

Bottom-up control regulates fisheries production at the scale of eco-regions in European seas

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ABSTRACT: We used primary productivity data derived from remote sensing images and catch data for the period 1998 to 2004 to characterize the productivity of eco-regions in the northeast Atlantic, Mediterranean, Black and Baltic Seas, and then analyzed the strength of the trophic linkage between primary productivity and marine fisheries production in European seas. Mean annual primary production (PP) derived from an ocean-color based model was highly contrasted among eco-regions, exceeding $500 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Marmara and North Seas but being less than $150 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Faroes, Adriatic-Ionian and Aegean-Levantine Seas. Fisheries production expressed in mean annual yield and primary production required to support catches (PPR) varied greatly among eco-regions, from 0.02 t km^{-2} and $0.7 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the oceanic northeast Atlantic eco-region to 6 t km^{-2} and $130 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Marmara Sea respectively. Linear regression models showed significant positive relationships between PP and yield as well as between PP and PPR, suggesting a strong linkage between marine productivity and fisheries production in European seas. Moreover, this bottom-up control appeared consistent over time: recent mean annual yield for the period 1998 to 2004 reflected the long-term yield averaged over the last 3 decades. We argue that such large-scale coupling is due to energy transfer along the food web (from phytoplankton to predators) through predation processes, primary productivity driving the production of living marine resources and their exploitation at the scale of eco-regions. Our findings have an important bearing for ecosystem approaches to fisheries, particularly for the estimation of the capacity of eco-regions with regard to sustainable exploitation. This is further relevant in a context of climate change, because variations in PP linked to global warming could strongly modify fisheries production in the future.

KEY WORDS: Bottom-up control · Fisheries production · Primary productivity · Ocean-color remote sensing

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INTRODUCTION

For some time, ecologists have debated what controls the processes that determine marine biomass production, i.e. whether the primary control is exerted by resources (bottom-up) or predators (top-down) (Hunter & Price 1992, Power 1992). Top-down control has been shown to be important for the structure and function-

ing of lake and marine ecosystems, the regulation by the upper food-web components sometimes affecting more than 1 trophic level through trophic cascades (Pace et al. 1999, Frank et al. 2005). Conversely, other authors argued that the regulation of all food-web components depends on the availability of food resources, so that variations in primary production (PP) can propagate up the system and affect population

dynamics at all trophic levels (Hunter & Price 1992). Some food webs are also controlled by a number of key species at intermediate trophic levels through 'wasp-waist' control, as observed for small pelagic fish in upwelling ecosystems (Cury et al. 2000). Actually, ecosystems may not be driven by only 1 type of control: these processes probably act on populations and communities simultaneously, and the balance of bottom-up vs. top-down control might depend on the ecosystem's state, diversity and integrity (Hunter & Price 1992, Cury et al. 2003).

The practical and theoretical issues raised by the debate are important because oceanic food webs support most of the world's fisheries and the balance of top-down vs. bottom-up control provides insights into our understanding of the structure and functioning of marine ecosystems (Reid et al. 2000). Following a bottom-up perspective, PP has long been considered a good predictor of the potential yield of the world's oceans (Ryther 1969). Indeed, the control of marine fish production by PP was suggested after a comparative cross-system analysis based on *in situ* data (Iverson 1990). More recently, Ware & Thomson (2005) used satellite-derived estimates of mean annual chlorophyll *a* (chl *a*) concentration to analyze the trophic coupling between biomass of primary producers and long-term sustainable fish catches in the northeast Pacific. They showed strong bottom-up trophic linkages between phytoplankton, zooplankton and catches of resident fish at the scale of regional (100 000 km²) and sub-regional (10 000 km²) areas. Furthermore, based on mean chl *a* concentration derived from remote sensing and a greenness index from Continuous Plankton Recorder (CPR) surveys, both used as proxies for PP, Frank et al. (2006) showed the dependence of long-term fishery yields on PP in the northwest Atlantic but demonstrated the necessity of considering temporal dynamics in order to quantify the balance of top-down vs. bottom-up control, which can vary spatially and temporally.

In the present analysis, we used PP estimates derived from satellite observations of surface chl *a* and fisheries data to investigate whether bottom-up forcing regulates fisheries production in the large marine eco-regions of the northeast Atlantic, Mediterranean, Black and Baltic Seas. The advent of ocean-color remote sensing that provides synoptic fields of phytoplankton biomass associated with large databases of catch statistics allowed us to conduct the study over appropriate scales of time and space. We focused both on total and plankton-feeder fisheries, because the latter fisheries could be more dependent on PP than are upper trophic levels. In order to account for energy transfer within the food web and trophic categories of species harvested, the relationship between primary

production required to support catches (PPR; Pauly & Christensen 1995) and PP was also considered. The objectives of the present study were to (1) characterize the European eco-regions by PP, catch and PPR estimates, (2) analyze the strength of the trophic linkage between primary productivity and marine fisheries production in European seas at short and long time scales, and (3) investigate the temporal consistency of this large-scale coupling over the last 3 decades.

MATERIALS AND METHODS

This section presents (1) the spatial scale of the analysis and European eco-regions; the origin and time span of the (2) primary productivity, (3) fisheries data, (4) equation and parameters required to estimate PPR; and (5) statistical models used to analyze the trophic linkage between primary and fisheries production.

European eco-regions. The geographical scope of the present study includes the marine areas of the Barcelona, Bucharest, Helsinki and OSPAR Conventions, i.e. the Atlantic Ocean east of a line from the south of Greenland (42°W), north of a line drawn west from the straits of Gibraltar (36°N), and east as far as longitude 51° E, to include the Baltic Sea, the Black Sea and the Mediterranean Sea. The Advisory Committee on Ecosystems (ACE) of the International Council for the Exploration of the Sea (ICES) recently proposed to split these areas into 13 eco-regions for the implementation of an ecosystem approach to fisheries in European waters (ICES 2004). These eco-regions were defined on the basis of biogeographic and oceanographic features, and also aimed to account for political, social, economic and management components. In the present analysis, eco-region boundaries were set to match the boundaries of the ICES and General Fisheries Commission for the Mediterranean (GFCM) statistical areas that composed them. We included the western Channel (ICES Area VIIe) into the Celtic Seas eco-region because the physical structure and phytoplankton dynamics differ between the western and eastern parts of the Channel, the western part being more stratified and oceanic (Hoch & Garreau 1998). The Marmara Sea was separated from Aegean-Levantine Seas and considered as a specific eco-region because it is a 'sea of transition' characterized by particular nutrient availability (de Leiva Moreno et al. 2000) and is considered as a statistical division within GFCM. This resulted in a total of 14 eco-regions (Fig. 1).

Primary productivity data. In the present analysis, PP was estimated in each eco-region and for each year over the period 1998 to 2004 from satellite data, using an ocean-color based approach. Satellites currently

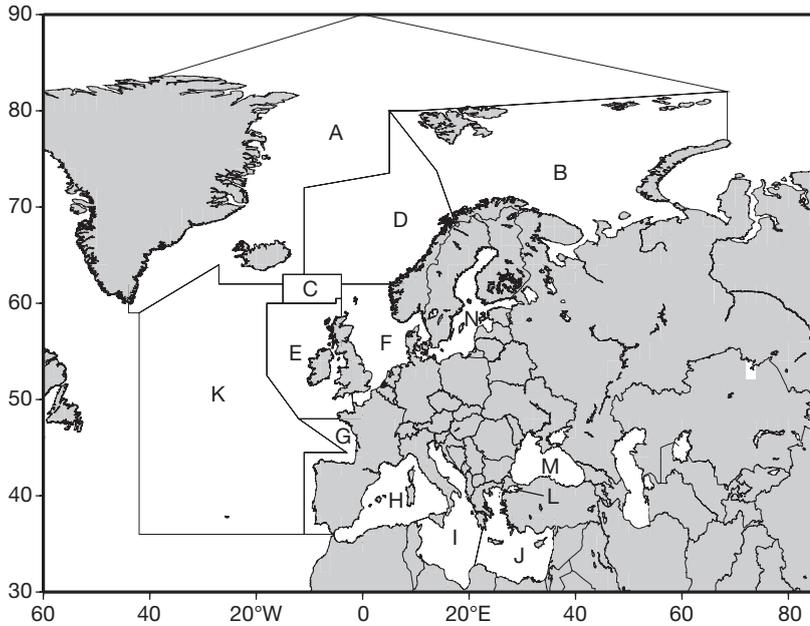


Fig. 1. Boundaries of the 14 eco-regions. (A) Greenland and Iceland Seas, (B) Barents Sea, (C) Faroes, (D) Norwegian Sea, (E) Celtic Seas, (F) North Sea, (G) south European Atlantic Shelf, (H) western Mediterranean Sea, (I) Adriatic-Ionian Seas, (J) Aegean-Levantine Seas, (K) oceanic northeast Atlantic, (L) Marmara Sea, (M) Black Sea, (N) Baltic Sea

provide ocean color images, allowing the quantification of basin-scale variability in phytoplankton production (e.g. Longhurst 1998). This is a very useful alternative to *in situ* measurements, which require significant extrapolation owing to the undersampling of ship-based estimates of global PP.

The calculations were performed using monthly global maps of surface concentrations of chl *a* provided as SeaWiFS product by the Goddard Space Flight Center (NASA). This data set has emerged as a high-quality, consistent time series that is appropriate for temporal analysis (McClain et al. 2004). PP was computed with a wavelength- and depth-resolved model that essentially follows the principles of Platt & Sathyendranath (1988), implemented on a global scale by Longhurst et al. (1995). The main elements of the model are recalled below for completeness, and the details of the changes from the original implementation of Longhurst et al. (1995) are detailed by Mélin (2003).

The spectrum of direct and diffuse solar irradiance at the ocean surface was described by the clear-sky model of Gregg & Carder (1990) with a correction for cloud cover. Subsequently, the light spectrum is propagated down the water column with a diffuse attenuation coefficient $K_d = (a + b_b)/\mu$, where a and b_b are the total absorption and back-scattering coefficients, respectively, and μ is the mean cosine of the angle of light propagation (Sathyendranath & Platt 1989). All

inherent optical properties of sea water are parameterized as a function of the chl *a* concentration. The vertical shape of the chl *a* profile is fixed for a given biogeographic province and season (Longhurst et al. 1995), and its magnitude is scaled with the surface SeaWiFS-derived chl *a*. Therefore, the value of the satellite-derived surface chl *a* sets all optical properties of the water column.

In practice, the contributions by pure sea water for a and b_b are defined according to Pope & Fry (1997) and Buitelvelde et al. (1994), respectively. The absorption term additionally includes the contributions from phytoplankton, detritus and chromophoric dissolved organic matter. The particulate back-scattering coefficient is modelled according to Morel & Maritorena (2001). The bio-optical model was operated until the spectrally integrated irradiance field became less than 0.1% of the surface photosynthetically available radiation (PAR).

PP at each depth level is proportional to chl *a*, and is a function of light through a light-photosynthesis curve defined by the photosynthetic rate at light saturation and the initial slope of the curve. With respect to Longhurst et al. (1995), updated parameters were listed by Mélin (2003) on the basis of biogeographic province and season. These calculations were conducted for 12 time steps during a day representative of the month, and PP is finally obtained by integration over depth and time. PP is then used as a proxy of all production available to upper trophic levels, because bacterial production generally represents less than 10% of PP and shows similar profiles at the scale of the Atlantic Ocean (Hoppe et al. 2002).

Fisheries data. Catch data by species, year and subdivision were available for the period 1973 to 2004 for the northeast Atlantic and Mediterranean eco-regions and were extracted from the ICES and GFCM databases. Data include all quantities caught and landed for both food and feed purposes but exclude discards. Trophic information from the FishBase database (www.fishbase.org) was used to determine which commercial species were 'plankton feeders' following de Leiva Moreno et al. (2000). Hence, 428 and 71 fish categories, i.e. all species or trophic groups recorded in the catch database, were taken into account in the study of total fish and plankton feeders respectively.

Primary production required to support catches (PPR). PPR ($\text{g C m}^{-2} \text{ yr}^{-1}$) allows a comparison of fish catches regardless of their position in the food web by expressing each species yield relative to PP (Ryther

1969, Pauly & Christensen 1995). PPR estimates were calculated for total and plankton feeders following

$$\text{PPR} = \sum_i^n \left(\frac{Y_i}{9} \right) \times \left(\frac{1}{\text{TE}} \right)^{\text{TL}_i - 1}$$

where Y_i is the yield (in metric tons) of species i , TE is the trophic transfer efficiency, i.e. the proportion of prey production converted to predator production, TL_i is mean trophic level of species i , and n is the number of species harvested. PPR estimates were based on a conservative 9:1 ratio for the conversion of wet weight to carbon (Strathmann 1967). Mean values of trophic levels assigned to each species were extracted from the FishBase database, and were assumed to be stable from year to year and valid for the total area covered by the study. TE was assumed to be constant for each trophic level within the area covered by the study and during the period considered, i.e. 1973 to 2004. A range of TE estimates (0.1 to 0.15) was used, consistent with those reported in other marine ecosystems (Ryther 1969, Pauly & Christensen 1995). Preliminary analysis showed that the rank of eco-regions relative to PPR was not modified by changes in TE, but that the absolute values of PPR were. Thereafter, a TE of 0.125 was assumed. PPR:PP ratios were calculated in each eco-region to quantify the portion of PP required to sustain the reported catches.

Relationships between PP, PPR and yield. First, we investigated whether yield was correlated with PP on short time scales in each of the eco-regions. Linear regression models and Spearman rank correlation tests were performed to analyze whether the interannual variability in fish yield (total and plankton feeders) could be explained by the interannual variations in PP between 1998 and 2004. Non-parametric Spearman tests were used because of the shortness of the time series. These temporal correlations were estimated considering a time-lag ranging from 0 to 2 yr between PP and fisheries production. Although the influence of PP on spawning and larval survivorship and the subsequent recruitment to the fishery can take more than 2 yr, young age classes of several fish can represent a large part of the total catch in several eco-regions. For instance, this is the case for anchovy *Engraulis encrasicolus* in the Mediterranean eco-regions, sandeels *Ammodytes* spp. in the North Sea and blue whiting *Micromesistius poutassou* in the North Sea and in the Greenland and Iceland Seas.

Second, correlations between yield and PP averaged from 1998 to 2004 were examined when considering the 14 eco-regions through linear regression models. The relationship between PPR (in $\text{g C m}^{-2} \text{ yr}^{-1}$) and PP was also investigated to assess how PP was used by the European fisheries. No spatial correlation was taken into account in the analysis because eco-regions were

defined on the basis of oceanographic, biogeographic and ecological criteria (ICES 2004), and were therefore considered as comprising independent data. Finally, long-term average yield (1973 to 1997) was compared with yield averaged for the most recent period (1998 to 2004) in order to assess changes that occurred in fisheries production among eco-regions in the long-term and examine the temporal consistency of the previous results.

RESULTS

Characterization of European eco-regions

The remote sensing images available for the period 1998 to 2004 reveal highly variable levels of primary production in the European eco-regions (Fig. 2a). The Mediterranean eco-regions, i.e. the Western Mediterranean Sea, Adriatic-Ionian Seas and Aegean-Levantine Seas, were characterized by low primary production ($<200 \text{ g C m}^{-2} \text{ yr}^{-1}$). In contrast, the Black Sea and especially the Marmara Sea appeared very productive (400 and $600 \text{ g C m}^{-2} \text{ yr}^{-1}$ respectively). In the northeast Atlantic, the less productive areas ($<200 \text{ g C m}^{-2} \text{ yr}^{-1}$) were located west and north, i.e. oceanic northeast Atlantic, Faroes, Greenland and Iceland Seas and the Norwegian Sea. In contrast, the eco-regions that include an important part of continental shelf, i.e. the Barents, Baltic, North and Celtic Seas and South European Atlantic Shelf were more productive (mean annual production ranging between 250 and $550 \text{ g C m}^{-2} \text{ yr}^{-1}$).

During this period, fisheries production in the eco-regions of European seas was also highly variable (Fig. 2b). Catches were highest in the Marmara Sea and North Sea, with an annual production exceeding 3.5 t km^{-2} for total fish and 2.0 t km^{-2} for plankton feeders. The Baltic Sea and Faroes were also productive, with total fish yields higher than 2 t km^{-2} . The Norwegian, Celtic and Black Seas showed intermediate fishery production of between 1.0 and 1.4 t km^{-2} . The production in the other eco-regions was lower than 1 t km^{-2} . The proportion of plankton feeders comprising total catch varied from 0% in the oceanic Northeast Atlantic to 78% in the Black Sea. Although some productive areas such as the Faroes could comprise a low proportion of plankton feeders in their total production (4.3%), total and plankton feeder fish production were highly correlated (slope = 1.62, adjusted $R^2 = 0.82$, $p < 0.001$).

The Faroes and Norwegian Sea exhibited the highest PPR:PP ratios, with values exceeding 30% for a TE of 0.125 (Fig. 2c). Such high values indicate that a large portion of the aquatic PP in these eco-regions

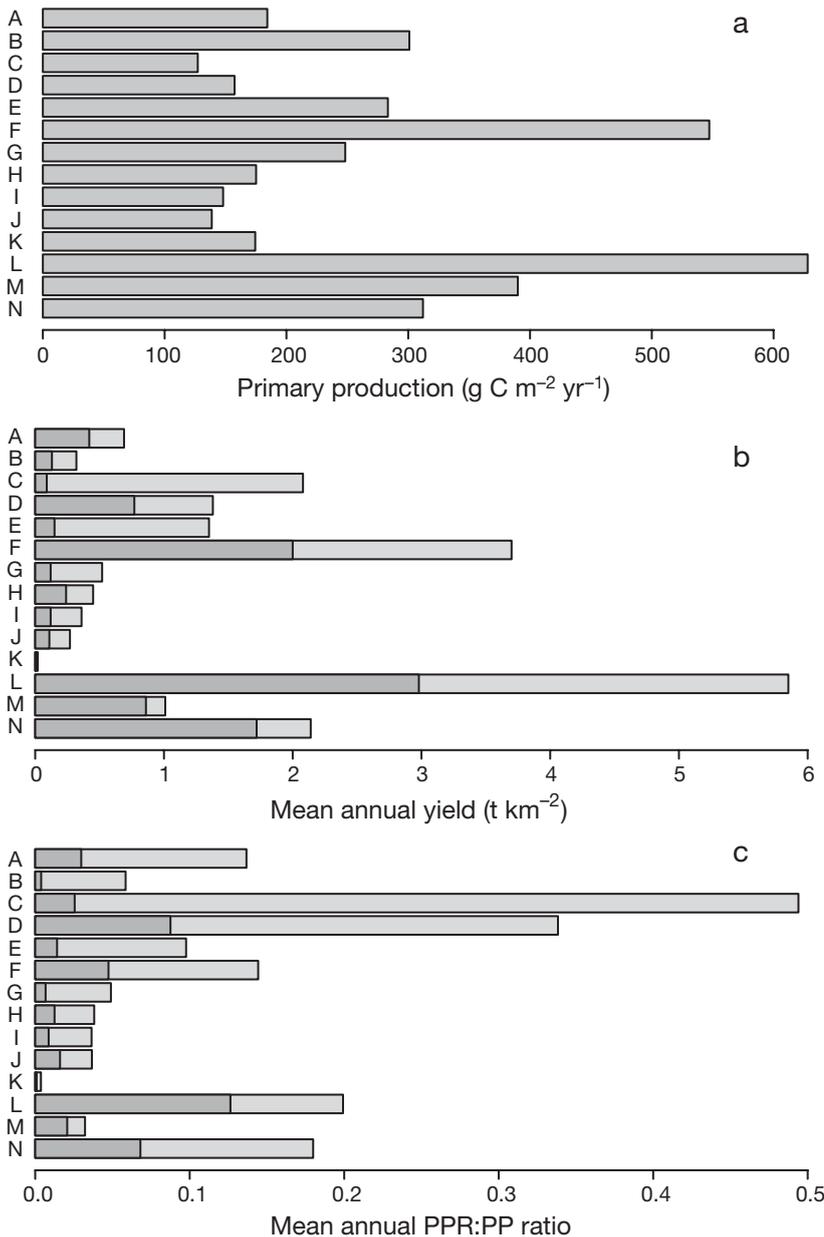


Fig. 2. Characteristics of the 14 eco-regions considered in the study for the period 1998 to 2004. (a) Mean annual primary production, (b) mean annual yield and (c) mean annual PPR:PP ratio. For (b,c), dark grey: plankton feeders; light grey: total fish

was devoted to support the fisheries that harvested high-trophic-level fish such as saithe *Pollachius virens* and cod *Gadus morhua* characterized by TLs > 4.3. The Marmara, Baltic, North, Greenland and Iceland Seas and Celtic Seas were characterized by intermediate ratio values of PPR:PP that varied between 10 and 20%. The South European Atlantic shelf, Mediterranean and Black Sea eco-regions exhibited low ratio values of PPR:PP, varying between

3 and 5%. These low values were mainly resultant from the importance of plankton feeders in total catches, namely anchovies *Engraulis encrasicolus* (TL = 2.92) and sardines *Sardina pilchardus* (TL = 2.78) and to the low contribution of high-trophic-level fish in the total yield. The oceanic north-east Atlantic had the lowest PPR:PP ratio, less than 1% regardless of the value of TE considered. This eco-region is mostly composed of open ocean in which few high trophic level species, mainly tunas, are exploited.

Interannual variability in PP and yield

Most of the eco-regions exhibited low interannual variability in PP for the period 1998 to 2004, with the exception of the Marmara Sea, which displayed a high increase from 550 g C m⁻² yr⁻¹ in 2002 to more than 750 g C m⁻² yr⁻¹ in 2004 (Fig. 3, top graphs). Despite interannual variations and increasing (e.g. Faroes) or decreasing (e.g. Greenland and Iceland Seas, Black Sea) trends observed for some of the eco-regions, the spatial differences were greater than the temporal differences.

The low level of interannual variability with regard to spatial gradients was also mostly verified for total fish yield (Fig. 3, middle graphs) and PPR to support total fish catches (Fig. 3, bottom graphs); however, the Faroes and Barents Sea exhibited important interannual changes in yield and PPR during this period.

No interannual correlation was found between PP and yield (total and plankton feeders) or between PP and PPR when using linear regression models and Spearman rank correlation tests with 0, 1 or 2 yr time lags. Interannual variations in PP do not seem to explain the temporal variability in catches.

Spatial trophic linkage

A significant positive relationship was found between mean annual PP (g C m⁻² yr⁻¹) and mean annual yield (t km⁻²) when considering total fish

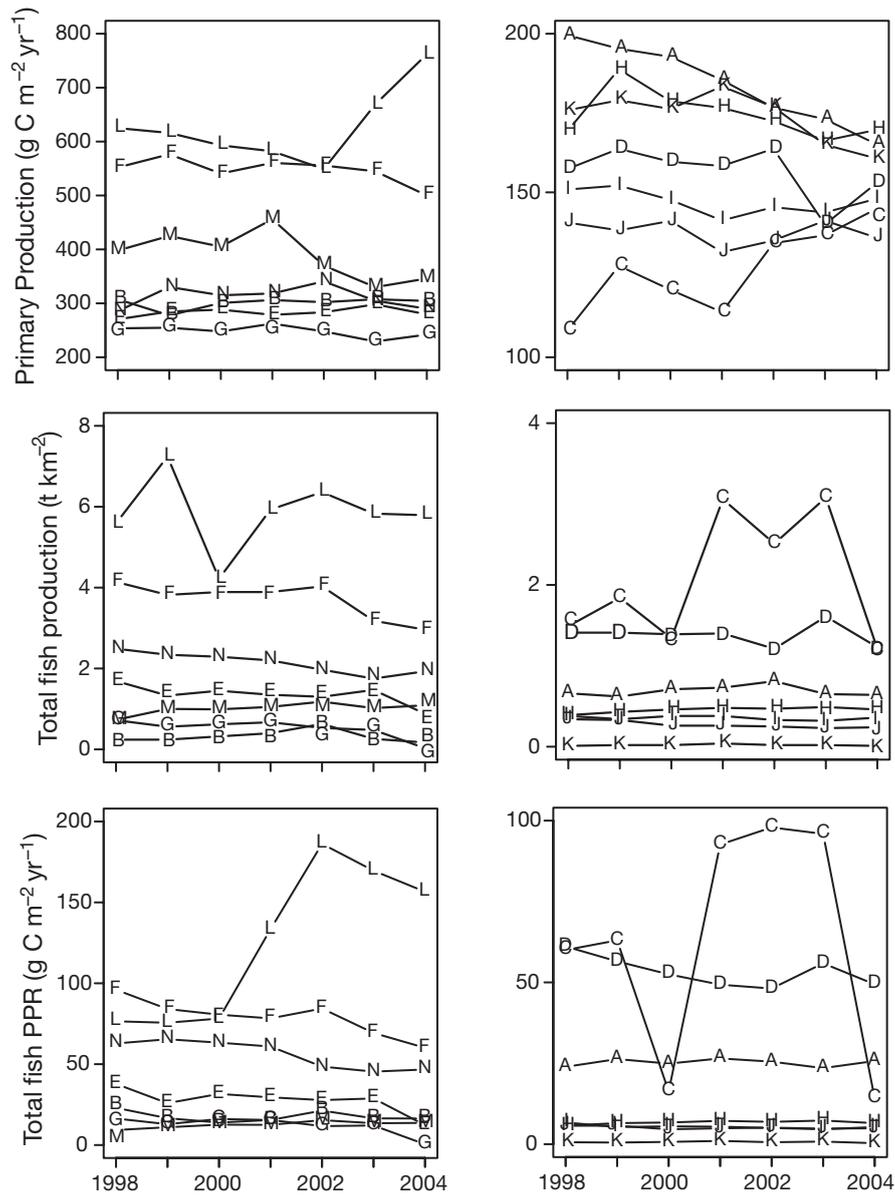


Fig. 3. Annual values of (top) primary production (PP), (middle) total fish production and (bottom) primary production required to support catches (PPR) for each of 14 eco-regions, 1998–2004. Scales were selected for readability along y-axes. See Fig. 1 for eco-region codes

(slope = 0.0085, adjusted $R^2 = 0.64$, $p < 0.001$; Fig. 4a). These findings were reinforced by the strong correlation between PP and mean annual yield of plankton feeders, these species being more directly related to phytoplankton production (slope = 0.0051, adjusted $R^2 = 0.73$, $p < 0.001$; Fig. 4b). These relationships suggest a strong bottom-up trophic linkage between the productivity of the eco-regions and fish catches. Spatial variability in annual PP accounted for more than 60% of the spatial variance in mean fish yield in European seas. This reveals a dominant bottom-up control

between PP and marine fish communities in the north-east Atlantic and the Mediterranean, Black and Baltic Seas at the ecosystem scale.

Furthermore, the relationship between PP and PPR was significant when considering either total fish (slope = 0.16, intercept = -9.2, adjusted $R^2 = 0.45$, $p < 0.01$; Fig. 5a) or plankton feeders (slope = 0.11, adjusted $R^2 = 0.62$, $p < 0.001$; Fig. 5b). Because PPR quantifies fish yield on the same basis, i.e. relative to the phytoplankton considered as Trophic Level 1 in the food web, these linear models confirm

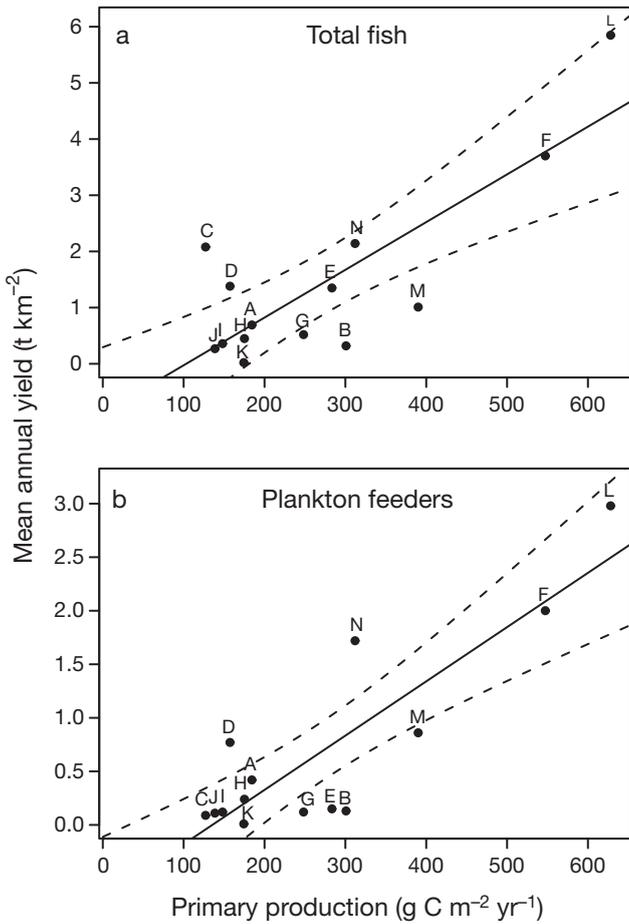


Fig. 4. Mean annual yield as a function of primary production (PP) in each of 14 eco-regions for (a) total fish and (b) plankton feeders. Solid lines: linear regressions fitted to data (see text for details); dashed lines: 95% confidence levels around regression lines. See Fig. 1 for eco-region codes

the strong bottom-up trophic coupling between primary and fisheries production in the European seas.

Long-term trophic linkage

The significant relationship found between long-term (1973 to 1997) and recent yield (1998 to 2004) (slope = 0.72, adjusted $R^2 = 0.70$, $p < 0.001$; Fig. 6) revealed that the current fish production observed in European seas reflected the long-term average fish production in the different eco-regions. Catch levels were thus time-consistent in most of the eco-regions with the exceptions of the Marmara and North Seas, which exhibited an important increase and decrease in fisheries production, respectively, during the recent (1998 to 2004) period. A highly sig-

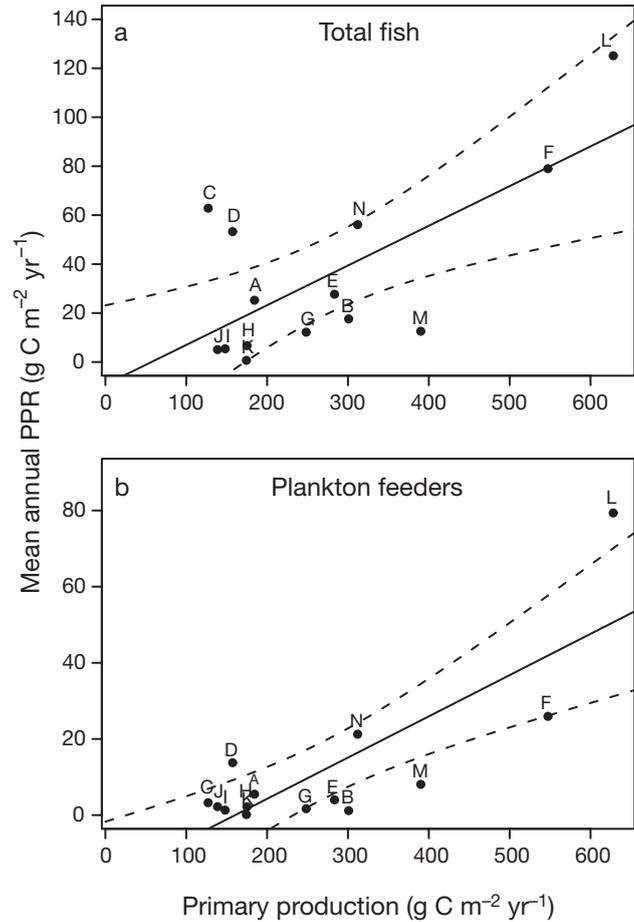


Fig. 5. Mean annual primary production required to support catches (PPR) as a function of primary production (PP) in each of 14 eco-regions for (a) total fish and (b) plankton feeders. Solid lines: linear regressions fitted to data (see text for details); dashed lines: 95% confidence levels around regression lines. See Fig. 1 for eco-region codes

nificant relationship (slope = 0.007, adjusted $R^2 = 0.66$, $p < 0.001$) was found when fitting a linear regression model to PP and long-term annual yield, i.e. averaged over the period 1973 to 1997. This demonstrates the long-term consistency of the trophic linkage between PP and yield in the study area, assuming that PP estimates for the period 1998 to 2004 reflect the large-scale spatial gradients in PP over time.

DISCUSSION

The present study indicates that bottom-up forcing regulates the production of marine living resources in the European seas, i.e. fisheries production levels in European eco-regions are largely determined by the PP of the underlying marine ecosystems. We showed

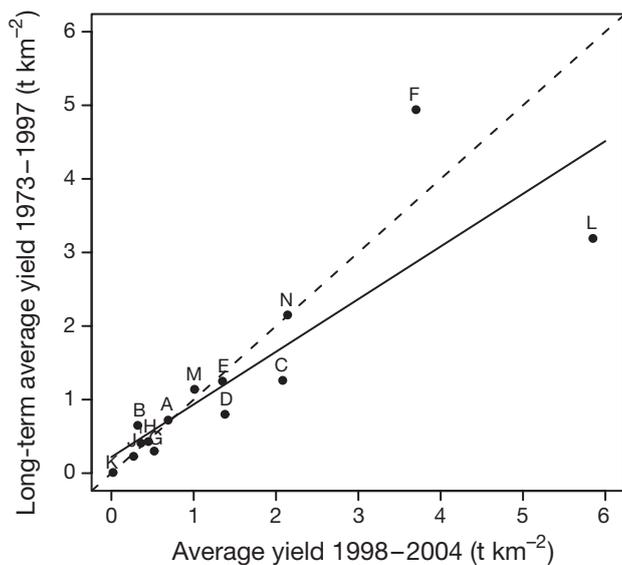


Fig. 6. Long-term average yield for the period 1973–1997 vs. recent average yield for the period 1998–2004. Solid line: linear regression fitted to data; dashed line: first bisecting line. See Fig. 1 for eco-region codes

that this bottom-up control acts at an ecosystem level over very large spatial scales (eco-regions: millions of km²). Moreover, comparison of long-term yield vs. recent yield showed that the gradient between high and low productive regions has not been modified over the last 3 decades. These findings, together with the predominance of spatial over temporal variability in PP (Fig. 3), suggest that bottom-up trophic linkages have been controlling fish production in the European seas for more than 30 yr.

Data reliability

Several caveats regarding the data and assumptions made in the analysis that could bias our quantitative results were identified. PP estimates were issued from an ocean-color based model that takes into account the light-photosynthesis curve and chl *a* depth profile (Mélin 2003). In the framework of an international inter-comparison exercise, the outputs of the PP model were generally consistent with global or basin estimates of marine PP given by 24 models relying on ocean-color data (Carr et al. 2006). Although more work is needed on the comparison of model outputs with *in situ* data, preliminary results indicate that the considered PP model performs relatively well with respect to other models when its outputs are compared with field measurements (Mélin 2003). The main sources of uncertainty for the PP estimates are

- The retrieval of chl *a* concentration from ocean-color remote sensing, which is still associated with reasonably large uncertainties in the optically complex waters of some coastal areas, especially when turbidity becomes greatly increased owing to suspended and dissolved material. This is typically the case in the coastal North Sea and might explain some the differences between the PP averages used in the present study and some values derived from field measurements as reviewed by Greenstreet et al. (1997). The accuracy of the SeaWiFS chl *a* product is much better constrained for open ocean waters
- The simplified model representation of phytoplankton physiology and its vertical distribution, which results in discrepancies when model outputs are directly compared with measurements of individual stations. This uncertainty is somewhat alleviated by taking spatial and/or time averages (Siegel et al. 2001)

In spite of these caveats, PP 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).

Catch data can be altered by discards, dishonesty and the logistic difficulties of collecting statistics. Because data used in the present study have been managed by ICES and GFCM for quite some time, we should expect good homogeneity in the data sets despite possible dissimilarities in the accuracy of catch reports among member countries. Thus, possible bias owing to unreliable data should be small, and the large scale of the study and aggregation of catch at the eco-region level enable us to suppose that our results are not a consequence of artifacts arising from these problems.

PPR estimates were based on constant TLs; however, individual TLs can vary in space and time according to prey availability and ontogenic changes (Jennings et al. 2002a). Furthermore, changes in size structure owing to fishing can affect species TL (Jennings et al. 2002a). The FishBase database remains the best source of available information on fish trophic ecology at such a large scale, and contrasts in species' TLs generally exceed the more subtle declines caused by shifts in species' size structures. Also, TE was assumed constant despite the fact that it can vary among TLs and ecosystems (Ryther 1969). Given the lack of precise information on TE in the complex marine food webs of European seas, we assumed a mean TE of 0.125, which corresponds well with values reported in the literature (Ryther 1969). In the future, methods coupling analyses of size and trophic structure would facilitate the improvement of our knowledge on trophic TE in marine ecosystems (Jennings et al. 2002b).

Despite all these caveats, when the large degree of spatial heterogeneity in PP, catch and PPR among eco-regions is considered—i.e. the broadness of the observed patterns—our main conclusion still stands: fisheries production levels in marine European ecosystems are largely determined by PP.

Bottom-up trophic linkage

PP computed from remote sensing data reflects large spatial gradients in marine and coastal primary productivity, which are consistent with knowledge and observations available on these systems. A large number of physical, biological and anthropogenic features are responsible for the spatial differences of PP in European seas. In the Mediterranean, the water exchange at Gibraltar could be one of the main causes of the oligotrophic nature of water masses. The impoverishment of Mediterranean waters (in terms of nutrient availability) increases from west to east as Atlantic surface water is progressively depleted of nutrients (de Leiva Moreno et al. 2000). By contrast, the Black and Marmara Seas are nutrient-rich eco-regions, notably owing to excess in nitrogen and phosphorus loadings from human activities on adjacent watersheds. The main effect of the increased nutrient load is greater PP by the phytoplankton, with blooms maintained during the whole vegetation period (Cederwall & Elmgren 1990). In the same way, the high productivity of the Baltic and North Seas is partly explained by the high levels of nutrient discharge from rivers, run-off and the atmosphere (EEA 2001). Compared with these regions, the Celtic Seas and South European Atlantic Shelf—mainly composed of continental shelf—are characterized by intermediate levels of PP because they are less subject to nutrient discharge and are more open towards the Atlantic ocean. Finally, the oceanic north-east Atlantic and Greenland and Iceland Seas are oligotrophic eco-regions mainly owing to their small continental shelf area and low nutrient load, which limit production rates.

Linear regression models were fitted to catch and PP data because there was no *a priori* reason to expect a non-linear relation between ocean fisheries production and phytoplankton production (Iverson 1990). As in the studies of Ware & Thomson (2005) and Frank et al. (2006), linear models were used to demonstrate the strong positive relationship between PP and fish production based on data from various oceanic and coastal ecosystems of the northeast Atlantic and European marginal seas; however, they were not used to explore the mathematical form of the underlying processes. It remains to be seen whether these processes are non-linear: they depend both on the ecological characteris-

tics of marine ecosystems (e.g. food chain length) and fishing patterns (e.g. fishing selectivity).

Our results indicate that large-scale spatial variability in PP determines large-scale spatial gradients in fisheries production. The strong coupling between marine productivity and fisheries production observed across wide spatial scales, as shown by the empirical relationships, reveals that similar mechanisms may underlie the functioning of the oceanic and coastal ecosystems, despite large differences in the marine food webs of European seas. In addition, the deviation of each eco-region from the average relationship between PP and fisheries production may provide interesting insights into their characteristics. For instance, the high yield observed in the Faroes for the period 1998 to 2004 is explained by large catches of blue whiting *Micromesistius poutassou* during their large annual migration from Porcupine Bank area west of the British Isles to the Norwegian Sea (Hansen & Jákupsstovu 1992). The anomalous high yield with regard to regional PP then reflects fisheries production imported from adjacent eco-regions and is due to the small size of the Faroe eco-region. In contrast, the negative outlier obtained for the Black Sea could be related to the poor environmental condition of the area, which is characterized by a high degree of eutrophication and is associated with the collapse of several demersal and benthic fish stocks (EEA 2001, Daskalov 2002).

We suggest that the consistent patterns observed result from energy transfer along the food web, i.e. from the biomass produced by phytoplankton photosynthesis transferred to upper trophic levels via predation. However, it remains difficult to distinguish between the various components of bottom-up control, which include direct effects of prey availability on predator growth, reproduction and larvae survival, and indirect effects such as competition for food between predators. Our findings are in accordance with the results of Menge et al. (1997), who demonstrated the effects of phytoplankton abundance on benthic communities. Patterns of bottom-up trophic linkage were also found in the northeast Pacific and northwest Atlantic (Ware & Thomson 2005, Frank et al. 2006). Based on the relationships between phytoplankton prey and herbivorous copepod abundance data, available on an ocean-basin scale from CPR surveys, Richardson & Schoeman (2004) recently provided evidence for dominant bottom-up control within the plankton community in the northeast Atlantic. Our analysis, which derived from different data sets, shows a similar type of control in the marine eco-regions of the northeast Atlantic, Mediterranean, Black and Baltic Seas, and leads to the conclusion that bottom-up effects propagate up food webs and

affect commercial fish communities and catch at the ecosystem scale.

Spatial gradients in fisheries production in European seas were consistent over time, despite variations in catch in the Marmara and North Seas. The increase in fisheries production in the Marmara sea is mainly explained by the low production in the 1970s and the development of the fisheries hereafter. The strong decrease in catch in the North Sea is attributed to the high levels of exploitation that led to the overfishing of many North Sea stocks (ICES 2004). In addition, although some ecosystems in the North Atlantic may have experienced changes in PP since the 1950s (Reid et al. 1998), the predominance of spatial over temporal gradients in PP (Fig. 3) allowed us to assume that PP estimates derived from ocean-color remote sensing for the period 1998 to 2004 sufficiently characterize the marine productivity of the eco-regions over time (see Ware & Thomson 2005). This suggests that European fisheries production has been driven by bottom-up control processes for >30 yr.

In contrast, interannual variations in PP did not explain short-term variability in fisheries production, suggesting that other ecological processes control marine fish production over short time scales. Variations in catch inherent to changes in PP might be concealed by time delays associated with the number of fish age classes or transitory situations and dampened by species interactions (Micheli 1999). In particular, top-down control has been shown to regulate fish and plankton communities, and this might explain the absence of a relationship between PP and fisheries production over short time scales (Cury et al. 2003, Frank et al. 2005). Analysis of temporal dynamics in the northwest Atlantic demonstrated that top-down effects combine with bottom-up control to govern functional group abundances, leading to spatial and temporal variance in trophic control at a regional scale (Frank et al. 2006). Therefore, top-down control can still matter at a species level, even if bottom-up control sets limits on total production (which is essential to fisheries and markets).

Consequences of bottom-up linkage for an ecosystem approach to fisheries

The strong trophic linkage between PP and fish catches has an important bearing for an ecosystem approach to fisheries because it clearly illustrates the link between an ecosystem's state and the capacity of that eco-region with regard to sustainable exploitation. Changes in environment can strongly affect marine fish productivity as well as ecosystem carrying capacity, and this clearly calls for a holistic view of fisheries

management that must be considered within an ecosystem framework.

This is critical for the European fisheries in the context of global change, because phytoplankton and zooplankton populations seem to be responding to a changing climate in the northeast Atlantic (e.g. Richardson & Schoeman 2004). The expected response of marine ecosystems to the predicted significant increase in Earth's surface temperature in the forthcoming years greatly differs among biogeographical provinces (Sarmiento et al. 2004). Although complex and still exploratory, predicted variations in PP in the north Atlantic as a response to climate warming, together with our findings, indicate that limits of fisheries production will be strongly modified over the next decades. A better understanding of the magnitude and trends of such changes, which are critical to fisheries management, will require stronger interaction between physical oceanographers and fisheries scientists.

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