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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

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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 \cdot Surplus production \cdot Multispecies models \cdot Aggregate biomass estimates \cdot Environmental covariates \cdot Fisheries management \cdot Hierarchical analysis

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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

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

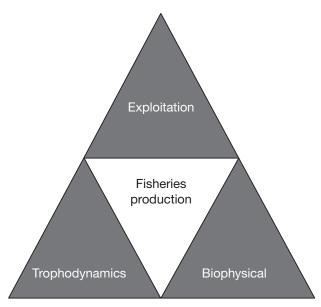


Fig. 1. The triad of drivers that can affect fisheries production

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.

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 densitydependent 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 agestructured 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 broadscale 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 | | NL | SGOSL | ESS | WSS | GOM | GB | North | BS | Norw |
|---------------------|-----|-----|----|----------------------------------|-----|-------|-----|-----|-----|-----|-------|-----|------|
| Pacific Ocean | | | | Atlantic/Arctic Ocean | | | | | | | | | |
| Alaska plaice | X | | | Aesop shrimp | X | | | | | | | | |
| Arrowtooth flounder | X | X | X | Alewife | | X | X | | | | | | |
| Curlfin sole | | | X | American lobster | | X | X | X | | | | | |
| Dover sole | | X | X | American plaice | X | X | X | | X | X | | | |
| Dusky rockfish | | X | | Atlantic argentine | | | X | | | | | | |
| English sole | | | X | Atlantic butterfish | | | | | | X | | | |
| Flathead sole | X | | X | Atlantic cod | X | X | X | X | X | X | X | X | |
| King crab | X | | 21 | Atlantic bagfish | 21 | 21 | X | 21 | 21 | 21 | 21 | 21 | |
| Lingcod | 71 | | X | Atlantic hagiish | X | X | X | | X | X | | | |
| Northern rock sole | X | | Λ | Atlantic herring | X | X | 71 | X | X | X | X | X | X |
| | Λ | v | | | Λ | Λ | | X | X | X | Λ | Λ | X |
| Northern rockfish | v | X | v | Atlantic mackerel | | 37 | 37 | | | | | | Λ |
| Pacific cod | X | X | X | Atlantic redfishes (NS) | 37 | X | X | X | X | X | | | |
| Pacific halibut | X | X | X | Atlantic wolffish | X | X | | | X | X | | | |
| Pacific herring | X | X | X | Beaked redfish | X | | | | | | | X | |
| Pacific ocean perch | | X | | Blue hake | X | | | | | | | | |
| Pacific salmon | | X | | Blue whiting | | | | | | | | | X |
| Pacific sanddab | | | X | Capelin | X | X | | | | | | X | |
| Petrale sole | | | X | Common sole | | | | | | | X | | |
| Quillback rockfish | | | X | Cusk | | | X | X | | | | | |
| Rex sole | | X | X | Eelpouts (NS) | X | | | | | | | | |
| Rougheye rockfish | | X | | European plaice | | | | | | | X | | |
| Sablefish | X | X | X | Fourspot flounder | | | | | X | | 2. | | |
| Sand sole | 71 | 71 | X | Golden redfish | | | | | 71 | | | X | |
| | | | X | Goosefish | | | X | X | X | X | | Λ | |
| Silvergray rockfish | | | | | | 37 | Λ | Λ | Λ | Λ | | | |
| Slender sole | | | X | Greenland cod | 3.7 | X | 3.7 | | | | | 3.7 | |
| Southern rock sole | | | X | Greenland halibut | X | X | X | | | | | X | |
| Spotted ratfish | | | X | Haddock | X | X | X | X | X | X | X | X | |
| Tanner crab | X | | | Jonah crab | | | X | | | | | | |
| Walleye pollock | X | X | X | Lesser sandeel | | | | | | | X | | |
| Yellowfin sole | X | X | | Longfin squid | | | | | X | X | | | |
| Yellowtail rockfish | | | X | Longhorn sculpin | | | X | X | | | | | |
| | | | | Lumpfish | X | | X | | | | | | |
| | | | | Northern prawn | X | | | | | | | | |
| | | | | Norway pout | | | | | | | X | | |
| | | | | Ocean pout | | | X | | X | X | 21 | | |
| | | | | Pandalid shrimps (NS) | | | X | | Λ | Λ | | X | |
| | | | | Pollock | | | X | X | X | X | X | X | |
| | | | | | | 37 | Λ | Λ | Λ | Λ | Λ | Λ | |
| | | | | Rainbow smelt | | X | 3.7 | 3.7 | 3.7 | 3.7 | | | |
| | | | | 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 | 71 | | X | X | | | |
| | | | | Silver hake | | 71 | X | X | X | X | | | |
| | | | | | | | Λ | Λ | Λ | | | | |
| | | | | Smooth dogfish | 3.7 | | | | | 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 | | | |
| | | | | Witch hounder Wolffishes (NS) | 71 | 11 | X | X | 71 | 21 | | | |
| | | | | Yellowtail flounder | X | X | X | 71 | X | X | | | |
| | | | | renowian nounder | Λ | Λ | Λ | | Λ | Λ | | | |
| Both oceans | | | | Both oceans | | | | | | | | | |
| Butter sole | | | X | Butter sole | | | | | | | | X | |
| Skates (NS) | | | X | Skates (NS) | | | X | X | X | X | | 21 | |
| Snow crab | X | | 11 | Snow crab | X | X | X | Λ | Λ | Δ1 | | | |
| | Λ | | X | Spiny dogfish | Λ | Λ | X | X | X | X | | | |
| Spiny dogfish | | | | | | | | | | | | | |

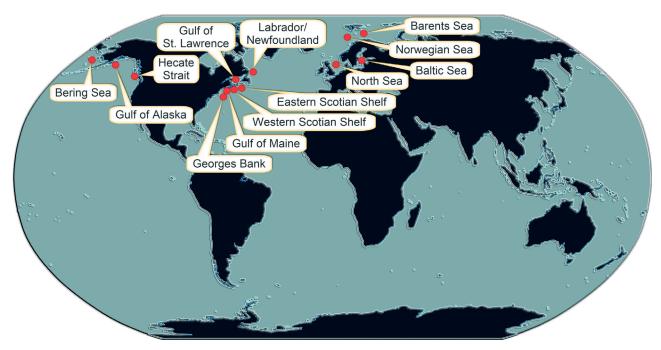


Fig. 2. Locations of the ecosystems included in the present comparative analyses

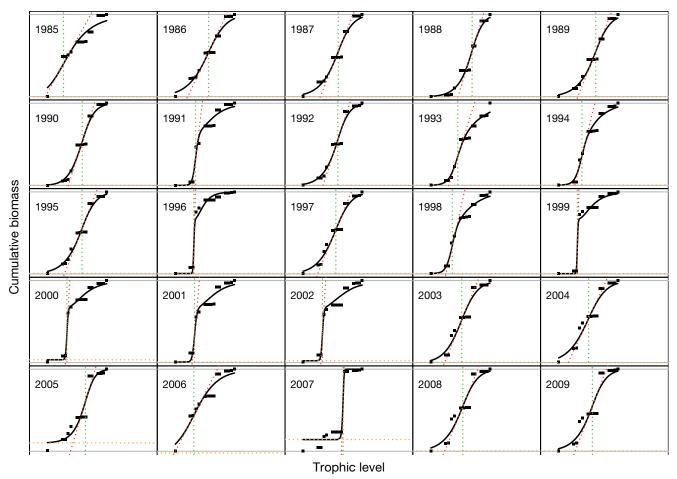


Fig. 3. Example of changes to the biomass accumulation curves across trophic levels over time for the Gulf of St. Lawrence ecosystem (adapted from Pranovi et al. 2012). Vertical dotted (green) line: trophic level intercept, or inflection point; horizontal dotted (orange) line: biomass intercept or starting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

 $\Sigma SS_{MSY} > Ecosystem_{MSY}$

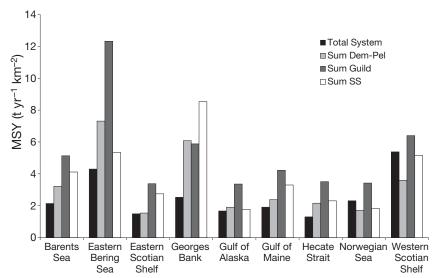


Fig. 4. Contrasts of maximum sustainable yield (MSY) estimates for the studied systems, summed functional guild aggregation, summed habitat aggregation (Dem: demersal; Pel: pelagic), and summed single species (SS) for several northern hemisphere ecosystems

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 systemlevel 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 rela-

tively 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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