

Primary productivity demands of global fishing fleets

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Abstract

To be sustainable, the extractive process of fishing requires biomass renewal via primary production driven by solar energy. Primary production required (PPR) estimates how much primary production is needed to replace the biomass of fisheries landings removed from marine ecosystems. Here, we examine the historical fishing behaviour of global fishing fleets, which parts of the food web they rely on, which ecosystems they fish and how intensively. Highly mobile European and Asian fleets have moved to ever more distant productive waters since the 1970s, especially once they are faced with the costs of access agreements for exclusive economic zones (EEZs) declared by host countries. We examine fleet PPR demands in the context of large marine ecosystems (LMEs), which are frequently fished with PPR demands well above their average primary productivity (PP). In some cases, this was mitigated by subsequent emigration of fleets or by management intervention. Fleet movements, however, have stressed additional marine areas, including the EEZs of developing countries. This suggests the potential for spatial serial depletion, if fishing capacity is not reduced to more sustainable PP removal levels. Fundamentally, fishing is limited by solar-powered PP limits. Fishing beyond solar production has occurred, but in the future, marine systems may not be as forgiving, especially if overfishing and climate change compromise their resilience.

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Introduction

Solar radiation and available nutrients control, and ultimately limit, primary productivity in the world's oceans (Chassot *et al.* 2010). The production of marine fishes (which include marine invertebrates) is limited and influenced by various factors, but primary production is arguably the most important and most fundamental (Pauly and Christensen 1995). Likely, upper limits for sustainable marine fisheries catches which range from 100 to 140 million tonnes per year have been estimated using a variety of methods (e.g. Granger and Garcia 1996; Pauly 1996; Chassot *et al.* 2010). For many years now, total reported global landings have stagnated around 80 million tonnes per year (Watson and Pauly 2001), with perhaps another 20 million tonnes of additional illegal catch (Agnew *et al.* 2009). There is, however, evidence that global landings have not been capped by conservative management (Mora *et al.* 2009; Alder *et al.* 2010), because fishing capacity expressed by the cumulative power of fishing vessels has continued to increase (Anticamara *et al.* 2011; Watson *et al.* 2012). Moreover, if fishing capacity is adjusted for known increases in efficiency (Pauly and Palomares 2010), catches taken per unit of fishing effort have actually declined (Watson *et al.* 2012). This suggests that, in general, global sustainable harvest limits have already been exceeded.

The expansion of global fishing fleets, driven by declining catches in inshore waters, aided by improved technology and supported by subsidies (Sumaila *et al.* 2010a,b), resulted in few resources that are now unfished (Swartz *et al.* 2010a; Watson *et al.* 2012), and fisheries now harvest even vulnerable slow-growing populations at great depths (Pauly *et al.* 2003; Morato *et al.* 2006; Pitcher *et al.* 2010; Norse *et al.* 2011). Invertebrate fisheries, in particular, have expanded with relatively little scrutiny in many parts of the world's oceans (Anderson *et al.* 2011). The expansion of fisheries has been accompanied by a general decline in biomass on a grand scale (Christensen *et al.* 2003), and distant water fleets account for a large proportion of global fisheries landings (Bonfil *et al.* 1998; Pauly *et al.* 2012). European and other fleets from developed countries now rely on resources from the developing world, such as West and East Africa (Alder and Sumaila 2004; Atta-Mills *et al.* 2004; Swartz *et al.*

2010b; Le Manach *et al.* 2012), increasingly obtained via inequitable access agreements (Kaczynski and Fluharty 2002; Le Manach *et al.* 2013). With the development of mapped global catch databases (Watson *et al.* 2004, 2005), it is now possible to track, via primary production required (PPR), how much primary productivity is captured by global fisheries through time on fine spatial scales. Thus, Swartz *et al.* (2010a) showed how the PPR levels increased and high PPR demands spread globally. They did not, however, explore how various global fleets contributed to these changes, and whether differences in the species targeted explained changes in their PPR demands, and their map of primary production (PP) was limited to only a single year. Some marine systems are more resilient and differ in both their average primary production levels, but also in how much net production is imported from other areas. Here, we address the PPR demands of fleets on individual large marine ecosystem (LME, Sherman and Duda 1999; Sherman *et al.* 2005) areas, and a PP map based on over 10 years of satellite observations. This analysis can assist policy makers and fisheries scientists to understand the dynamics of the highly mobile global fishing fleets and their demands on innate, and often limited, marine ecosystem productivity.

Methods

Primary production

Primary production estimates were derived using the model described by Platt and Sathyendranath (1998), which computes depth-integrated primary production from chlorophyll pigment concentration based on satellite data (SeaWiFS, <http://seawifs.gsfc.nasa.gov/> accessed 31 Oct 2012) and photosynthetically active radiation as calculated in Bouvet *et al.* (2002). The primary production estimates we used were processed at the Inland and Marine Waters Unit (IMW), Institute for Environment and Sustainability, EU Joint Research Center (JRC), Ispra, Italy <http://gmis.jrc.ec.europa.eu/> (accessed 31 Oct 2012), under the responsibility of Nicolas Hoepffner (nicolas.hoepffner@jrc.it) and Frédéric Mélin (fredreric.melin@jrc.it) and made available on a monthly basis from October 1997 with a spatial resolution of 9 km. The primary production estimates presented here pertain to an average value for the period 1998–2007 inclusive,

which, for the purpose of our analysis, was assumed to be representative of the entire period (1950–2006).

Large marine ecosystem areas

Large marine ecosystem (LMEs) refer to 66 marine ecosystems with unique sets of ecological, oceanographic and biogeochemical characteristics (Sherman and Duda 1999; Watson *et al.* 2003). They were ecologically defined to serve as a framework for the assessment and management of transnational coastal fisheries and environments, including LMEs (Pauly *et al.* 2008). The LMEs are identified in Table 1 and presented at <http://www.lme.noaa.gov/>. The coefficient of interannual variation (CV) in primary production estimates for each LME area from satellite data (1998–2007 inclusive) is included.

Catch data

Annual catch data were taken from the spatially disaggregated global catch database of the *Sea Around Us* project (Watson *et al.* 2004). This online database (www.seaaroundus.org) is derived mainly from corrected Food and Agriculture Organization of the United Nation’s (FAO) global fisheries landings statistics (www.fao.org/fishery/statistics/en), complemented by the statistics of various international and national agencies, and some reconstructed data sets (Zeller and Pauly 2007). These statistics, after harmonization, are disaggregated into a spatial grid system that breaks down the world’s ocean into 180 000 cells (0.5° latitude by 0.5° longitude) based on the geographical distribution of over 1500 commercially exploited fish and invertebrate taxa and using ancillary data such as the fishing agreements regulating foreign access to the exclusive economic zones (EEZs) of maritime countries.

Catch sourced here is defined as reported landings. Catch data were adjusted to account for illegal and unreported catch (IU) on the global estimates (Agnew *et al.* 2009), but this did not include adjustments for discarding. Agnew *et al.* (2009) provided 5-year average estimates of IU catches (for 1980–2003) reported for most FAO statistical reporting areas. We assigned the average global IU catch value to fish groups not included in their publication. For periods prior to 1980, we assigned the 1980–1984 average value.

Table 1 Large marine ecosystem (LME) areas and the coefficient of interannual variation (CV) in primary production estimates from satellite data (1998–2007 inclusive). See also www.seaaroundus.org/lme/.

LME	CV	LME	CV
Agulhas Current	3.2	Indonesian Sea	4.0
Antarctic	12.8	Insular Pacific-Hawaiian	3.1
Arabian Sea	5.3	Kara Sea	14.1
Arctic	22.2	Kuroshio Current	4.4
Artic Archipelago	14.9	Laptev Sea	21.0
Baffin Bay/ Davis Strait	7.8	Mediterranean Sea	1.8
Baltic Sea	6.9	New Zealand Shelf	3.7
Barents Sea	9.5	Newfoundland-Labrador Shelf	1.9
Bay of Bengal	2.9	North Brazil Shelf	5.0
Beaufort Sea	24.2	North Sea	3.7
Benguela Current	1.7	Northeast Australian Shelf	1.6
Black Sea	7.1	Northeast U.S. Continental Shelf	3.3
California Current	5.2	Northern Australian Shelf	3.1
Canary Current	4.6	Northwest Australian Shelf	3.8
Caribbean Sea	1.7	Norwegian Shelf	2.7
Celtic-Biscay Shelf	2.5	Oyashio Current	4.4
Chukchi Sea	19.4	Pacific Central American Coast	9.2
East Bering Sea	4.2	Patagonian Shelf	4.2
East Brazil Shelf	3.0	Red Sea	4.9
East Central Australian Shelf	4.4	Scotian Shelf	2.2
East China Sea	1.6	Sea of Japan	2.6
East Greenland Shelf	6.9	Sea of Okhotsk	3.7
East Siberian Sea	25.9	Somali Coastal Current	9.5
Faroe Plateau	12.8	South Brazil Shelf	6.0
Guinea Current	4.1	South China Sea	2.9
Gulf of Alaska	3.7	Southeast Australian Shelf	3.2
Gulf of California	8.1	Southeast U.S. Continental Shelf	10.9
Gulf of Mexico	4.8	Southwest Australian Shelf	3.1
Gulf of Thailand	3.1	Sulu/Celebes Seas	4.6
Hudson Bay	6.3	West Bering Sea	6.7
Humboldt Current	6.1	West Central Australian Shelf	3.6
Iberian Coastal	3.9	West Greenland Shelf	8.8
Iceland Shelf	7.8	Yellow Sea	3.6

Agnew *et al.* (2009) reported a general decline in these illegal catch categories in recent years, as did Zeller and Pauly (2005) for discard-adjusted global landings. However, we treated this period more conservatively by assigning the 2000–2003 average values of illegal catch (the end of reporting in Agnew *et al.* 2009) to the 2004–2006 time period considered here. As Agnew *et al.* (2009) also showed that IU catch varies with taxonomic

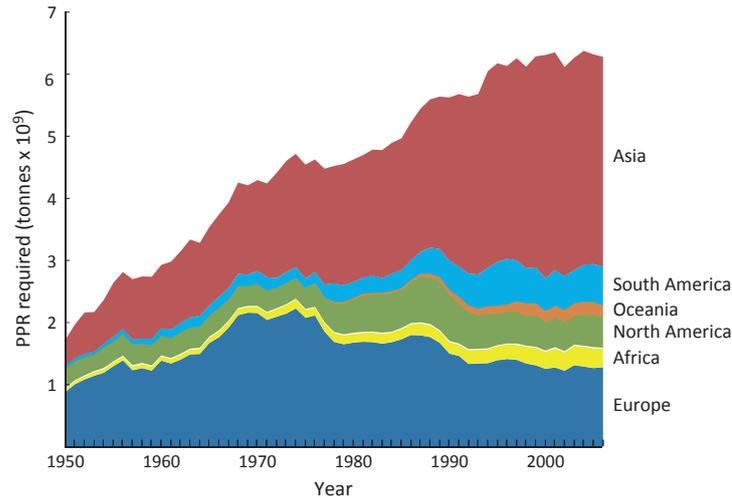


Figure 1 The annual primary production (million tonnes) required to supply the global catch of fishing fleets by continent from 1950 to 2006.

group, we assigned a value of only 5% to all large tuna and billfish landings, rather than the higher, and less representative, area averages. We consider that because we did not include discards that our PPR estimates are conservative.

Primary production required

The analysis, which covers the period from 1950 to 2006, defines fisheries exploitation based on the primary production that is required to generate the catches of marine fisheries. The primary production required (PPR, Pauly and Christensen 1995) is computed from:

$$PPR = \sum_{i=1}^n \frac{C_i}{CR} \times \left(\frac{1}{TE}\right)^{(TL_i-1)} \quad (1)$$

where C_i is the catch of species i , CR is the conversion rate of wet weight to carbon, TE is the transfer efficiency between trophic levels, TL_i is the trophic level of species i and n is the number of species caught in a given area. We applied a 9:1 ratio for CR and 10% for TE (Pauly and Christensen 1995). Species-specific trophic levels, usually derived from diet composition data, were taken from FishBase (www.fishbase.org) for fishes and SeaLifeBase (www.sealifebase.org) for invertebrates.

Results

Conversion of global annual landings (correcting for illegal and unreported catches) into the PPR by fishing fleets (as designated by continent of origin)

showed a rising demand that began stagnating in the late 1990s when global landings failed to increase (Fig. 1). Most of this growth in PPR was driven by fleets from Asia, while PPR demand from some fleets (such as Europe) actually declined in recent decades.

Primary production required (Equation 1) is a product of the carbon-converted catch mass and the conversion ratio for the trophic level of the taxa involved. Hence, differences in the PPR of fishing countries differ not only in the catch taken, but also in the trophic level of the taxa landed (Pauly *et al.* 1998). With a trophic transfer efficiency of 10% and a conversion of wet weight to carbon of 12.5%, the PPR of 100 t landed of trophic level 2 (animals consuming primary producers directly) would be 125 t. If, however, the taxa taken were at trophic level 3, then the PPR would be ten times, or 1250 t. Fig. 2 shows how total

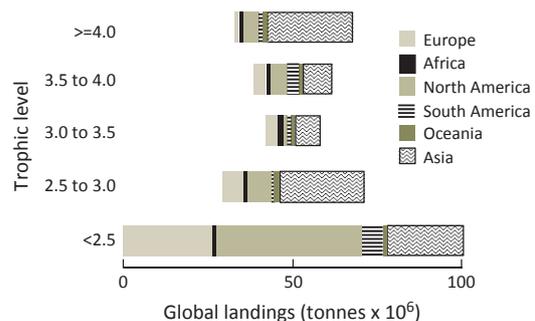


Figure 2 The landings taken (1950 to 2006 inclusively) in tonnes by global fleets broken down to trophic slices. Trophic level is highest at the top.

landings (1950 to 2006) taken by the fleets from different continents were broken down by slices of the trophic level spectrum. In this figure, the total landings taken by each continent's fleets are separated into the trophic level of the taxa in an arrangement suggestive of a crude trophic pyramid, with the bottom being animals that consume plants directly and those at the top being top predators. Thus, landings taken at the top are equivalent in PPR about at least 100 times that at the bottom. European fleets (the left segment of each bar) took most of their catch at the lowest trophic levels with very little taken at the highest levels (>4), where catches are dominated by piscivorous species. In contrast, fleets from Asia (right-most segment in each bar) took significant landings across the trophic spectrum. At the highest trophic level, fleets from Asia took the majority of landings (76%) of all global fleets. Therefore, in addition to increasing landings, the targeting of higher trophic level species partially explains why the PPR by Asian fleets has increased the most in Fig. 1.

To place PPR values in perspective, we need to compare them with the underlying productivity (PP) available within fished area. PP varies from place to place and there is some interannual variation as well. Large marine ecosystems (LMEs, Table 1) in the Arctic or near-Arctic have the highest variability in PP (coefficient of variation of 20–25%); however, this may also be partially due to poorer satellite coverage. The majority of LME areas have a coefficient of interannual variation in PP of <5%, suggesting that average PP levels are representative and that it is unlikely that levels deviated greatly from the average during our study period (1950–2006).

To track where global fleets have intensified or shifted their PPR demands over time, we created maps of PPR by fleet and decade (Fig. 3). These maps show the change in PPR by 30-min spatial cells per decade, demonstrating how demand was changing in space and time. Generally, PPR levels intensified decade by decade. The Asian fleets expanded and increased their PPR intensity throughout the Pacific starting in the 1950s (Fig. 3b). In the 1960s, Asian fleets (mainly Japan) targeted the west coast of Africa, and more recently, a Chinese-led PPR demand increase in African waters has been suggested (Pauly *et al.* 2012). In more recent times (1990s and 2000s), the Asian fleets have also increasingly targeted eastern Pacific waters (Fig. 3b).

Fleets from Europe, as expected, made already very high demands on the waters in the north-eastern and north-western Atlantic in the 1950s; however, already by the 1960s, we see intensification of PPR on NW African waters (Fig. 3c). Thereafter, demand in African waters appears to decline, but it is known that many European vessels reflagged at that time and appeared as African vessels (Alder and Sumaila 2004). Most PPR demand, however, still identifiable as European has more recently shifted back to northern European waters.

Examination of PPR demand by fleets within individual large LME areas provided more detailed insights into the changes that have occurred. LME areas are relatively homogenous in their basic ecosystem structure and primary productivity regime, making them very suitable for examination of PPR. We focus here on six of the 66 defined LME areas that we examined (Fig. 4, see Data S1). The six LMEs presented here account for approximately 20% of global reported landings. For each figure panel, we provide two vertical axis scales. The left hand axis provides the tonnes of annual PPR, whereas the right hand axis shows the proportion of average annual primary production (PP) available in that LME that this PPR accounts for.

Some biomass related to regional primary productivity may originate outside of LME areas and be imported; however, most PP occurs within the LME areas as especially that associated with coastal upwellings. Large pelagics can travel large distances and enter LME areas from oceanic areas. Landings of large pelagics from these mid-ocean areas (outside of LMEs) comprised 19% of all landings from these areas. Some LME areas such as those associated with the northern Australian shelf areas or those of Hawaii have an even larger component of large pelagic landings; however, this is rare. Those LME areas featured below, however, do not have significant external PP imports, and the average of large pelagic landings is <1%.

The Humboldt Current LME is a highly productive system fished predominately by Peruvian and Chilean vessels (see contributions in Bertrand 2008; Heileman *et al.* 2008). In the mid-1990s, PPR increased to levels that approached 80% of the average available PP levels. It is worth noting that some of the most productive global fishing areas are associated with ocean currents and rich nutrient upwellings. Here, they combine to create

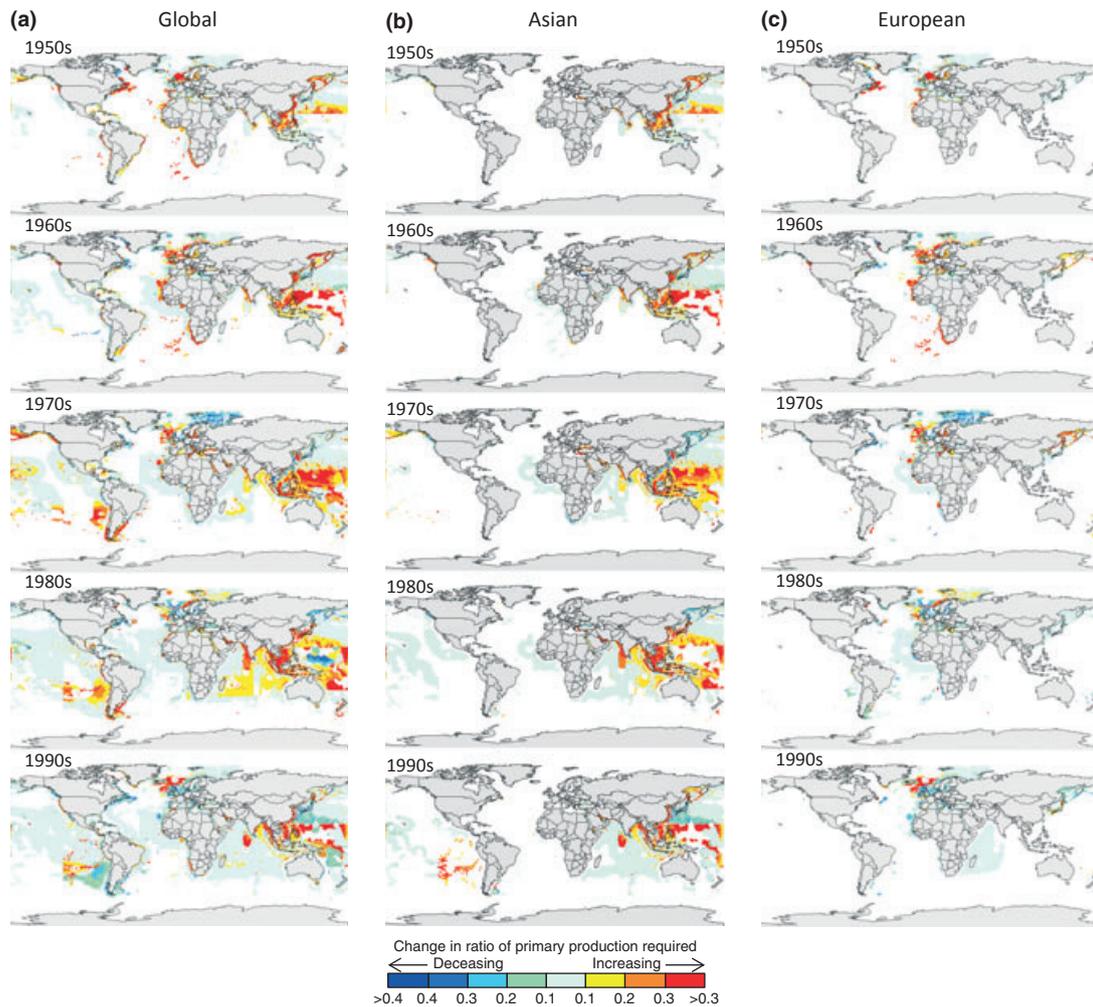


Figure 3 Maps of the inter-decadal changes in the ratio between primary production required to produce global landings from 30-min spatial cells and the average primary production for that same spatial cell for (a) global fleets, (b) for those originating from Asia and (c) for those from Europe.

some of the largest landings of small pelagics reported.

The PPR for the North Sea LME (Fig. 4) peaked at high levels (about 2 times the average PP) in the early 1970s, but has steadily declined since. Fisheries management has attempted to intervene to reduce this unsustainable demand to lower levels. The demand of European fleets, however, is an international story, and to understand it, better you need to also examine the Scotian Shelf and Canary Current LME areas. European fleets have fished in the Newfoundland area since the first decade of sixteenth century (Kurlansky 1999), and fishing resources here were instrumental to European interests in this region. On Canada's Scotian Shelf, European fleets continued to exert a

strong PPR demand until the declaration of exclusive economic zones (EEZ) in the 1980s, combined with the collapse of the cod fishery on Canada's east coast in the early 1990s (Walters and Maquire 1996; Fig. 4). Thereafter, European fleets had to find more productive waters and they did so in waters off NW Africa. The plot for the Canary Current LME area (Fig. 4) shows the increasing demand of European fleets in the early 1970s and thereafter. In recent decades, there has been a tendency for European vessels to reflag themselves as African vessels, which in part accounts for the increasing PPR demand by 'African' fleets in this area (Bonfil *et al.* 1998; Alder and Sumaila 2004).

On the New Zealand Shelf, there was also a significant PPR demand by foreign fleets in the

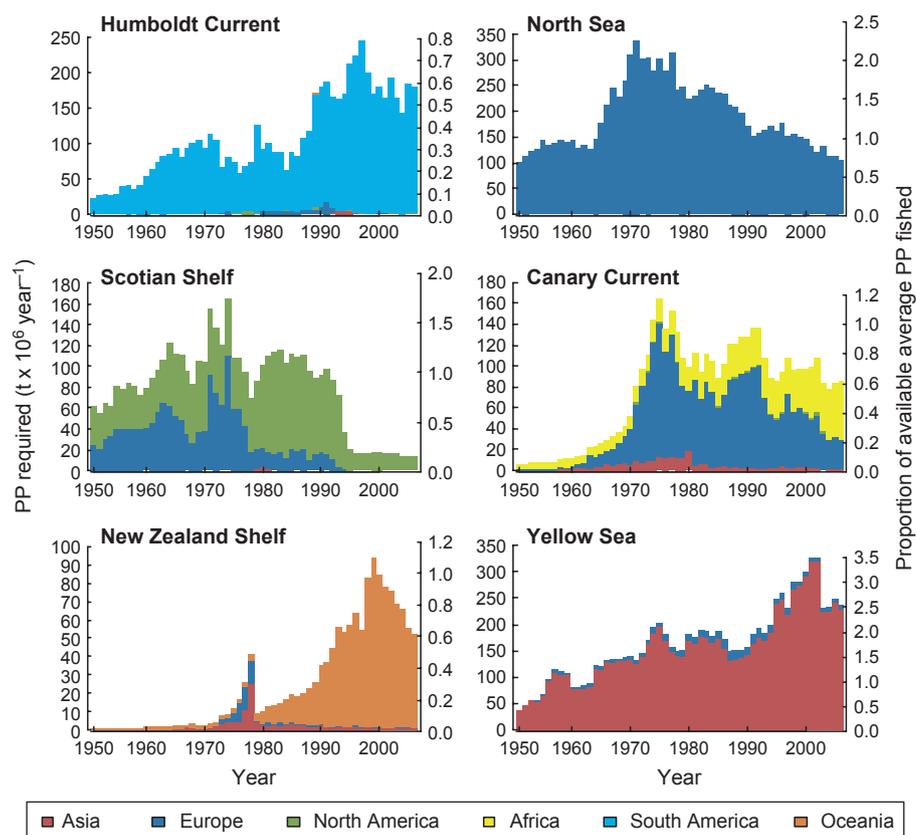


Figure 4 Primary productivity required (tonnes $\times 10^6 \text{ year}^{-1}$) taken by continental fleets from 1950 to 2006 compared to average primary productivity (as a proportion) for Large marine ecosystem (LME) areas Humboldt Current, North Sea, Scotian Shelf, Canary Current, New Zealand Shelf and Yellow Sea.

1970s that peaked at around 50% of available primary production (Fig. 4). Due to strong national interests, this foreign fishing was replaced by New Zealand or other flag carriers from Oceania in the 1980s and thereafter. PPR demand increased rapidly to unsustainable levels exceeding 100% by the late 1990s. Changes in fisheries management appears to have brought PPR demand down in recent years, which can be attributed to a range of measures including reductions in total allowable catches, gear and capacity (Worm *et al.* 2009). However, concerns about very high levels of unaccounted discarding in the New Zealand fisheries have recently surfaced, which could alter this picture.

In the Yellow Sea LME (Fig. 4), there had long been very high and increasing PPR levels exceeding 100% of available PP already by the mid-1960s (Heileman and Jiang 2008). These values may be unreliable due to the over-reporting of Chinese catches from these waters (Watson and Pauly 2001).

Discussion

One of the main trends revealed by our analysis is the increase in the primary production required by all global fleets, but especially those from countries in Asia. Increase in PPR demand is widespread and includes targeting the highest trophic levels. The expansion and intensification of exploitation levels are of concern not only to the future supply of marine-sourced protein and industry profitability (Srinivasan *et al.* 2010, 2012; Tremblay-Boyer *et al.* 2011), but also to global marine biodiversity (Butchart *et al.* 2010; Anderson *et al.* 2011; Mouillot *et al.* 2011). It could impact on all aspects of the marine environment, ranging from critical habitats to vulnerable populations of marine mammals and seabirds. Particularly vulnerable are the deeper, less productive areas, which are often outside of currently managed areas and EEZ claims (Pitcher *et al.* 2010; Norse *et al.* 2011). High seas fisheries also include the tunas and billfishes, whose life strategy and high value makes

them very vulnerable to over-exploitation (Collette *et al.* 2011). Coll *et al.* 2008 reported that the spatial dynamics of exploitation indicated that signs of ecosystem overfishing were already detectable in various LMEs of Northern Europe, the North Atlantic, East Asia and the Gulf of Mexico during the 1950s, and they found that generally this phenomena expanded to new areas as fishing effort increased, although some areas subsequently improved as a result of better fisheries management.

Increases in PPR have typically occurred in the most productive fishing areas, with levels approaching, or greatly exceeding the local average PP available. In recent years, some of the fleets fishing in these areas have had to moderate their demands and PPR has decreased. For highly mobile fleets, such as those from Europe and Asia, however, there have been other avenues, notably fishing in the waters of other countries (where access is available) and returns (after subsidies, Le Manach *et al.* 2013) are high. European fleets have long fished on the east coasts of Canada and the USA (Kurlansky 1999; Roberts 2007). When these countries declared their EEZ, it required negotiating access agreements for European fleets to continue to fish in these waters. The exclusion of foreign vessels from the Northeast Shelf LME was due to the depleted condition of virtually all groundfish species by the mid-1970s. In particular, the decline of the important Atlantic cod fishery in this area further signalled the general departure of European fleets from these waters. In European waters, the era of heavy exploitation started well before 1950 (Kurlansky 1999; Roberts 2007), and this area was already heavily fished at the time of US and Canadian EEZ declaration (Christensen *et al.* 2003). The solution for Europe was to send more vessels south. New entrants to the EU were not necessarily afforded fishing access to the overfished waters of the North Sea or other European waters. We can see the expansion to and intensification of European fishing in areas of NW Africa in the 1970s and 1980s (Alder and Sumaila 2004; Atta-Mills *et al.* 2004; Watson 2005). European countries like Spain have long fished in northern and north-western Africa (Watson 2005). When EEZs were declared, European aid programs and heavily subsidized access agreements (Le Manach *et al.* 2013) made this relatively easy to continue. More recently, however, European companies have made individual

arrangements with African countries and one of the consequences is that their activities became less visible due to a lack of transparency and accountability of such side agreements (Le Manach *et al.* 2013). Increased reflagging to the African host country or the use of flags of convenience has also added to the complexity and increased lack of accountability (Bonfil *et al.* 1998; Alder and Sumaila 2004). Fisheries in West Africa have generally declined in response to this additional fishing effort (Christensen *et al.* 2005).

Asian fleets have expanded their range and fishing intensity considerably (Anticamara *et al.* 2011; Watson *et al.* 2012). We have seen that they fish across all trophic levels of marine systems and this can bring additional dangers to sustainability (Coll *et al.* 2008). China has large and expanding fishing fleets, which increasingly also fish in Africa (Pauly *et al.* 2012). As with other mobile fleets, this has allowed their PPR demands to be 'satisfied' through spatial expansion to 'new' ocean areas.

Our calculations assumed a fixed transfer efficiency of 10% between higher trophic levels in the food chain, and further assumed that this efficiency did not vary significantly from place to place, or through changes in the ecosystem such as heavy fishing or other factors can induce. Pauly and Christensen (1995) found a range of efficiency values (3% to 18%), but suggested that these were extreme and that a rate of 10% was most representative of all but limited areas. This is, however, an important area of future research and there is some evidence of spatial and ecosystem variations in efficiency (Libralato *et al.* 2008), even suggestions that these rates can change with exploitation (Coll *et al.* 2009a,b).

In general, all global fleets moved to exploit more distant waters, increasingly in the waters of the southern hemisphere (Swartz *et al.* 2010a; Watson *et al.* 2012). This expansion comes at an increasing energy cost (Tyedmers *et al.* 2005) as the fuel expended per tonne of fish landed makes for economics that often require subsidies to remain profitable (Sumaila *et al.* 2010a). Often, the 'new' fishing areas are already fished and the expansion of these fleets increasingly comes at the cost of local small-scale fisheries in developing countries (Alder and Sumaila 2004; Atta-Mills *et al.* 2004; Christensen *et al.* 2005). These small-scale fisheries are of crucial food security importance, and competition through highly industrialized foreign fleets

leads only to further marginalization of this crucial fisheries sector (Pauly 2006). Overall, the solar-powered productivity of the oceans has become a global commodity, and as a vital environmental service, it is over-used and under stress.

What about future productivity of the world's oceans? Expected and observed changes in global ocean temperature, oxygen and acidity all suggest that marine ecosystems are and will continue to be altered (Cheung *et al.* 2010). Certainly, the sun will continue to supply the energy to power the ocean ecosystems. It is, however, less certain what changes in the diversity and resilience of marine systems will occur, and how this will change what the ocean can provide for us, and the efficiencies at which it does so. If marine food webs are greatly altered through overfishing and climate change, we could find more of the sun's energy being funnelled to organisms such as jellyfish, which often compete with fisheries (and do not provide much nourishment) (Pauly *et al.* 2009; Brotz *et al.* 2012). Our data show that in the past it was possible to fish for many years at PPR rates that surpassed average *in situ* PP levels. This may have been a function of a well-networked ecosystem supported by the evolved resilience that biodiversity brings (Worm *et al.* 2006; Butchart *et al.* 2010). It has now, however, become necessary to restrict catches so that marine ecosystems can rebuild their productive potential and diversity. With future changes to marine food webs, we may not be able to extract as much from these systems as we have in the past, and they may be less forgiving.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Data S1. Primary productivity required (million tonnes per year) taken by continental fleets from 1950 to 2006 compared to average primary productivity (as a proportion) for global Large Marine Ecosystem (LME) and Exclusive Economic Zones (EEZ) areas.