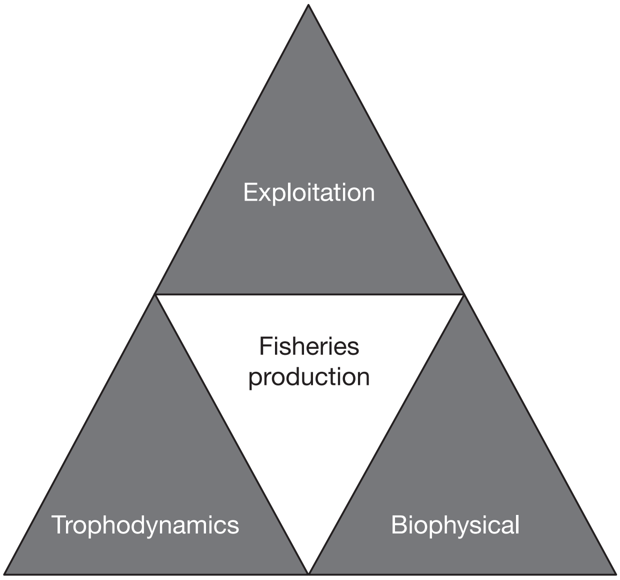

Fig. 1. The triad of drivers that can affect fisheries production

An essential element of comparative ecosystem analysis is the development of a common analytic platform that produces a standardized measure to enable adequate comparisons across ecosystems. The need for such a standardized method precludes the application of complex, detailed models tailored to the specifics of any particular ecosystem and instead favors simpler, abstract representations of key ecological processes. In ecology, simple density-dependent population models have commonly proved to be useful in this type of application; in fisheries ecology, these approaches are easily adapted to also account for removals from fisheries, using models commonly called surplus production models (SPMs). These models relate the production of a population to the current population size, intrinsic rates of productivity, and density-dependent effects. Although there has been debate about the applications of such modeling approaches, particularly regarding assumptions or perceptions of equilibrium and lack of age-structured dynamics (Mohn 1980, Ludwig & Walters 1985, 1989, Punt 2003), there is consensus that they play a useful and important role in ecology in general (Mangel et al. 2006) and fisheries science in particular (Ludwig & Walters 1985, 1989, National Research Council 1998). Other benefits of SPMs are noted by Gaichas et al. (2012a). Importantly for this application, the data inputs to conduct SPM are relatively simple and often readily available across ecosystems. Moreover, SPMs are often used to derive common biological reference points (BRPs); classic examples include maximum sustainable yield (MSY) and the biomass or fishing rates at MSY (B_{MSY} and F_{MSY} respectively), which are used to assess the status of exploited stocks. Thus, the reference points generated by these models provide familiar outputs that serve as a consistent platform for comparison of fisheries production across ecosystems and at different levels of ecosystem aggregation (e.g. species, aggregated foraging guild or habitat group, or full system).

Marine ecosystems are complex and respond to external drivers at multiple temporal, spatial, and organizational scales. This inherent complexity precludes an experimental approach at appropriate spatio-temporal scales; thus, to explore the questions addressed here, a comparative approach is required (Murawski et al. 2010). Placing ecosystem responses into a broader context enables the elucidation of both common, generic patterns and processes that are unique to particular ecosystems. Our objectives here are to highlight the fundamental features of marine ecosystems that emerged from the comparative analyses presented in this TS. Here, we synthesize that body of work, highlighted as major themes in the sections below, to emphasize major findings that are apt to be valuable and informative for EBFM and may indeed be fundamental features of marine ecosystems.

PATTERNS IN EMPIRICAL INFORMATION

In compiling the database of catch, biomass, and environmental time series for this comparative work (for data descriptions, see Bundy et al. 2012, Fu et al. 2012, Pranovi et al. 2012, Gaichas et al. 2012a, all in this TS) (Table 1 lists the main species considered), several key empirical relationships were identified across the ecosystems (Fig. 2) prior to the application of production models. Fu et al. (2012) compared the relative importance and effect of fisheries, trophodynamic, and biophysical drivers on a range of metrics across ecosystems. The results indicate that each component of the triad of drivers was important for all of the studied ecosystems, as found in other studies (e.g. Coll et al. 2010, Link et al. 2010a,b); however, the relative importance of each driver and the indicators they most affected varied among ecosystems, suggesting that an examination of a suite of indicators and drivers is required. Temporal variability in derived metrics of fish biomass and fisheries catches across ecosystems indicated distinct differences between the Pacific and Atlantic Ocean basins for many but not all ecosystem indicators (Fu et al. 2012). Some similarity among these and related ecosystems within an ocean basin has been shown before, with coherency in basic biological responses readily and repeatedly observed (e.g. Link et al. 2009, Megrey et al. 2009, Nye et al. 2010).

A fundamental feature derived from these data is the sigmoidal relationship of cumulative biomass curves across trophic levels (Pranovi et al. 2012). It appears from the generality of the patterns observed that biomass tends to accumulate, either proportionally or in absolute magnitude, at middle trophic levels; this is apt to be a common feature in most marine ecosystems. As biomass accumulates across trophic levels, the sigmoidal shape appears to be robust across ecosystems, time, and many very distinct types of taxa. This common feature could potentially be used as a system-level BRP. For instance, as perturbations occur in a given ecosystem, the inflection point and steepness parameters reflect such changes by flattening out the curve (Fig. 3) (Pranovi et al. 2012), indicative of a potential system-level threshold similar to that presented in other attempts to define ecosystem overfishing (e.g. Gascuel et al. 2005, Link 2005, Tudela et al. 2005, Coll et al. 2008, Libralato et al. 2008). The value of modelling sigmoidal biomass accumulation curves is that it is a simple derivation of readily extant data, not requiring involved multi-species, food web, or ecosystem models. As such, this might be an important fundamental feature that could be useful for fisheries management, especially EBFM.

PROMINENCE AMONG DRIVERS

No single driver emerged as consistently dominant across all ecosystems, based on both direct empirical descriptions (Fu et al. 2012, Pranovi et al. 2012) and statistical modeling (Bundy et al. 2012, Holsman et al. 2012, this TS). Measures of exploitation and broad-scale climate indices were some of the more consistently prominent drivers that emerged across all ecosystems, but no single factor was the most dominant across all ecosystems. However, while not the dominant signal, temperature affected production in nearly all systems based on both empirical and full-system SPM approaches (Bundy et al. 2012, Fu et al. 2012). These observations are consistent with similar empirical studies of some of these and other ecosystems (Coll et al. 2010, Link et al. 2010b).

Including environmental covariates in the SPM similarly exhibited no obvious pattern indicating the major driver influencing fisheries production (Bundy et al. 2012, Holsman et al. 2012). The prominence among environmental, trophic, and fishing metrics all varied across the ecosystems, levels of aggregation, and type of model fitting. However, inclusion of such covariates almost always lowered estimates of key BRPs, especially MSY (e.g. Bundy et al. 2012, Holsman et al. 2012). Simulation studies (Gaichas et al. 2012b, Gamble & Link 2012, both in this TS) also exhibited lower MSY and associated BRP estimates, albeit with higher variances about them, when environmental or ecological factors were included. Furthermore, simulations showed that climate change can have larger effects than species interactions, which can have larger effects than fisheries removals (Gaichas et al. 2012b, Gamble & Link 2012).

Table 1. Species list for each ecosystem used in the sum of the single-species (SS) maximum sustainable yield (MSY) analysis shown in Fig. 4 (cf. Bundy et al. 2012, their Table A1 and Pranovi et al. 2012, their Table 2 for more details). EBS: Eastern Bering Sea; GOA: Gulf of Alaska; HS: Hecate Strait; NL: Newfoundland; SGOSL: southern Gulf of St. Lawrence; E/WSS: eastern/western Scotian Shelf; GOM: Gulf of Maine; GB: Georges Bank; North: North Sea; BS: Barents Sea; Norw.: Norwegian Sea. NS: species not specified

	EBS	GOA	HS
Pacific Ocean			
Alaska plaice	X		
Arrowtooth flounder	X	X	X
Curlfin sole			X
Dover sole		X	X
Dusky rockfish		X	
English sole			X
Flathead sole	X		X
King crab	X		
Lingcod			X
Northern rock sole	X		
Northern rockfish		X	
Pacific cod	X	X	X
Pacific halibut	X	X	X
Pacific herring	X	X	X
Pacific ocean perch		X	
Pacific salmon		X	
Pacific sanddab			X
Petrale sole			X
Quillback rockfish			X
Rex sole		X	X
Rougheye rockfish		X	
Sablefish	X	X	X
Sand sole			X
Silvergray rockfish			X
Slender sole			X
Southern rock sole			X
Spotted ratfish			X
Tanner crab	X		
Walleye pollock	X	X	X
Yellowfin sole	X	X	
Yellowtail rockfish			X
Both oceans			
Butter sole			X
Skates (NS)			X
Snow crab	X		
Spiny dogfish			X

	NL	SGOSL	ESS	WSS	GOM	GB	North	BS	Norw.
Atlantic/Arctic Ocean									
Aesop shrimp	X								
Alewife		X	X						
American lobster		X	X	X					
American plaice	X	X	X		X	X			
Atlantic argentine			X						
Atlantic butterfish						X			
Atlantic cod	X	X	X	X	X	X	X	X	
Atlantic hagfish			X						
Atlantic halibut	X	X	X		X	X			
Atlantic herring	X	X		X	X	X	X	X	X
Atlantic mackerel				X	X	X			X
Atlantic redfishes (NS)		X	X	X	X	X			
Atlantic wolffish	X	X			X	X			
Beaked redfish	X							X	
Blue hake	X								
Blue whiting									X
Capelin	X	X						X	
Common sole							X		
Cusk			X	X					
Eelpouts (NS)	X								
European plaice							X		
Fourspot flounder					X				
Golden redfish								X	
Goosefish			X	X	X	X			
Greenland cod		X							
Greenland halibut	X	X	X					X	
Haddock	X	X	X	X	X	X	X	X	
Jonah crab			X						
Lesser sandeel							X		
Longfin squid					X	X			
Longhorn sculpin			X	X					
Lumpfish	X		X						
Northern prawn	X								
Norway pout							X		
Ocean pout			X		X	X			
Pandalid shrimps (NS)			X					X	
Pollock			X	X	X	X	X	X	
Rainbow smelt		X							
Red hake			X	X	X	X			
Rock crab		X	X						
Roughhead grenadier	X								
Roundnose grenadier	X								
Saithe								X	
Scup					X				
Sea scallop			X	X					
Sea raven									
Shad			X						
Shortfin squid		X			X	X			
Silver hake			X	X	X	X			
Smooth dogfish						X			
Spotted wolffish	X								
Squids (NS)			X	X					
Summer flounder					X	X			
Toad crabs (NS)		X							
White hake	X	X	X	X	X	X			
Whiting							X		
Windowpane		X			X	X			
Winter flounder		X	X		X	X			
Witch flounder	X	X	X		X	X			
Wolffishes (NS)			X	X					
Yellowtail flounder	X	X	X		X	X			
Both oceans									
Butter sole								X	
Skates (NS)			X	X	X	X			
Snow crab	X	X	X						
Spiny dogfish			X	X	X	X			

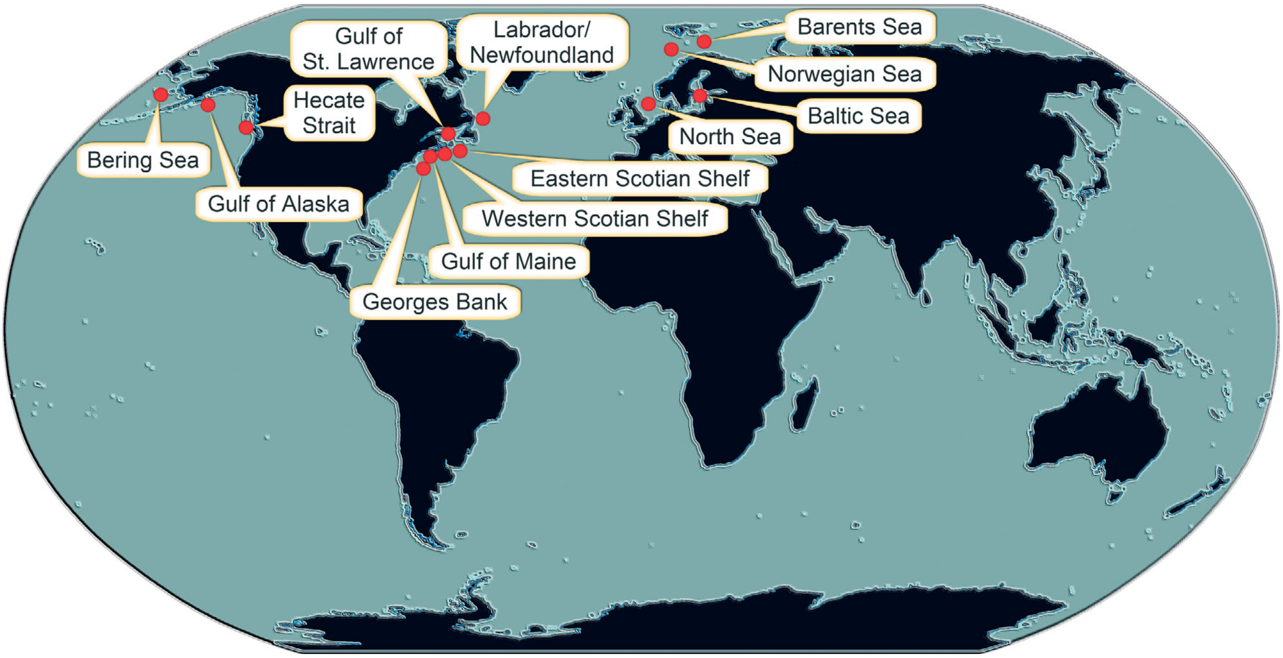

Fig. 2. Locations of the ecosystems included in the present comparative analyses

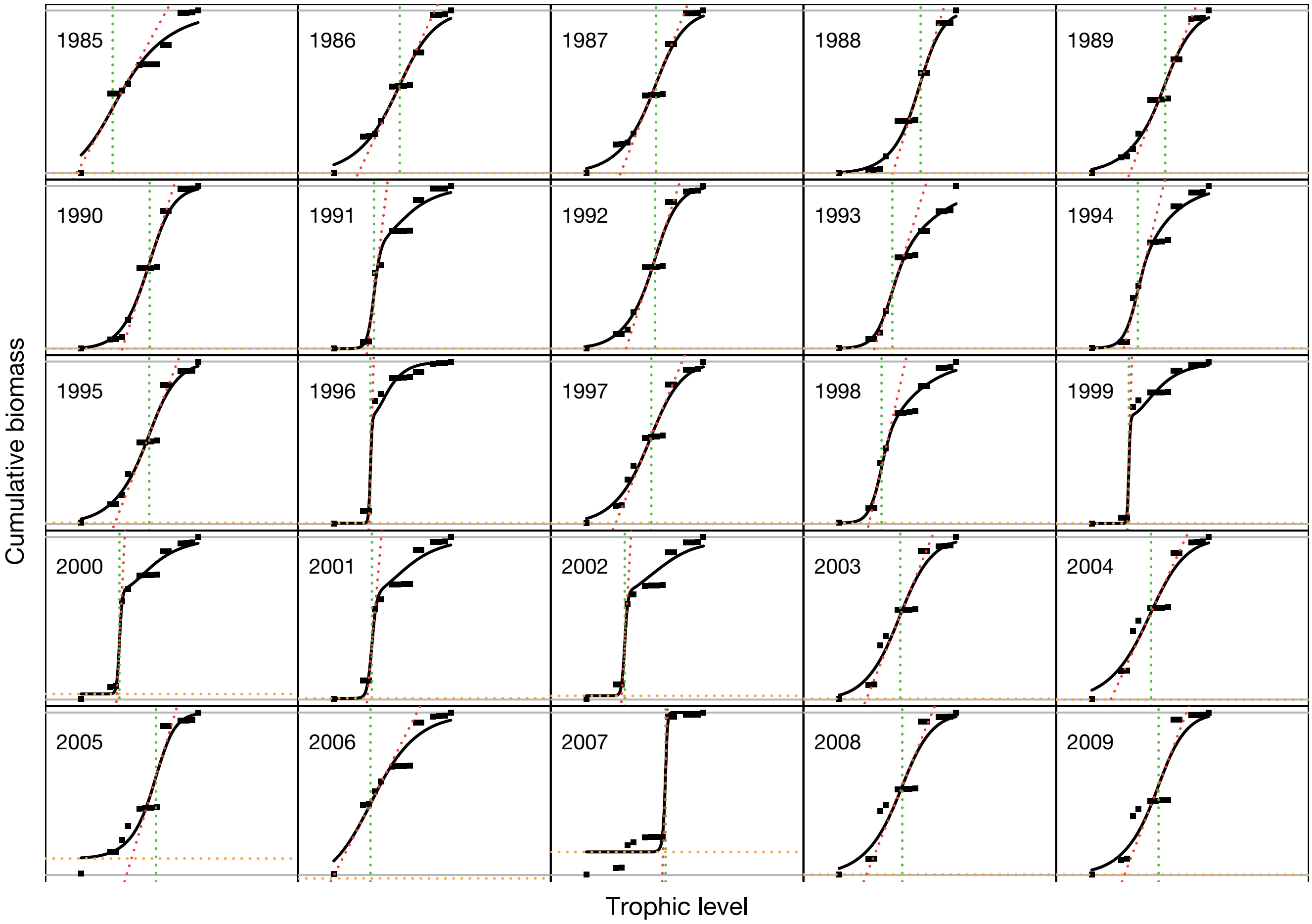

Fig. 3. Example of changes to the biomass accumulation curves across trophic levels over time for the Gulf of St. Lawrence ecosystem (adapted from Pranovi et al. 2012). Vertical dotted (green) line: trophic level intercept, or inflection point; horizontal dotted (orange) line: biomass intercept or starting biomass level; diagonal dotted (red) line: tangent of the curve through the inflection point

One fundamental feature that did emerge from this work is that, despite the lack of a consistent dominant driver across all ecosystems, the addition of biophysical or ecological covariates often improved the fit of SPMs (Bundy et al. 2012, Holsman et al. 2012). This implies that multiple factors, in addition to fishing, can influence fisheries production, and those factors should no longer be omitted from exploration, modeling, and provision of fisheries management advice, consistent with calls for EBFM. Moreover, although the inclusion of the covariates improved model fits, they also altered estimated reference points. This suggests not only that environmental variability can be an important source of observation error affecting survey data, but also that failure to include biophysical and trophodynamic covariates can be an important source of process error in assessments.

Clearly, further work is warranted to determine if there are major, dominant, consistent drivers as a fundamental feature of all marine ecosystems (Longhurst 2010). It may very well be that all facets of the triad can be important under any given situation, that they have different time scales, that they all have the potential to be dominant at any given time, and that all are occurring at various levels of magnitude within an ecosystem (Hunt & McKinnell 2006). However, determining what conditions make one set of drivers more prominent than others, and why, remains to be more fully elucidated. For now, the present work clearly indicates that including covariates in investigations of fishery production is important, but that the covariates must be tailored to individual systems. Temperature data in particular are widely available and have improved fits in many situations across systems; thus, perhaps future investigations could include a thermally related and relevant covariate as a matter of course.

AGGREGATION OF FISHERIES PRODUCTION

This TS is some of the first work to systematically examine production at intermediate levels of aggregation between single species (SS) and full systems using a comparative approach. Using both simulation and SPM fitting approaches, the relative productivity of aggregated groups becomes apparent. For example, aggregate pelagic habitat groups nearly always had higher MSYs than the aggregate demersal groups (Gaichas et al. 2012b, Lucey et al. 2012, this TS). Similarly and not surprisingly, planktivores were nearly always the most productive feeding aggregate. However, the size-based groups performed counter-intuitively, with aggregates of small species showing generally higher productivity than large species, but with medium species less productive than larger sizes. Similarly, simulation results based on parameters for Georges Bank showed large species as the most productive. Overall, habitat-based groups had the most consistent production patterns in the SPM fitting study (Lucey et al. 2012), while taxonomic aggregates appeared to perform well to balance dual management objectives of maximal yield and minimal depletion (Gaichas et al. 2012b; see next section).

Aggregate groups at intermediate levels of organization may also provide effective ecosystem indicators. Changes in aggregate biomass for particular groups (gadoids or clupeids) were more indicative of ecosystem or fishery change than total system biomass in empirical studies (Fu et al. 2012). This information on the productivity of aggregate groups may be useful in setting BRPs in areas or for groups where information is limited; the patterns in relative productivity reported here could generally inform such data-poor situations.

IMPLICATIONS FOR ECOSYSTEM-BASED FISHERIES MANAGEMENT

An emergent fundamental feature from simulation modeling is that enforcing tradeoffs across ecosystem-use objectives may not be as bad as was once thought. Management strategy evaluation simulations demonstrate that the loss in yield required to maintain conservation objectives is usually small, on the order of <10% of the maximal system yield (Gaichas et al. 2012b, their Fig. 2). This is consistent with prior studies of some of these and other ecosystems (Worm et al. 2009). A key implication is that avoiding stock collapse and maximizing yield do indeed form a set of contrasts, but the differences in optimizing both goals may be rather small. Foregoing a small fraction of yield to avoid endangering targeted (or even non-targeted or endangered) species has other benefits as well, including market dynamics that may compensate (in terms of value) for what was not landed (in terms of volume) (Edwards et al. 2004). Clearly, further simulations, analytical modeling, empirical evaluations, and ultimately fitting to multiple objective-function frameworks with explicit social implications are warranted, but these preliminary results indicate a probable win-win scenario for fisheries management, consistent with calls for EBFM.

A significant finding from the modeling work reported in this TS is that the ranges of system-level MSY values across these ecosystems are usually within 1 to 5 t yr^{-1} km^{-2} (Bundy et al. 2012, their Fig. 5). This may also be a key fundamental feature of northern hemisphere, boreal or temperate ecosystems. Certainly, a 4 to 5-fold difference can be important, but it is a previously unspecified range and likely represents a range of production within which these types of ecosystems may be bound. Estimates of other BRPs, especially B_{MSY}, appear to be similarly constrained within a relatively limited range of values (5 to 20 t yr^{-1} km^{-2}). Although this represents potentially up to a 4-fold difference, our point in highlighting it is that this range is still within an order of magnitude, not across several. Whether this observation will hold for other northern hemisphere, temperate or boreal ecosystems is unknown. Future efforts to extend and explore this approach should certainly include southern hemisphere and tropical examples. Yet, we suspect the range will not greatly expand for 3 reasons. First, as we conducted the workshops, when we added other ecosystems into this body of work, they tended to fall within this reported range. Second, global meta-analyses that have examined landings data (slightly distinct from the biomass and landings data used here) all tended to estimate annual yields within similar ranges when examined on an areal basis (Ryther 1969, Pauly & Christensen 1995, Ware & Thomson 2005, Chassot et al. 2010), although the range presented here is smaller than those of other studies. Third, the primary production to support fisheries production in these mid- to higher latitude systems generally falls within a similarly limited range and, although variable, has not fundamentally changed (orders of) magnitude over time. We do not know whether this observation will hold for other types of marine ecosystems; this finding clearly merits further examination. Additionally, the spatial extent of the ecosystems examined here was generally quite large; whether these patterns would be retained in smaller ecosystems similarly merits examination, particularly to ensure that major production features or locales are not omitted. Given these caveats, if this pattern holds, it represents a significant basis for developing limits to fishery removals from ecosystems, even if only for the northern ecosystems included in the studies in this TS (Gaichas et al. 2012a). This empirically confirmed range should serve as one of the more robust system-level BRPs, ultimately limiting what can be produced, and thus harvested, from an ecosystem. Ultimately, if further research supports this limited range of sustainable harvests, expectations of fisheries yields from all stakeholders should be tempered accordingly.

Another major finding is that with increasing levels of aggregation, the summation of yields at lower levels of aggregation is almost always higher than yield estimates executed at the higher levels (Fig. 4) (Bundy et al. 2012, Holsman et al. 2012, Lucey et al. 2012. For instance, total system-level estimates of yield are always lower than sums of similar estimates at the functional guild or habitat aggregated levels. Further, the total system-level estimates of yield are always lower than the sum of such yields estimates at the SS level. Certainly the types and levels of intermediate aggregations can be important and alter the results (Gaichas et al. 2012b, Lucey et al. 2012), and some of the aggregate group summations can exceed the SS sums (due to vagaries of how productivity is allocated across reinforcing species in an aggregate group), but certainly at the system level and SS level, the fundamental pattern remains. Although noted multiple times in the past (e.g. May 1975, Pope 1975, 1979, Brown et al. 1976, Fukuda 1976, May et al. 1979) and more recently (Walters et al. 2005, Steele et al. 2011, Tyrrell et al. 2011), this fundamental inequality holds:

$$\Sigma \text{SS}_{\text{MSY}} > \text{Ecosystem}_{\text{MSY}}$$

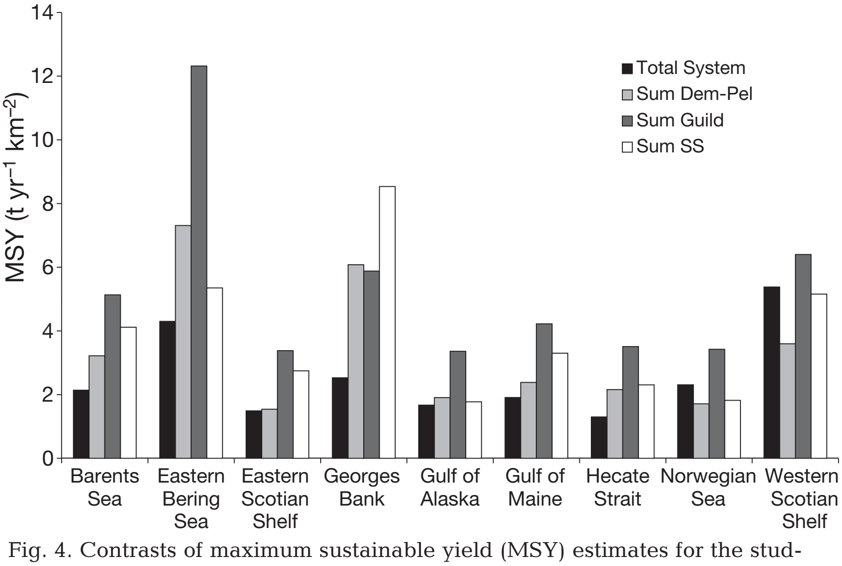

Fig. 4. Contrasts of maximum sustainable yield (MSY) estimates for the studied systems, summed functional guild aggregation, summed habitat aggregation (Dem: demersal; Pel: pelagic), and summed single species (SS) for several northern hemisphere ecosystems

We recognize that from an energetics perspective this is not surprising, as the more aggregated levels already account for species and technical interactions (Brown et al. 1976, May et al. 1979, Tyrrell et al. 2011). However, we assert that further empirical demonstration of the robustness of this pattern should reinforce to both managers and stakeholders that ecosystem-based approaches to management will inevitably involve addressing trade-offs (Link 2010). Moreover, this fundamental feature also represents a way to further augment and refine system-level BRPs for a specific ecosystem beyond the 1 to 5 t yr^{-1} km^{-2} rule of thumb noted above. Applying this approach would require consideration of the species mixes involved, such that managers are cognizant of the level of fishing those species and the system had already experienced, and of the need for any particular tradeoffs or compensation among species and aggregate groups. This would need to be done to ensure functional redundancies as well as affording specific stocks or aggregate groups adequate protection, particularly if the stocks were fished at low levels of abundance or productivity or otherwise warranted special consideration (Gaichas et al. 2012b). This inequality is one of the most consistent emergent features synthesized from these studies, as estimating total system-level yields is now demonstrated to be quite feasible, consistent with calls for EBFM. Continuing to estimate SS yields still has its place, but doing so without recognizing the system-level limitations and aggregated properties of a fished community is no longer defensible.

A final key finding from comparing the results of production models to other models in the Gulf of Maine is that production models can give similar results as more complex age-structured models (Fogarty et al. 2012, this TS). This suggests that applying the SPM approach to data-poor species or entire ecosystems with limited sampling resources can give reasonable advice for ecosystem-based fishery management.

SUMMARY

We reiterate the value of comparative studies (Murawski et al. 2010), as few marine ecosystems at these scales are amenable to experimental work, and even ecosystem modeling has its limitations, especially regarding the copious data required to validate a wide set of scenarios. We also note the value of simpler, integrative approaches, such as SPM. Keeping comparison platforms to approaches that are relatively simple and feasible and that leverage extant data are critical for conducting ecosystem comparisons. Here, the features that emerged from the contrasts and comparisons across the studied ecosystems shed insight into some common patterns and processes of marine ecosystems but would likely have not emerged from examination of those systems in isolation, via process-oriented studies or similar methods.

We note that all parts of the triad of drivers (environment, fisheries, and trophodynamics) (Fig. 1) can be important. Clearly, all have the potential to be important, and all operate to some degree in each system. Which drivers dominate under which conditions is still undetermined. Further work to elucidate a set of 'assembly rules' under which specific drivers are most prominent is warranted.

Several fundamental features emerge from this TS and related works. We particularly note the sigmoidal biomass accumulation curves across trophic levels, the improvement of model fits by inclusion of environmental or ecological covariates, the inequality of system MSY versus aggregated sums and SS sums of MSY, the 1 to 5 t yr^{-1} km^{-2} yield rule of thumb, and that tradeoffs among fishery-sector and protected-resources objectives may not be as harsh as was originally thought. Certainly, there may be other features that will emerge from future comparative ecosystem studies, and the ones noted here merit continued examination. Yet, we assert that these emergent features have the potential to alter our understanding of marine ecosystem dynamics and improve how we manage fisheries production therein. As practitioners continue to implement EBFM (Pitcher et al. 2009, Link 2010, Essington & Punt 2011), a robust data set of the features and properties of ecosystems and how they influence fisheries production shall be increasingly important. We trust that what we have synthesized here represents one step toward that goal.

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Ecosystems of Norway and the US (MENU I & II), and Norwegian-Canadian Collaborations (NORCAN). We also thank the anonymous reviewers who provided some excellent advice, resulting in an improved manuscript. Finally, we dedicate this work to the memory of Bern Megrey, who was an integral part of these efforts and whose untimely death was unfortunate but whose enthusiasm for this work was invaluable.

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