Fishery production potential of large marine ecosystems: A prototype analysis ☆

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Summary and key messages

- Satellite-based estimates of primary productivity by size classes, and a more complete food web relative to earlier approaches, were used to estimate marine ecosystem productivity. Including microbial, benthic, and microplankton components of production resulted in an overall fishery production potential of 140–180 million metric tonnes and an additional 30–50 million metric tonnes of benthos.
- Increased exploitation of components of this production such as mesopelagic fishes or benthic organisms may have serious ecosystem wide negative consequences and other problems. Accordingly, a full risk analysis will be necessary before considering increased exploitation of these ecosystem components.
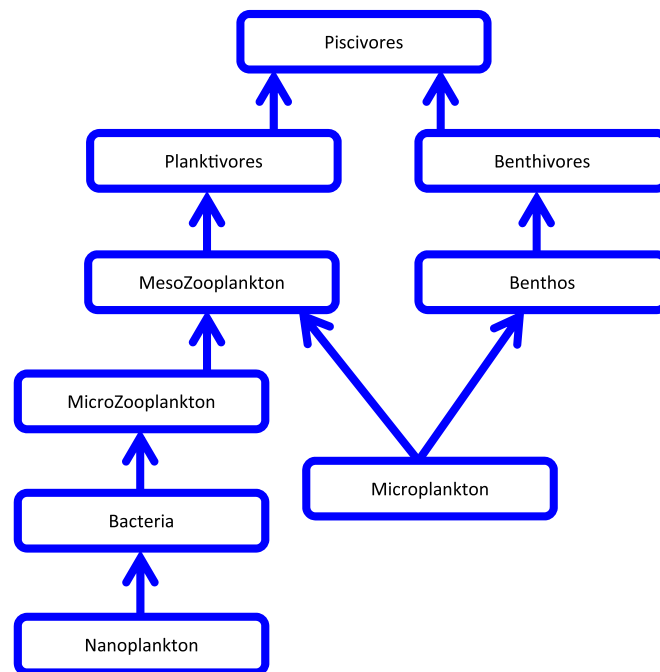
- The fishery production potential estimates can be used in concert with observed catch data to estimate ecosystem exploitation rates for major ecosystem components including benthos, benthivores, planktivores, and piscivores.

1. Introduction

Attempts to define the fishery production potential of marine systems based on energetic considerations have an extensive history (Kestevan and Holt, 1955; Graham and Edwards, 1962; Schaefer, 1965; Moiseev, 1969; Ricker, 1969; Ryther, 1969; Gulland, 1970, 1971; Moiseev, 1994). Bottom-up control of fish production has now been demonstrated in many regions of the world ocean (Ware, 2000) supporting the general approach of tracing pathways involved in the translation of primary production to fishery yields. Our ability to estimate primary production was revolutionized by Steeman-Nielsen's (1951) development and application of the ^{14}C method, paving the way for elaboration of simple models of energy flow from the base of the food web through fish production.

Earlier estimates of fishery production potential based on energetic principles were based on estimates of primary production over all phytoplankton size classes, inferred ecological transfer efficiencies from laboratory experiments and other observations, and observed or assumed levels of the mean trophic level of the catch. The general strategy was laid out by Kestevan and Holt (1955). Graham and Edwards (1962) provided an estimate of potential global fish yield of 115 kkt (10^6 mt) for bony (teleost) fishes supporting 'conventional' fisheries using this method. In contrast, their estimate of potential yield based on extrapolations of catch histories in space and time was less than half this value at 55 kkt. Schaefer (1965), applying somewhat higher estimates of transfer efficiencies, estimated the potential yield to be on the order of 200 kkt. Ricker (1969) followed with a projection of approximately 150 kkt. In a widely cited evaluation, Ryther (1969) estimated the world fish production potential to be on the order of 100 kkt, and was the first to apply a partitioning of fishery production potential among different oceanic domains including coastal, offshore, upwelling, and open ocean systems. Ryther (1969) further applied different estimates of food chain length in these different system types to reflect fundamental differences in ecosystem structure and patterns of energy flow. An overall reliance on key elements of the analysis such as transfer efficiencies and mean trophic level of the catch, characterized by high levels of uncertainty in food-web based analyses, led Pauly (1996) to infer that the concordance of Ryther's estimates (1969) with current observations may largely reflect countervailing errors, that is, the answers may be 'right' for the wrong reasons (Pauly, 1996).

Here we describe elements of a prototype fishery production analysis for large marine ecosystems around the world, developed as part of a study commissioned by the Fisheries and Aquaculture Department of the FAO. This project – Developing New Approaches to Global Stock Status Assessment and Fishery Production Potential of the Seas – was designed to explore new approaches to (1) determining single-stock status with particular reference to assessments in data-limited

Fig. 1. Food web structure employed in this analysis. Nano-pico plankton, bacteria, and microzooplankton comprise the microbial food web in this representation. The classical grazing food web is fuelled by microphytoplankton production. Species characterized by ontogenetic shifts in diet and/or mixed feeding strategies can occupy multiple compartments in this representation.
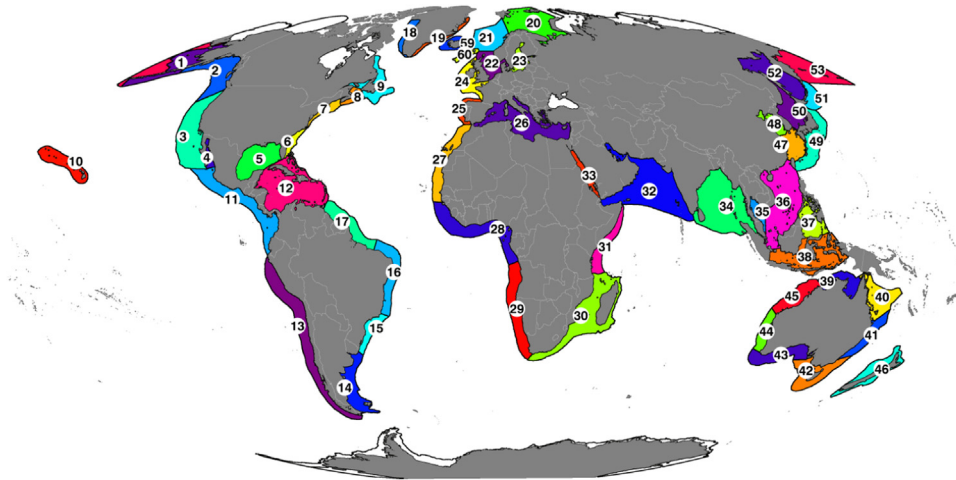
Fig. 2. Strata used in estimating global fishery production potential based on LME boundaries (individual LMEs designated by colour; LME numbers in circles).

situations, and (2) developing estimates of ecosystem-level production potential. To meet the second objective, we developed a prototype model of energy flow in fishery systems that expands the basic food chain models underlying earlier fishery production potential models to a simple food web architecture.

2. Methods and data sources

Ecosystem network models have now been applied for all the LMEs considered in this report using the well-known Ecopath with Ecosim (EwE; Christensen et al., 2008, 2009) formulation based on the original developments by Polovina (1984) and Christensen and Pauly (1992). Here, we seek to complement these analyses using a simple characterization of fishery production systems. Our approach entails projections of available production at different trophic levels given information on estimates of primary production. This method is therefore in keeping with the earlier analyses noted above (Graham and Edwards, 1962; Schaefer, 1965; Ricker, 1969; Ryther, 1969). We have expanded the implicit food chain approach in these analyses to a very simple but broadly applicable food web model. We have specified removals from discrete ecosystem components (including benthos, planktivores, benthivores, and piscivores) to more fully characterize fishery dynamics directed at different functional groups, often by different fleet sectors. However, we have ignored potential production coming from detrital or demersal primary production, as it was not possible to obtain global estimates of these. Nor have we explicitly accounted for recycling in our estimates of production. We acknowledge that in systems where these elements collectively are a significant proportion of the primary basal resources, our estimates will be conservative.

In our analysis, we recognize two pathways for transfer of primary production in the system: the classical grazing food web tracing the fate of production of microplankton (phytoplankton cells > 20 μm: principally diatoms and large dinoflagellates), and production involving transfer through the microbial food web originating with combined nanoplankton (2–20 μm) and picoplankton (< 2 μm) production (nano-picoplankton; Fig. 1). The former involves grazing by mesozooplankton and filtering of diatom production by benthic invertebrates, particularly bivalves. The latter pathway entails consumption of nano-picoplankton by heterotrophic bacteria and feeding of microzooplankton on bacteria. In this representation, carnivorous zooplankton (mesozooplankton) prey on microzooplankton. The microbial pathway therefore involves two or more trophic transfer steps before reaching mesozooplankton as a bridge to higher trophic levels. We note that the functional groups represented in the upper food web depicted in Fig. 1 do not strictly correspond to taxonomic groups. Individual taxa may feed at multiple trophic levels, reflecting both ontogenetic shifts in diet and generalist feeding strategies with life stages.
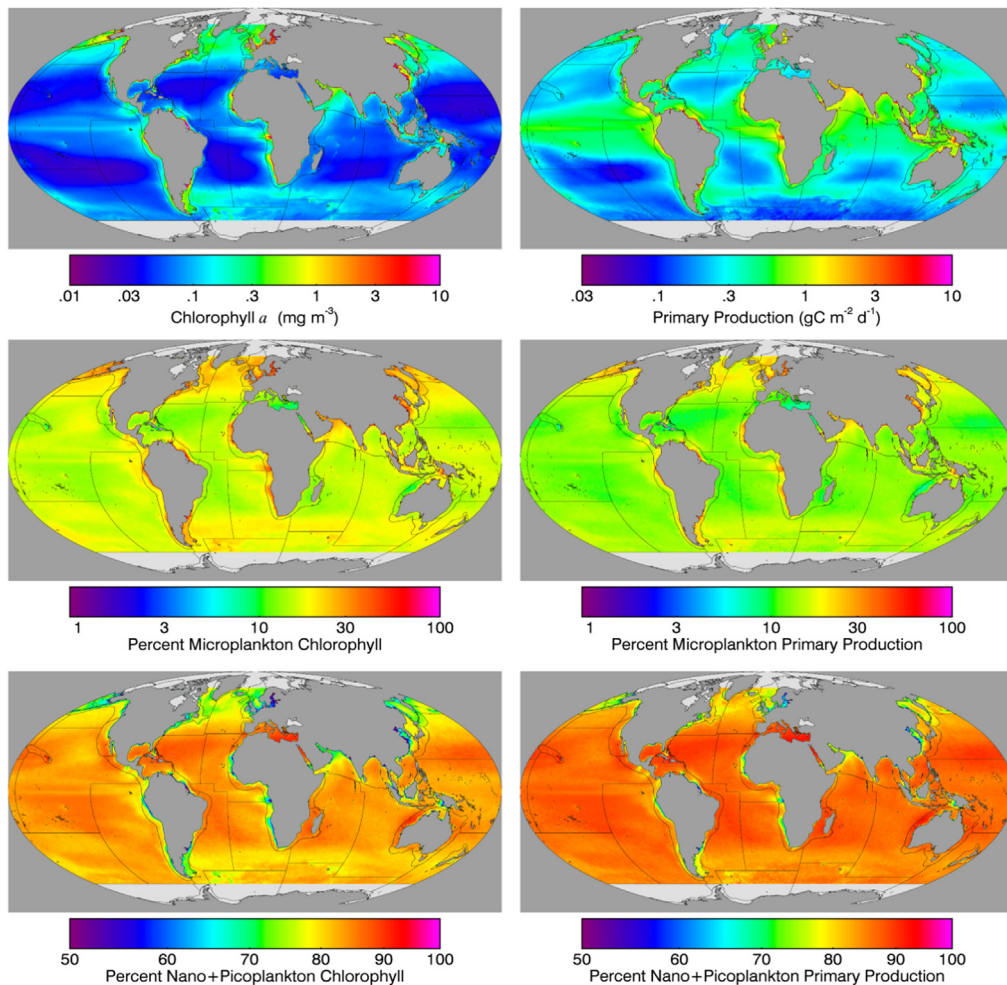
For this analysis we used designated LMEs as strata (Fig. 2). LMEs are differentiated by similar physical and ecological features, such as hydrography, productivity, and tropically dependent populations (Sherman and Alexander, 1986; Sherman, 1991), accounting for approximately 80–90 per cent of the global fisheries catch (Christensen et al., 2008). To account for some of the near shore versus offshore variability in production within some regions, each LME was subdivided using the 300 m isobath. The < 300 m subareas included the characteristically more productive continental shelf areas and the near shore areas of the upwelling regions. In general, the > 300 m subareas were characterized by lower overall levels of production by microphytoplankton. Inland seas and high latitude regions, including Hudson Bay, Black Sea, Arctic Ocean, Kara Sea, Laptev Sea, East Siberian Sea, Beaufort Sea, Chukchi Sea, and Antarctica, were not included in this analysis due to the seasonal effects of cloud cover and high solar zenith angles on estimates derived from satellite coverage in these regions.

2.1. Primary production

Ocean colour remote sensors provide an unprecedented view of the global ocean and are the only means to obtain basin-scale, synoptic high frequency measurements of global primary production. Annual estimates of primary production were calculated using data from the Sea-viewing Wide Field-of-View Sensor (SeaWiFS, NASA) and a modified version of the Vertically Generalized Productivity Model (VGPM; Behrenfeld and Falkowski, 1997). This modified VGPM model replaces the original temperature-dependent description of photosynthetic efficiencies with the exponential Eppley function (Eppley, 1972), which was modified by Morel (1991). The modified VGPM model allows a more mechanistic representation of the production dynamics.

We computed monthly chlorophyll concentration and primary production on a pixel by pixel (9 km × 9 km) basis and summed over all pixels within an LME to generate estimates of the total for each region. Our approach differs from previous analyses of fishery production potential in treating the satellite-derived data as a census rather than a sample in which mean productivity was applied over selected coastal and ocean areas. This approach preserves the spatial variability in phytoplankton production dynamics within an LME.

To estimate the proportion of primary production attributed to the microplankton component, we first estimated the microplankton total chlorophyll a (biomass) fraction and then used an empirical relationship to calculate per cent of microplankton production. Recent advances in ocean colour remote sensing have led to the development of several phytoplankton size classes (PSC) and phytoplankton functional type (PFT) models. However, most of these models are not recommended for use in continental shelf waters (i.e. < 200 m). Because of the importance of the continental shelf regions to global fisheries, we used a regional model by Pan et al. (2011), who developed a chemotaxonomic method to measure PFTs on the Northeast US Continental Shelf LME (NES LME) using satellite-derived phytoplankton pigment measurements (Pan et al., 2010). The diatom and dinoflagellate biomasses were combined to represent the microplankton fraction, and the

Fig. 3. Distribution patterns for total chlorophyll a (mg m^{-3}) and primary production (g C m^{-2} d^{-1}) (upper); per cent microplankton chlorophyll a and primary production (middle); and per cent nano-picoplankton chlorophyll a and primary production (lower).

remaining functional groups were combined in the nano-picoplankton group (Vidussi et al., 2001).

2.2. Transfer efficiencies

To objectively assess trophic transfer efficiencies throughout our generic food web, we evaluated estimates of transfer efficiencies derived from 240 published Ecopath with Ecosim (EwE) models. Rather than assume or assign trophic transfer efficiencies at different steps in the food web for the models for each LME, we used these model estimates to define probability distributions characterizing transfer probabilities at different steps in the food web. Our characterization of transfer efficiencies between discrete trophic levels based on these Ecopath models followed the approach of Ulanowicz (1993).
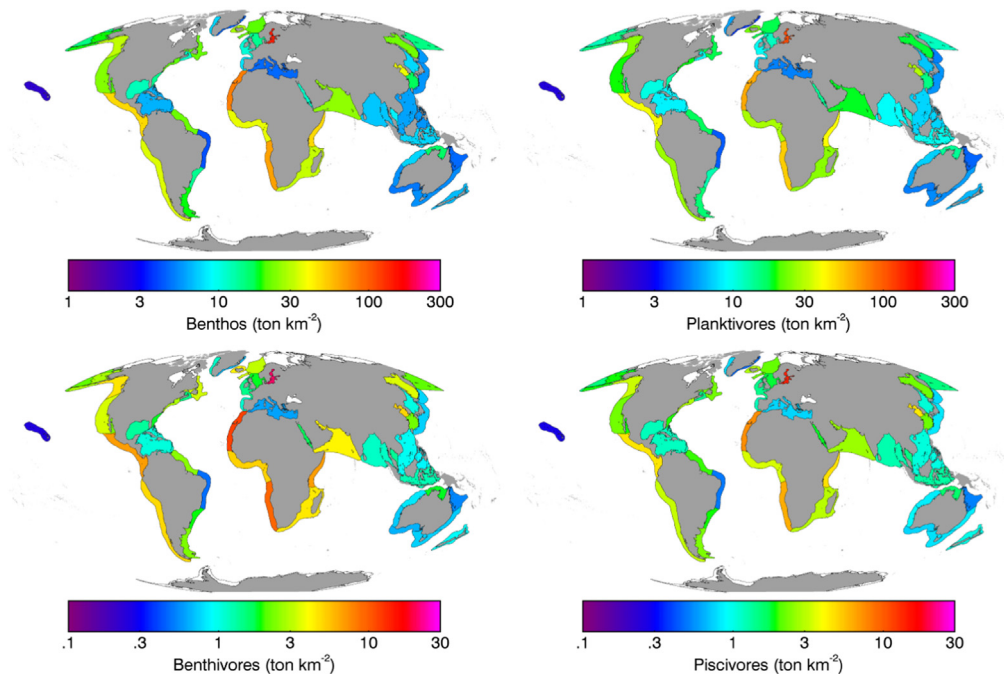
2.3. Ecosystem reference points

As noted earlier, the estimates of fishery production potential described above typically assumed that 50–70 per cent of production at a defined mean trophic level could be extracted as catch (e.g. Graham and Edwards, 1962; Ryther, 1969; Schaefer, 1965; Ricker, 1969; but see Moiseev (1994)). These proposed extraction rates were predicated on prevailing single-species recommendations based on the (implicit) assumption that fishing mortality rates could equal natural mortality for the stock (Pauly and Christensen, 1995). It is now recognized that these earlier target levels for single-species management were too high and led to risk-prone decisions (Pauly and Christensen, 1995). Standard reference points have not been fully established to guide overall extraction policies for marine ecosystems. Iverson (1990) proposed that exploitation rates should not exceed the *f*-ratio (the ratio of new primary production to total primary production) in marine systems. This suggestion is based on the underlying recognition that new production (primarily by larger phytoplankton species) is more readily available to fuel production at the higher trophic levels of principal economic interest while the production derived from the nano-picoplankton is largely, but not exclusively, consumed within the microbial food web. Although direct estimates of the *f*-ratio are not broadly available for large marine ecosystems throughout the world ocean, we can consider the ratio of microplankton production to total primary production as a limit reference point not to be exceeded.

3. Results

3.1. Primary production

Chlorophyll concentration and primary production are highest in coastal locations characterized by important inputs of

Fig. 4. Estimated production levels (t km^{-2}) in the absence of exploitation by functional group for LMEs represented in this study. Note change to logarithmic scale for the benthivore and piscivore functional groups.

nutrients from land and strong mixing processes driven by winds and tides (Fig. 3). High chlorophyll and production levels are concentrated in upwelling regions. Overall primary production is dominated by nano-picoplankton production, especially in the deeper coastal locations and the ocean basins. Within the 300 m isobath, microplankton production accounted for 25.1 per cent of the total production on average. For deeper water components (> 300 m) within individual LMEs, microplankton production accounted for 20.1 per cent of the total production. As expected, the microplankton contribution to production was smallest (14.2 per cent) in the open ocean regions outside LME boundaries.

3.2. Production by functional group

Production estimates for the major functional groups of potential or realized importance to harvesting are provided in Fig. 4 by LME. Individual species can be represented in more than one trophic level compartment, reflecting both ontogenetic shifts in diet and mixed or omnivorous feeding strategies. Characteristically high production levels for these groups are found in the dominant upwelling regions of the world ocean and in regions where at least seasonal upwelling patterns are important (e.g. the Arabian Sea). Western boundary current regions are characterized by moderately high production levels (e.g. Oyashio and Kuroshio Current systems, Northwest Atlantic LMEs, and Agulhas Current region). Intermittent and localized upwelling patterns in these regions, coupled with high nutrient concentrations in several of these systems, contribute to relatively high production levels.

3.3. Fishery production potential

Estimates of fishery production potential depend on the available production at different trophic levels, the proportion of the production comprising species suitable for harvest (including considerations of species composition, marketability, and economic efficiency of harvesting operations), and the determination of sustainable exploitation levels. We have provided estimates of the overall available production by ecotype and functional group for potentially harvestable components of the LMEs considered in this report. In the following, we apply the proposed limiting exploitation level set by the fraction of microplankton production.

Under this set of assumptions, we estimate an overall potential yield of approximately 140-180 million tonnes for the benthivore, planktivore, and piscivore functional groups for the LMEs considered here and approximately 30–50 million tonnes of benthic organisms depending on the assumed percentage of the benthic production is suitable for harvest. Although this level of benthic fishery yield may not be fully attainable by capture fisheries under current market preferences and economic conditions, we note that the energetic pathways supporting natural benthic production could also potentially support enhanced mariculture production for molluscs in particular. Aquaculture production has been rapidly increasing (FAO, 2012). Although freshwater aquaculture remains dominant, important increases in mariculture are possible but would of course require adequate environmental controls.

4. Discussion

Understanding the prospects for sustainable production potential from the seas assumes particular importance given the likely demands for animal protein to meet the needs of a burgeoning human population. Currently, 3 billion people obtain nearly 20 per cent of their dietary animal protein needs from aquatic sources, and 4.3 billion obtain approximately 15 per cent of these requirements from fishery and aquaculture products (FAO, 2012). Global per capita consumption of aquatic food products has increased steadily in recent years (FAO, 2012), but sharp regional differences in availability and utilization between developed and developing countries signal an important issue in global food security. Here, updated earlier estimates of global fishery production potential from marine capture fisheries are provided to place the prospects for meeting human protein and essential micronutrients in context.

We have developed and provided a first application of a new approach to estimating fishery production potential. The earlier fishery production potential analyses (e.g. Graham and Edwards (1962), Schaefer (1965), Ryther (1969), Ricker (1969) and Gulland (1970,1971)) relied on a combination of methods including temporal and spatial extrapolations of catch trends and simple food chain models. The latter entailed consideration of overall phytoplankton primary production, ecological transfer efficiencies (typically a single value applied to all trophic levels), and the designation of a single mean trophic level at which catch is extracted. Our approach broadens the consideration of energetic pathways through the classical grazing and microbial food webs. We allow for differential ecological transfer efficiencies for different trophic levels and for extraction of catches at multiple levels in the food web. We attempt to strike a balance between these simple earlier models and more complex ecological network models that often require specification of parameter estimates for a large number of nodes representing different species or species groups. The model involves a projection through this simplified food web starting with phytoplankton production. Therefore, it explicitly considers bottom-up forcing of the food web to be the dominant factor in production dynamics of these systems. We recognize that the interplay between bottom-up and top-down controls can be important in many food webs.

Ryther (1969) was the first to partition ocean provinces into fishery production domains in his analysis of simple food chain models. The approach adopted here expands this approach using Large Marine Ecosystems as strata (see also

Christensen et al. (2008, 2009)). Pauly (1996) suggested that drawing on multiple methods of estimation and spatial domains can help provide more robust overall determinations of fishery production potential. In the absence of other information, we have assumed that the inputs and outflows of energy and organisms within each LME are in balance. We implicitly assume that the overall analysis captures these dynamics when we integrate over LMEs to generate estimates over broader geographical scales.

The determination of a harvest reference level is critical in estimating fishery production potential. We have proposed linking the ecosystem harvest rate to the fraction of microplankton production in the system. This provides estimates centred about 20 per cent. Moiseev (1994) suggested that exploitation rates not exceed 20–25 per cent although the exact rationale for this level was not specified. However, Moiseev's recommendation is broadly consonant with the microplankton production reference level for the LMEs considered in this report. Direct consideration of the energetic requirements of other ecosystem components must also be made. Cury et al. (2011) noted that when pelagic prey items of seabirds was reduced to below one third of their presumed maximum levels, fledging success was significantly impaired. In a consideration of forage fish management to meet the needs of a broad suite of predators including mammals and seabirds, Pikitch et al. (2012) recommended that precautionary exploitation rates should be established that halve the values assigned under conventional single species management. Simulations which considered a 25 per cent harvest rate resulted in increased overall economic returns and reduced impact on upper trophic level predators (Pikitch et al., 2012). Christensen (1996) had earlier noted that estimates of the consumption of groundfish often are higher by a factor of three relative to catches. The early estimates of fishery production potential implicitly or explicitly were based on an assumption that the fishing mortality rate and natural mortality rate of the harvested species were equal at the recommended reference point, implying that half the production could be taken as yield. The observations on the actual consumption by natural predators make clear that the harvest rate should be substantially lower. Collectively, these independent recommendations and observations suggest that exploitation rates generally not exceed 25 per cent of available production and are consonant with our recommendation for a reference point.

Our first-order estimates of fishery production potential based on this new approach suggest a potential yield of approximately 140–180 kkt for planktonic and nektonic organisms within the LMEs considered here. Our estimates of the fishery production potential for benthic organisms are approximately 30–50 kkt depending on the assumed percentage of the benthic production that is suitable for harvest. Perhaps a more likely scenario for benthic production would entail a combination of expanded capture fisheries and some form of sustainable mariculture, principally for molluscs. If these potential yields are to be realized, an overall diversification of the complex of harvested species will have to be attained and a reduction of exploitation rates on overfished species accomplished. Although our analysis is motivated by consideration of food security in the 21st century, any consideration of expansion in harvest levels to 'latent' resources would require careful consideration of all ecological risks that might be incurred. It is clear that the greatest prospect for potential increase in fish yield is for planktivorous species. If this expansion is to occur, it must be undertaken with consideration of the forage needs for other species in the system. It must be further recognized that many of the species that can potentially support such an increase (for example, mesopelagic fish) will be processed for fish meal and oils and not used for direct human consumption. They can contribute to an expansion of mariculture for upper trophic level species and as food supplies for farmed animals.

Moiseev (1994) estimated global fishery production potential of 120–150 kkt for conventionally harvested species and an additional 60–80 kkt for lower trophic level species including krill, deep sea squids, and mesopelagic species. Moiseev (1994) departed from previous estimates of potential yield in recommending that ecosystem exploitation rates not exceed 20–25 per cent.

Significant advances in satellite oceanography are being made that will improve our estimates of size-fractionated chlorophyll concentrations. Attempts to correct for potential biases in chlorophyll concentration in near shore waters due to particulate matter other than phytoplankton in the surface layer are under constant development resulting in improved estimates. Further, we have used a coarse partitioning of phytoplankton community structure. While allowing us to make an important distinction among energetic pathways through microbial food web and the classical 'grazing' good web, we note that much more highly resolved phytoplankton community structures have been employed in other size-based models (e.g. Jennings et al. (2008) and Boyce et al. (2015)). Our estimates of trophic transfer efficiency and energetic pathways through the benthos and mesozooplankton can be re-evaluated with examination of additional food webs constructed for marine systems. A critically important need is to refine the estimation of the harvestable component of the benthic and planktivore compartments of the food web. In this prototype analysis, we deliberately employed a highly simplified food web structure to minimize data requirements and associated assumptions. Explorations of the scope for refinement in the microbial food web and benthic compartments in particular, however, could provide important benefits in model realism with relatively low cost in terms of additional complexity.

Many of the data and model inputs used here are drawn from analyses conducted over the last two to three decades. Accordingly, our baseline for attempting to estimate fishery production potential largely reflects contemporaneous conditions and the current state of the world ocean. We note however, that large-scale changes due to fishing and other stressors in continental shelf ecosystems over the last century or more have been documented (e.g. Jackson et al. (2001), Roberts (2010), Tremblay-Boyer et al. (2011), and Christensen et al. (2015)). These changes hold important implications for energetics, system carrying capacity, and productivity and our perceptions of production potential. The risk of succumbing to the shifting baseline syndrome is clearly evident here.

Acknowledgements

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Acronyms and glossary of terms

14C: method
kkt: 10^6mt
mt: 1000 kg

FAO: Food and Agriculture Organization of the United Nations
EwE: Ecopath with Ecosim
microplankton: phytoplankton cells $> 20\ \mu m$: principally diatoms and large dinoflagellates
nanoplankton: plankton cells 2–$20\ \mu m$
picoplankton: plankton cells $< 20\ \mu m$
nano-picoplankton: combined nanoplankton and picoplankton production
f-ratio: the ratio of new primary production to total primary production isobaths