

## Global marine primary production constrains fisheries catches

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## Abstract

Primary production must constrain the amount of fish and invertebrates available to expanding fisheries; however the degree of limitation has only been demonstrated at regional scales to date.

30 Here we show that phytoplanktonic primary production, estimated from an ocean-color satellite (SeaWiFS), is related to global fisheries catches at the scale of Large Marine Ecosystems, while accounting for temperature and ecological factors such as ecosystem size and type, species richness, animal body size, and the degree and nature of fisheries exploitation. Indeed we show that global fisheries catch since 1950 have been increasingly constrained by the amount of primary  
35 production. The primary production appropriated by current global fisheries is 17 to 112% higher than that appropriated by sustainable fisheries. Global primary production appears to be declining, in some part due to climate variability and change, with consequences for the near future fisheries catches.

## INTRODUCTION

40 Fisheries have long been thought inexhaustible because of the vastness of the oceans that represent more than 70% of the surface of planet Earth. Over time, technology has advanced and fishing has progressively spread over the world oceans to affect marine species at lower trophic levels and in offshore deeper waters (Pauly *et al.* 2003; Essington *et al.* 2006). After a long period of steady increase, cumulative world marine fisheries catches stabilised in the mid-1990s at  
45 between  $75$  and  $85 \times 10^6$  tons (Watson & Pauly 2001). Such stability might actually be spurious, instead it is likely that global fisheries catches are declining and the decline has been masked by underreporting and misreporting of catch by countries combined with large environmentally-forced fluctuations in the catch of small pelagic species, such as the Peruvian anchoveta (Watson & Pauly 2001). The decrease in global catch might be explained by the sequential depletion of individual  
50 stocks, which in the past would have been balanced by fisheries expansion to new opportunities in the high seas and into deeper water or by the exploitation of lower trophic levels (Pauly *et al.* 2002). Although limited empirical evidence has been provided to date, the attainment of a maximum of global catch is consistent with fundamental energetic limits to fisheries exploitation (Ryther 1969).

55 Solar radiation is the main external source of energy for marine ecosystems. More than 90% of oceanic productivity is fixed by phytoplankton which is then transferred through food webs by predation and lost through metabolism (Lindeman 1942; Duarte & Cebrian 1996). The total fish and invertebrate production in an ecosystem results from the conversion of organic matter at each trophic level. This production depends on ecological features such as the number of feeding links,  
60 the efficiency of energy transfer from one trophic level to the next, and temperature-dependent metabolic kinetics in aquatic food web (Lindeman 1942; Ryther 1969; Iverson 1990; Ernest *et al.* 2003; Gascuel *et al.* 2008), and on ecosystem-specific features such as ecosystem size (Post *et al.* 2000), species richness (Frank *et al.* 2007), and consumer body size (Denney *et al.* 2002). In addition, the total secondary production available to fisheries depends upon the degree of fishing  
65 mortality and the nature of fisheries targeting of different trophic levels in the food web. Fisheries focusing only on lower trophic levels have the potential to appropriate orders of magnitude more energy than those focused on top predators (Pauly & Christensen 1995; Gascuel & Pauly 2009).

Two opportunities enable a global scale exploration of the relationship between primary production and fisheries catches: the recognition and description of large biogeochemical and

70 biologically consistent provinces (Large Marine Ecosystems) and the advent of satellite monitoring  
of ocean color and primary productivity. Large Marine Ecosystems encompass similar physical and  
ecological features, such as hydrography and productivity and provide convenient spatial units to  
test whether patterns of correlations between primary production and fisheries catches observed for  
75 some regions also persist at a global scale (Ware & Thomson 2005; Chassot *et al.* 2007; Frank *et al.* 2007). Ocean primary productivity is inherently variable over short temporal (daily) and spatial  
(meter) scales, synoptic views are difficult to achieve with oceanographic ships which cross oceans  
at the speed of a bicycle. The only high frequency, basin-scale sampling of oceanic primary  
production is available from satellites (Longhurst 1998).

Here, we test the relationship between marine primary production and fisheries catches across  
80 the world's Large Marine Ecosystems. Primary production estimates in each LME were combined  
with global catch statistics that account for illegal and unreported fishing (Agnew *et al.* 2009).  
First, we test the degree to which primary production but also ecosystem features (type and size of  
ecosystem, sea surface temperature, species richness) and the degree and nature of fisheries (level  
of pressure, trophic and size structure of the catch) explain the spatial variation in fisheries catches.  
85 Second, we explore the degree to which global fisheries catches are constrained by primary  
production using quantile regression models.

## MATERIALS AND METHODS

### Estimating primary production

Annual estimates of primary production (PP) in each Large Marine Ecosystem over the period  
90 2000-2004 were derived from averaged monthly global maps of surface concentrations of  
chlorophyll-a based on the Sea-viewing Wide Field-of-View Sensor (SeaWiFS, NASA) global time  
series (McClain *et al.* 2004). PP was computed from the surface concentration of the chlorophyll-a  
pigment, which serves as a proxy for algal biomass, using a wavelength- and depth-resolved model  
(Longhurst *et al.* 1995), further details are in the supplementary material online (Fig. S1). The PP  
95 estimates obtained at global scales with this approach were broadly consistent with those from  
other models driven by ocean colour data in terms of global average (47 Pg C yr<sup>-1</sup>) as well as  
spatial distribution (Carr *et al.* 2006) and compared favourably with a set of PP field measurements  
collected in the Equatorial Pacific and assembled for an international inter-comparison exercise  
(Friedrichs *et al.* 2009). For long term analysis, we assumed that PP estimates during 2000-2004

100 reflect the large-scale spatial gradients in PP since 1950; this assumption is later discussed.

### **Fisheries catches**

Annual catch data, including all quantities landed for both food and feed purposes, were available from spatially resolved global catch datasets prepared by the Sea Around Us project (<http://www.searoundus.org/>). Time series of catch data were derived from the harmonized global catch statistics of the Food and Agriculture Organization (FAO) of the United Nations and several other sources including collaborative national catch reconstructions using rule-based procedures which assign catch to 30-minute spatial cells based on taxon distribution, and on the fishing patterns/arrangements of reporting countries (Watson *et al.* 2004). Catch data were corrected for illegal and unreported catches that can represent a substantial amount of fisheries catches (Agnew *et al.* 2009) The dataset was available for the period 1950-2004 and excluded (i) ecosystems where data were incomplete, insufficiently detailed or suspected to be unreliable (e.g. Yellow Sea; Watson & Pauly 2001), (ii) catches from distant-water fleets (not allocated to fishing areas), and (iii) large and medium pelagic species that can migrate outside and between LME boundaries. Thus, the dataset included resident species defined as populations that occupy the continental margin year-round and undertake only spatially limited seasonal migrations (Ware & Thomson 2005). As a result, the following 10 of the 64 LMEs were excluded from the analysis: Antarctic, Arctic Ocean, Beaufort Sea, Chukchi Sea, East China Sea, East Siberian Sea, Hudson Bay, Kara Sea, Laptev Sea, and Yellow Sea. The remaining 54 LMEs considered here represented more than 68% of the world fisheries catches during 1950-2004. The selected resident non-migratory fishes and invertebrates corresponded to 90% of total catch in these LMEs during 1950-2004.

### **Primary production required to support fishery catches**

To convert fisheries catches into comparable energy units, we calculated the primary production required (PPR) to support fishery catches in t C km<sup>-2</sup> y<sup>-1</sup>. This allows comparison of fisheries catches consisting of species from different trophic levels (Ryther 1969; Pauly & Christensen 1995). The primary production required to produce the catches was calculated as following:

$$PPR_j = \sum_{i=1}^n \left( \frac{C_{ij}}{9} \right) \times \left( \frac{1}{TE_j} \right)^{TL_i-1} \quad (1)$$

where  $C_{ij}$  is the catch (in metric tons) of species  $i$  in LME  $j$ ,  $TE$  is the trophic transfer efficiency in LME  $j$ , i.e. the proportion of prey production converted to predator production,  $TL_i$  is the trophic level of species  $i$  and  $n$  is the number of species harvested in the LME. PPR estimates were based on a conservative 9:1 ratio for the conversion of wet weight to carbon (Strathmann, 1967).

Trophic levels derived from stomach content data were extracted from the FishBase database (Froese & Pauly 2009) and assigned to each species, assuming they were stable from year to year and valid for the area covered by the study.

### **Potential covariates of the primary production and fisheries catch relationship**

Several candidate covariates that represent major physical and ecological processes within large marine ecosystems were considered as predictors of fisheries catch. In addition to primary production, we selected 7 covariates for which data are available at LME scale: ecosystem type, sea surface temperature (Jennings *et al.* 2008), ecosystem size (Post *et al.* 2000), species richness (Frank *et al.* 2007), fishing pressure (Coll *et al.* 2008), mean trophic level (Gascuel *et al.* 2008), and maximum average body length (Denney *et al.* 2002). In doing so we explore the link between energy and fisheries production while accounting for all other major hypotheses.

#### **a. Ecosystem type**

Three ecosystem types were considered: upwelling, temperate, and tropical. Transfer efficiency  $TE$  was derived from a synthesis of ecosystem models and set equal to 5%, 10%, and 14% for upwelling, temperate and tropical ecosystems, respectively (Libralato *et al.* 2008; Coll *et al.* 2008), and assumed constant for each trophic level during 1950-2004.

#### **b. Sea surface temperature (SST)**

The SST distributions, obtained from the Physical Oceanography Distributed Active Archive Center (PO. DAAC, Jet Propulsion Laboratory), are provided by the AVHRR Pathfinder data set (version 5) as monthly maps (1985-2004) with a resolution of 4 km (<http://podaac.jpl.nasa.gov/>). Only the data points associated with the highest level of quality flags were considered.

#### **c. Ecosystem size (ES)**

The surface area of each Large Marine Ecosystem was computed using a geographic information system and assumed to be a good proxy of ecosystem size.

155 d. Species richness (SR)

The number of marine fishes in each Large Marine Ecosystem was derived from the Sea Around Us project (<http://www.seaaroundus.org/>). We calculated species richness per unit of area in each LME to account for the underlying species area relationship.

e. Fishing pressure ( $P_{\text{sust}}$ )

160 Fishing has both direct and indirect effects on fish populations and marine ecosystems (e.g. decline  
in stock abundance and habitat degradation), eventually affecting their structure and functioning  
(Garcia *et al.* 2003). Overexploitation of single species limits the catch that can be taken, but in a  
multispecies context the removal of relatively unproductive high trophic level predatory species  
can lead to increased fisheries catch potential through the proliferation of smaller, more-productive  
165 individuals and species (e.g. Gascuel *et al.* 2008). As marine ecosystems exhibit large differences  
in fisheries history, levels of exploitation, and trophic structure of the catch; an index of the overall  
ecosystem effects of fishing was used to account for differences in fishing pressure. The mean  
annual probability of sustainable fishing ( $P_{\text{sust}}$ ) was recently developed to assess the level of  
overfishing at ecosystem scale based on the total removal of secondary production compared to  
170 reference levels derived from ecosystem models (Libralato *et al.* 2008; Coll *et al.* 2008). The mean  
annual value of  $P_{\text{sust}}$  calculated for the period 2000-2004 accounting for discards and 30% illegal  
and unreported catch estimates was used. Lower probabilities of sustainable fishing  $P_{\text{sust}}$  indicate  
higher fishing pressures (Coll *et al.* 2008).

f. Mean trophic level of the catch (MTL)

175 For each LME, the Mean Trophic Level (MTL) of the catch, computed as the weighted average of  
trophic level of harvested species, was used to describe the position of the fishery in the food web  
during 2000-2004 (Froese & Pauly 2009).

g. Average maximum length ( $L_{\text{max}}$ )

180 Fisheries yield and sustainability is, to some degree, determined by the intrinsic population growth rate of the target species – for a given fishing mortality, shark fisheries are likely to be less sustainable and less productive than anchovy fisheries (Reynolds *et al.* 2005). We used body size as a proxy for the intrinsic rate of population increase, based on theoretical and empirical evidence for a scaling relationship between body size and the intrinsic rate of population increase (Denney *et al.* 2002, Savage *et al.* 2004). The average maximum length of the fish catch within each LME  
185 (Froese & Pauly 2009), computed as the weighted average of maximum length of harvested species, was used as a surrogate for the intrinsic growth rate of increase of the fish community (Denney *et al.* 2002).

### Testing for covariates of fisheries catch production

We used linear models to test for the effects of fishing pressure, average maximum length, sea surface temperature, mean trophic level, ecosystem size, species richness, log-primary production and ecosystem type on fisheries catches (log-PPR) during the period 2000-2004. No interaction effect was included in the model. Log-transformation of the response variable (PPR) and the primary production covariate enabled to remove skew and minimize the large standard deviations in the data. The following model was considered:

$$195 \quad \log(PPR_j) = P_{sust_j} + L_{max_j} + SST_j + MTL_j + ES_j + SR_j + \log(PP_j) + ET_j + \varepsilon_j \quad (2)$$

where  $j$  indexes LME,  $P_{sust}$  is the probability of sustainable fishing,  $L_{max}$  is the average maximum length of the catch,  $SST$  is the sea surface temperature,  $MTL$  is the mean trophic level of the catch,  $ES$  is the ecosystem size,  $SR$  is the species richness,  $PP$  is the primary production,  $ET$  is the ecosystem type.  $\varepsilon_j$  was modeled as an independent, normally distributed random variable with  
200 mean zero and constant variance. The assumptions of homoscedasticity and Gaussian error were checked through the residuals. Models were evaluated using the Akaike information criterion (AIC).

### Inferring constraints or limits using quantile regression

Changes in the slope of the regression models were used to investigate whether primary production

205 may constrain fishery catches. Quantile regressions are used to identify limiting factors when relating ecological variables (e.g. fish abundance) to environmental indices (Cade & Noon 2003; Planque & Buffaz 2008). A factor is inferred to be limiting when the slope tends to be steeper for upper quantiles and when it is significantly different from zero for high quantiles (Planque & Buffaz 2008). In particular, linear regression models for quantiles ranging from 10% to 90% by  
 210 steps of 10% were used to describe how the range of catch and PPR levels varied according to PP over long- (1950-2004) and short-term scales (2000-2004). The 90% quantile was used as a proxy of the maximum fishery production, although the upper regression quantiles do not describe the exact limit of the distribution function.

We tested whether the fishery catch changed over time through the slope of linear model fitted  
 215 between mean annual values of catch and PPR per LME averaged over (i) the recent period (2000-2004) and (ii) the long-term (1950-2004). We then estimated the slope of the 90% quantile regressions fitted to data grouped by 5-year periods over 1950-2004 to analyse the temporal changes in the maximum of PPR/PP ratio, considered as an index of LME exploitation (Pauly & Christensen 1995; Libralato *et al.* 2008).

220 Defining the upper limit of fisheries catch is a prerequisite to assess current levels of fishing relative to benchmarks and give insights into future fisheries catch. We used the slopes estimated from the 90% quantile linear regression models to predict the maximum global fisheries catches for 2000-2004, considering that all Large Marine Ecosystems could be exploited at maximum levels given their ecosystem-specific primary production. Similarly, sustainable levels of maximum  
 225 global fisheries catch have been calculated from the 90% quantile regression slopes estimated using solely LMEs where the probability of sustainable fishing  $P_{sust}$  was higher than 75% and 95%. Quantile regression models were all fitted to data without intercept and performed using the R package *quantreg* (Koenker 2009).

## RESULTS

### 230 **A large spatial variability in fisheries catch**

The mean annual catch during 2000-2004 for all species in the 54 LMEs was  $68 \times 10^6$  t  $y^{-1}$  (SD =  $4 \times 10^6$  t  $y^{-1}$ ), corresponding to a PPR of  $3.5 \times 10^9$  t C  $y^{-1}$  (SD =  $0.09 \times 10^9$  t C  $y^{-1}$ ). The LMEs showed strong differences in fishery catch over the long term (1950-2004) and recent period (2000-2004),

without any clear pattern associated with ecosystem type (Fig. 1a,c). In the 2000s, approximately 1  
235 t km<sup>-2</sup> y<sup>-1</sup> of fish catch is derived from 600 t C km<sup>-2</sup> y<sup>-1</sup> of primary production. Three of the 54  
LMEs showed high levels of mean annual catch when averaged over the whole period 1950-2004  
(Fig. 1a): the North Sea (PP = 919 t C km<sup>-2</sup> y<sup>-1</sup>, catch = 5.6 t km<sup>-2</sup> y<sup>-1</sup>), the Humboldt Current (PP =  
822 t C km<sup>-2</sup> y<sup>-1</sup>, catch = 4.0 t km<sup>-2</sup> y<sup>-1</sup>), and the Iceland shelf (PP = 561 t C km<sup>-2</sup> y<sup>-1</sup>, catch = 3.9 t  
240 km<sup>-2</sup> y<sup>-1</sup>). These LMEs were still the most productive in 2000-2004, with the Humboldt LME  
reaching an average fisheries catch of 7.0 t km<sup>-2</sup> y<sup>-1</sup>, being by far the most productive ecosystem of  
the world (Fig. 1c). The high catch levels in these LMEs in the recent period were mainly due to the  
catch being comprised largely of low trophic level (TL) species, i.e. sandeels (*Ammodytes* spp.; TL  
= 3.1), anchovy (*Engraulis ringens*; TL = 2.7), and capelin (*Mallotus villosus*; TL = 3.05) for the  
North Sea, Humboldt, and Iceland Shelf, respectively.

245 The conversion of catch weights into the Primary Production Required to support these fisheries  
reduced the spatial variability in fishery catch among LMEs (Fig. 1b,d) and showed that eastern  
boundary upwelling systems exhibit the highest values of PPR. The LMEs where the highest  
proportion of primary production is appropriated by fisheries catch over 1950-2004 include the  
Canary, Humboldt, and Benguela eastern boundary current upwelling ecosystems, with values of  
250 44%, 50%, and 24%, respectively in the 2000s. Again the high PPR can be attributed to the high  
catches of small low trophic level pelagic species such as anchovies (*Engraulis* spp.), sardines  
(*Sardina pilchardus* and *Sardinops* spp.), and sardinellas (*Sardinella* spp.) in upwelling LMEs and  
the low transfer efficiency of this type of ecosystems.

### **Disentangling the major factors explaining fisheries catch**

255 The spatial variance in global fisheries catches was best explained by four variables which  
explained 77% of the inter-LME variance in log-PPR: primary production (log-PP), the probability  
of sustainable fishing ( $P_{\text{sust}}$ ), the average maximum length ( $L_{\text{max}}$ ), and ecosystem type (ET). Primary  
production, ecosystem type, and fishing pressure explained most of the variance (Table 1). Other  
potential covariates, sea surface temperature (SST), mean trophic level (MTL), ecosystem size  
260 (ES), and fish species richness (SR) were not significantly different from zero and hence removed  
from the final model. The estimates of the ecosystem type parameters were higher for upwellings  
than tropical and temperate ecosystems, in accordance with the transfer efficiency we used to  
calculate PPR.

The prediction of Primary Production Required in each LME was reasonably accurate (Normalized  
265 Root Mean Square Error = 12%). The model prediction of global PPR was  $3.74 \times 10^9$  t C  $y^{-1}$  which  
is very similar to the actual PPR computed from the data ( $3.46 \times 10^9$  t C  $y^{-1}$ ). More sustainable  
fisheries would decrease the PPR, the negative coefficient suggests PPR significantly decreased  
with higher values of  $P_{\text{sust}}$  (Table 1). Exploitation of smaller-bodied fishes results in greater fisheries  
270 catch; the negative coefficient shows that PPR significantly decreased with  $L_{\text{max}}$  (Table 1). Primary  
production appears to constrain fisheries catches since PP positively and significantly affects PPR,  
once ecosystem type, degree ( $P_{\text{sust}}$ ) of the fisheries, and intrinsic population growth ( $L_{\text{max}}$ ) are  
accounted for (Table 1).

### Primary production as a limiting factor of fisheries catch

Primary production limits average and maximum fisheries catch across the world at the LME scale  
275 over both short and longer time scales (Fig. 1a, c and S2). The limitation has become increasingly  
apparent as regression slopes become steeper in more recent time periods (Fig. 2). The significant  
relationship found between long-term (1950-2004) and recent catch (2000-2004) (slope = 0.76,  
adjusted  $r^2 = 0.82$ ,  $p < 0.001$ ) revealed that the spatial gradients in fisheries catches were consistent  
through time (Fig. S3-S4).

### 280 Increasing levels of fishing exploitation through time

There has been a steady increase in the level of exploitation (PPR/PP) with a maximum value of  
16% during 2000-2004, based on the change in the 90% quantile regression slope (Fig. 3 and S5).  
The stability of the PPR/PP ratio in the last 20 years could suggest that current fishing patterns, and  
especially the fishing strategy currently applied in term of trophic levels that are targeted, may not  
285 allow any further increase in LME fisheries catch relative to primary production levels.

### Predictions of maximum global fisheries catch

The potential maximum of global catch was predicted to be  $146 \times 10^6$  t  $y^{-1}$  during 2000-2004 based  
on the 90% quantile regression model (Table 2). The mean total catch during 2000-2004 exceeded  
the maximum global fisheries catch predicted from the Large Marine Ecosystems where fishing is  
290 considered sustainable by 17% and 112% for  $P_{\text{sust}} > 75\%$  and  $P_{\text{sust}} > 95\%$ , respectively (Table 2).

These results emphasize the dependence of the current levels of fisheries catch on the unsustainable exploitation of these Large Marine Ecosystems.

## DISCUSSION

### Linkage between primary production and fisheries catches

295 Globally, fisheries catches are increasingly constrained by the primary productivity of the  
underlying Large Marine Ecosystems (Pauly & Christensen, 1995). While this has been shown at  
regional scales (Ware & Thomson, 2005; Chassot *et al.*, 2007), the novelty of the present work is to  
show that primary production constrains fisheries catches, while accounting for ecosystem and  
fisheries features. Here, we show that the primary production appropriated by fisheries catches  
300 depends on the scale and nature of fisheries, with heavily-exploited fisheries and those fisheries  
targeting the smallest fish species appropriating more primary production per tonne of catch. In  
addition, comparison of long-term vs. recent catches showed that the regional gradients in fisheries  
catches have not been modified during the last half century, in spite of different histories and  
developments of the LME fisheries combined with increasing exploitation intensity. This coupling  
305 between marine production and fisheries catches reveals that similar mechanisms underlie the  
functioning of marine ecosystems worldwide. Based on the trophodynamic approach of Lindeman  
(1942), we suggest these patterns are consistent with energetic transfers along the food web, from  
the biomass produced by phytoplankton photosynthesis to upper trophic levels.

### Global open-access databases for characterizing ecosystem-level ecological patterns

310 The advent of open-access global datasets derived from remote sensing, the compilation of  
ecological studies, i.e. estimates of trophic levels, average maximum length, transfer efficiency,  
and species richness, and fishery statistics allowed us to unveil the relative importance of bottom-  
up and extrinsic control of fisheries catch at global scale. The availability of global databases such  
as SeaWiFS, FishBase, and ECOwEB (Cohen, 1989) has proven to be a fundamental tool for  
315 detecting ecosystem-level ecological patterns and for testing for hypotheses on general laws and  
rules in ecology (e.g. Pimm *et al.* 1991). The development of access web services and data  
management infrastructures based on international collaborative work (e.g. SeaDataNet;  
<http://www.seadatanet.org/>) combined with openness of datasets collected through public funds is a

major step toward the improvement of our knowledge on the structure and functioning of marine ecosystems.

Due to the short span of SeaWiFS data, we assumed time-consistency in the spatial gradients of primary production although significant changes in phytoplankton may have occurred in the last decades (Reid *et al.* 1998). Comparison of chlorophyll climatologies derived from historical *in situ* data going back to the 1950s and remote sensing data sets showed that seasonal and spatial patterns are consistent at global scale (Conkright & Gregg 2003). This was supported by our data as the spatial differences in primary production were generally greater than the temporal variations observed in the Large Marine Ecosystems for the period 2000-2004. There are still large uncertainties associated with estimates of primary production in the optically complex waters of some coastal areas, especially when turbidity is increased owing to suspended and dissolved materials. Furthermore, annual primary production estimates are seasonally-biased in Large Marine Ecosystems of northern and southern latitudes due to cloud and ice coverage. However, these high latitude ecosystems face the biggest but uncertain anticipated potential impacts from climate change on primary production due to reduced sea ice and early impact from ocean acidification. Some of these physical changes are anticipated to lead to high species turnover due to local extinction and invasion in the Arctic and the sub-polar region of the Southern Ocean (Reid *et al.* 2007; Cheung *et al.* 2009). Primary production distributions provided by ocean color and appropriate models remain the major source of information for a synoptic and consistent mapping of phytoplankton activity over large spatial and temporal scales (Longhurst, 1998). A better knowledge of climate impacts on fisheries will require focusing on understanding primary production and energy transfers in both coastal waters and high latitude Large Marine Ecosystems.

Given the lack of precise information on transfer efficiency in the complex marine food webs of the Large Marine Ecosystems, we assumed constant ecosystem type-specific transfer efficiency values (Libralato *et al.* 2008). These values were based on a set of ecosystem models constructed from large datasets and steady state assumptions. Assuming constant transfer efficiency in dynamic food webs might affect our perception of the spatio-temporal variability of energy transfers from primary production to upper trophic levels. Further fundamental work is required to analyse trade-offs between transfer efficiencies and predator-prey mass ratio and how these parameters vary across environments (Jennings *et al.* 2008).

We used the probability of sustainability (Coll *et al.* 2008) as a measure of fishing pressure in the Large Marine Ecosystems. Despite some limitations, this index is based on a suite of indicators of overfishing that account for fishing effects at both population and ecosystem levels (Murawski 2000, Coll *et al.* 2008). In addition to the direct impact of overfishing on stock dynamics, the probability of being sustainably fished includes several components such as non-harvest mortality and habitat degradation that affect ecosystem properties and fisheries catches (Murawski 2000). Estimating an index of fishing pressure, i.e. fishing mortality at the scale of a population from observations of fishing effort (e.g. number of days at sea) is already a major task faced by fisheries scientists when assessing the state of fish stocks. Inferring fishing pressure estimates from the population to the community and whole ecosystem can be very complex due to interaction effects such as prey release which can increase secondary production and other fishing effects such as habitat degradation (Garcia *et al.* 2003). A better compilation and accessibility of global fishing effort and mortality estimates from Regional Marine Fisheries Organisations (RMFOs) and research institutes will ultimately facilitate comparative analyses among exploited ecosystems.

Life-history traits have been shown to affect the response of fish stocks to fisheries exploitation, with larger and later maturing species being less able to withstand a given rate of fishing mortality than their smaller earlier maturing counter-parts (Jennings *et al.* 1998). Maximum length is a key life-history trait and has been shown to be highly correlated with recruit and adult production and density dependence (Denney *et al.* 2002). Using the FishBase global information system (Froese & Pauly 2009), we computed an average maximum length within each Large Marine Ecosystem to synthesize life-history traits of the fish community in order to account for its capacity to sustain fishing mortality. Since detailed information on population dynamics (e.g. stock-recruitment relationship) is only available for fish stocks assessed within the framework of the RMFOs, maximum body size currently provides the most appropriate proxy for intrinsic population growth for the 901 exploited fish species considered in the present analysis (Denney *et al.* 2002).

### **Global fisheries catch in a context of climate change**

Our results confirm the linkage between primary production and fisheries catches to estimate the potential maximum catch of the world oceans based on marine systems described by different ecological transfer efficiencies (Ryther 1969; Pauly & Christensen 1995). In a context where cumulative world fisheries catches have already shown signs of decline since the mid-1990s after a long period of steady increase (Watson & Pauly 2001; Pauly *et al.* 2002), our estimates indicate

380 that current total fisheries catch could exceed sustainable reference levels, compared to LMEs  
where fishing is considered sustainable (Table 2). PPR predictions from the linear model were  
found to be in good agreement with observed data and consistent with global estimates of Pauly  
(1996) ( $\sim 3.10^9 \text{ t C y}^{-1}$ ).

385 Our model could be used to predict potential changes in fisheries catch given future mean  
maximum size, levels of fishing sustainability, and projections of marine production following the  
Intergovernmental Panel on Climate Change (IPCC) scenarios. The recent analysis of 50-year time  
series of sea surface temperature (SST) has shown warming trends in most of the LMEs of the  
world, with acceleration in the late 1970s-early 1980s and strong regional variations in SST change  
(Belkin 2009). Primary production remote sensing observations revealed that the recent surface  
390 temperature increase has triggered large spatial changes and a reduction in the global production of  
ocean phytoplankton since the early 1980s (e.g. Behrenfeld *et al.* 2006). This trend is especially  
marked outside the equatorial zone, where the areas of low chlorophyll production have recently  
expanded significantly (Polovina *et al.* 2008). Following our analysis, a reduction in primary  
production could have global negative impacts on fisheries catch and exacerbate current trends of  
395 overfishing. Predictions of chlorophyll-a concentrations to climate warming derived from coupled  
atmosphere-ocean general circulation models indicate little overall change in PP by 2050  
(Sarmiento *et al.* 2004). However these small changes at the global scale belie marked regional  
differences in the PP such as 17-42% contraction of productive marginal sea ice biomes and 7-16%  
expansion of the less productive subtropical oligotrophic gyres (Sarmiento *et al.* 2004). O'Connor  
400 *et al.* (2009) recently showed that the metabolic effects of temperature change will affect food web  
structure and productivity in mesocosms. Although the metabolic role of temperature is widely  
recognised (López-Urrutia *et al.* 2006; Jennings *et al.* 2008; Gascuel *et al.* 2008), temperature  
appears to be relatively unimportant compared to the other variables in our model. Outside the  
laboratory, the metabolic effect of temperature variation appears relatively unimportant at  
405 ecosystem scales compared to the level of primary production, mean body size, and degree of  
fisheries exploitation.

Our results have an important bearing for ecosystem approaches to fisheries and future climate  
change impact on global fisheries catches. First, our results show that many sustainably fished  
ecosystems may actually be drawing down the balance of ecological capital by taking fisheries  
410 catches beyond that which can be sustained by current primary production. Second, predicted  
decline in global primary production might exacerbate current trends of overfishing and may not

only lead to food security issues but also affect the human well-being and economies of many fishery-dependent countries.

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## Table captions

**Table 1** Primary production, fishing pressure, and average maximum length of fisheries catches best explain the spatial variance in fisheries catch among Large Marine Ecosystems. Summary table of the parameter estimates, degrees of freedom, standard errors, p-value, and percentage of deviance explained for the selected model.  $j$  index LME and  $\varepsilon$  is a normally distributed random variable with mean zero and constant variance

**Table 2** Global fisheries catch during 2000-2004 and maximum global fisheries catch (MGFC) predicted from quantile linear regression models for different levels of sustainability. MGFC,  $MGFC_{75}$ ,  $MGFC_{95}$  computed for all Large Marine Ecosystems, LMEs where  $P_{sust} > 75\%$ , and LMEs where  $P_{sust} > 95\%$ , respectively. Values between brackets indicate 95% confidence interval

## Figure captions

**Figure 1** Global marine primary production (PP) and fisheries production expressed in (a,c) catch (in  $t\ y^{-1}$ ) and (b,d) primary production required (PPR) to sustain catches (in  $t\ C\ km^{-2}\ y^{-1}$ ) over the long-term period (1950-2004) and recent period (2000-2004). Solid lines indicate quantile regression models with quantile  $\tau = 10\%$ ,  $50\%$ , and  $90\%$

**Figure 2** Slope of quantile regression as a function of quantile for (a,c) catch and (b,d) primary production (PP) over the long-term period (1950-2004) and recent period (2000-2004). Shaded area indicates the 95% confidence interval

**Figure 3** Change in the 90% quantile regression slope of the relationship between primary production (PP) and primary production required to sustain catches (PPR). Solid line indicates standard deviation around estimates

**Table 1**


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Selected model:  $\log(PPR_j) = P_{sust_j} + L_{max_j} + \log(PP_j) + ET_j + \varepsilon_j$

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Explanatory variable	Parameter value	Degrees of freedom	Standard Error	P-value	% Deviance explained
Probability of sustainable fishing $P_{sust}$	-0,0311	1	0,0046	< 0.001	28,24
Average maximum length $L_{max}$	-0,0384	1	0,0093	< 0.001	6,28
Primary production $\log-PP$	1,3755	1	0,2793	< 0.001	23,53
Ecosystem Type $ET$ ( <i>Tropical</i> )	1,2913		0,2577	< 0.001	30,35
Ecosystem Type $ET$ ( <i>Upwelling</i> )	3,0516	3	0,3770	< 0.001	

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**Table 2**

	Global fisheries catch 2000-2004	Maximum global fisheries catch MGFC	Maximum global fisheries catch MGFC <sub>75</sub>	Maximum global fisheries catch MGFC <sub>95</sub>
# of LMEs	54	54	31	16
Catch ( $\times 10^6$ t $y^{-1}$ )	68 (60–76)	146 (101–191)	58 (48–68)	32 (23–41)