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Is fisheries production within Large Marine Ecosystems determined by bottom-up or top-down forcing?

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Abstract

Understanding the mechanisms driving fisheries production is essential if we are to accurately predict changes under climate change and exploit fish stocks in a sustainable manner. Traditionally, studies have sought to distinguish between the two most prominent drivers, 'bottom-up' (resource driven) and 'top-down' (consumer driven); however, this dichotomy is increasingly proving to be artificial as the relative importance of each mechanism has been shown to vary through space and time. Nevertheless, the reason why one predominates over another within a region remains largely unknown. To address this gap in understanding, we identified the dominant driver of commercial landings within 47 ecosystems, encompassing a wide range of biogeochemical conditions and fishing practices to elucidate general patterns. We show that bottom-up and top-down effects vary consistently with past fishing pressure and oceanographic conditions; bottom-up control predominates within productive, overfished regions and top-down in relatively unproductive and under-exploited areas. We attribute these findings to differences in the species composition and oceanographic properties of regions, together with variation in fishing practices and (indicative) management effectiveness. Collectively, our analyses suggest that despite the complexity of ecological systems, it is possible to elucidate a number of generalities. Such knowledge could be used to increase the parsimony of ecosystem models and to move a step forward in predicting how the global ocean, particularly fisheries productivity, will respond to climate change.

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Introduction

The speed and magnitude of projected climatic changes will significantly impact life in the world's oceans (Hoegh-Guldberg and Bruno 2010). Global changes in sea surface temperature and primary production are projected to shift the distribution (Perry *et al.* 2005) and reduce the body size (Cheung *et al.* 2013) of species, in turn changing the composition of communities and altering the functioning of ecosystems (Doney *et al.* 2012). As oceans are fundamental to our economic welfare and well-being (Costanza 1999), concerns have been raised as to the impact of these changes upon the range of goods and services currently provisioned (e.g. Levin and Lubcehnco 2008); in particular, with burgeoning human populations and stagnating world fisheries catch, there is increasing concern regarding the impact of climate change upon fisheries production (Brander 2007; Garcia and Rosenberg 2010).

To date, attempts to project future fisheries production have been hampered by difficulties in evaluating the impact of environmental change upon marine ecosystems (Brander 2007); whilst field or laboratory-based studies can provide an insight as to how individuals or populations may respond (e.g. Riebesell *et al.* 2000; Wernberg *et al.* 2012), the complexity of ecosystems precludes experimental approaches. As a result, researchers frequently turn to mathematical models to provide a theoretical framework from which alternative hypotheses can be tested and projections made (e.g. Brown *et al.* 2010; Cheung *et al.* 2010). Nevertheless, whilst modern computing power makes this an attractive approach, models rely on user-specified assumptions regarding the dominant controls within a system; consequently, elucidating the drivers dictating production is an imperative step to ensure that models are specified accurately and their subsequent projections are reliable.

It is clear from a vast literature that a combination of bottom-up (e.g. environmental) and top-down (e.g. fishing) factors determines fisheries production; however, at present, the relative importance of each remains poorly understood. It has long been assumed that the effects of fishing dominate and that changes in production closely reflect changes in fishing effort. Nevertheless, whilst this theory is supported by the seminal work of Beverton and Holt (1957), results obtained from empirical studies have suggested otherwise that finding productivity at higher trophic levels to be driven from the bottom-up (Nixon *et al.* 1986; Ware and Thomson 2005; Chassot *et al.* 2007). Recently, however, a more balanced view has emerged in which both forces are seen to act in concert upon marine ecosystems (Mackinson *et al.* 2009), with the relative strength of each varying in space and time (Frank *et al.* 2007; Fu *et al.* 2012). Nevertheless, whilst the search for a simple, single pattern applicable across all situations has given way to more versatile approaches, the studies to date have investigated such issues within a single type of ecosystem (predominately temperate regions within the North Atlantic), making it difficult to infer the generality of the findings or the factors mediating the relative strength of each driver (Link *et al.* 2012). Consequently, within this study, we aim to determine the drivers of fisheries production upon a global scale, exploring the extent to which their relative importance varies across a diverse range of ecosystems, with differing climatic properties and community structure, in an attempt to reveal factors influencing their prominence.

As numerous biotic and abiotic variables that differ among systems may influence the relative importance of top-down and bottom-up effects, the three factors considered within this study, namely

(i) the average maximum length of the catch within a region; (ii) a region's biogeochemical environment; and (iii) its probability of being sustainably fished, are included based upon the results of previous studies and ecological theory:

The average maximum length of the catch landed within a region was considered for a number of reasons; firstly, body size is a fundamental biological characteristic that scales with many ecological properties (e.g. Woodward *et al.* 2005 and references therein); secondly, the distribution of smaller bodied species has been shown to change more rapidly in relation to environmental conditions compared with that of larger species (Perry *et al.* 2005); finally, the size of the species targeted by a fleet influences the quantity of, and variability in, its landings (Carscadden *et al.* 2001; Denney *et al.* 2002; Reynolds *et al.* 2005). The biogeochemical properties of a region (e.g. unproductive or productive; cold or warm) were considered based on the results of studies within terrestrial (Oksanen and Oksanen 2000), freshwater (Hoekman 2010) and marine (Finlay *et al.* 2007; Frank *et al.* 2007) systems demonstrating its influence upon the relative strength of bottom-up and top-down trophic forcing. The probability of a region being sustainably fished was considered to capture the multitude of ways in which fishing has influenced the dynamics, structure and functioning of marine ecosystems (Jennings *et al.* 1999; Stevens 2000; Anderson *et al.* 2008; Coll *et al.* 2008; Perry *et al.* 2010; Frank *et al.* 2011).

To evaluate the influence of these factors upon the driver of production within a region, we first determined the dominant driver within 47 of the 64 globally distributed Large Marine Ecosystems and subsequently tested for significant differences in the average sea surface temperature, primary productivity, maximum length of the fish landed and historical fishing pressure between regions driven from the bottom-up and top-down.

Methods

Large Marine Ecosystems (LME) (http://www.lme.noaa.gov/; accessed 12/12/2013) were selected as the spatial unit of study: LMEs are regions of the world's oceans characterized by distinct bathymetry, hydrography, productivity and trophically dependent populations (Sherman 1994). LMEs encompass a wide range of environmental conditions and levels of anthropogenic disturbance and subsequently provide an ideal spatial unit in which to explore the questions identified. Following Chassot *et al.* (2007) and Friedland *et al.* (2012), 17 of the 64 LMEs were excluded from the analysis based on the detail and reliability of the information, together with LMEs from an inland sea or where fishing was hampered by icy conditions. The time period selected (1998–2006) represented, at the time of this study, the longest continuous period for which all information was available.

Determining the drivers of fisheries production

A dynamic factor analysis (DFA) was used to determine, for each LME, the combination of explanatory variables that best explained temporal variance in its fisheries production. DFA is a multivariate time-series analysis method that attempts to identify underlying latent trends, the influence of explanatory variables and interactions between multivariate time series (Zuur *et al.* 2003). In a dynamic factor model, time series are expressed in terms of a linear combination of common trends, cycles, seasonal effects, explanatory variables and noise; each of these components is assumed to be stochastic. The structural time-series model is as follows:

$$s_n(t) = \sum\nolimits_{m=1}^{M} \gamma_{m,n}\alpha_{m(t)} + \mu_n + \sum\nolimits_{k=1}^{K} \beta_{k,n}x_k(t) + \varepsilon_n(t)$$
$$\text{and} \quad \alpha_m(t) = a_m(t-1) + n_m(t)$$

where $S_n(t)$ is the value of the nth response variable at time t, which in this case represents fisheries yield at time t. $\sum_{m=1}^{M} \gamma_{m,n}\alpha_{m(t)}$ is a linear combination of common trends, in which $a_m(t)$ is the mth unknown common trend at time t, and $\gamma_{m,n}$ is the factor loading or weighting coefficients for each $\alpha_m(t)$ trend. The terms $\varepsilon_n(t)$ and $n_m(t)$ are noise components. The term μ_n is the nth constant-level parameter (intercept term) which increases or decreases the linear combination of common trends. $\sum_{k=1}^{K} \beta_{k,n}x_k(t)$ represents a linear combination of explanatory variables, in which $\beta_{k,n}$ represents the regression coefficients for the kth explanatory variables $x_k(t)$. Fisheries yield was used as the response variable and time series of sea surface temperature (SST), chlorophyll *a* (ChlA) and fishing effort as explanatory variables. The models fitted ranged from the simplest (with no explanatory variable) to the most complex (including all explanatory variables and random noise), and model selection was performed using Akaike's information criterion (AIC).

To determine the relative importance of each explanatory variable, we first calculated the 'support' of each DFA model according to the AIC differences (Δ_i) between each model (i) and the AIC value of the top-ranked model, with models with $\Delta_i > 2$ dismissed (Burnham and Anderson 2002). Then, for the retained set of models (i.e. $\Delta_i < 2$), Akaike weights (w_i) were calculated to represent the relative likelihood of each model and the relative importance of each explanatory variable (j) calculated as the sum of w_i across all models where variable j occurred (Burnham and Anderson 2002).

Determining under what conditions top-down or bottom-up factors dominate

Large Marine Ecosystems in which ChlA or SST was the most important correlate of production were classified as being driven from the 'bottom-up', whilst regions where fishing effort was found to be of greater importance were classified as 'top-down'.

A pairwise t-test with Bonferroni's correction was used to test the null hypothesis that there would be no significant difference in four factors: the average maximum length of the fish landed; biogeochemical properties (chlorophyll *a* concentration and sea surface temperature); and probability of being sustainably fished, between LMEs driven from the top-down and bottom-up. Additionally, to determine and provide an indication of the importance of each of these factors, we used binomial logistic models to regress each factor against the dominant form of trophic control within a region. Model selection followed a stepwise procedure, combining both a forward and a backward approach minimizing Akaike's information criterion (AIC) and only retaining significant variables in the model, thereby arriving at the minimum adequate model explaining differences in the drivers of production between LMEs from the potential correlates considered.

Data collection

As a measure of annual sea surface temperature, we used Pathfinder (v.5.2; http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/) data derived from the Advanced Very High Resolution Radiometer infrared satellite (http://podaac.jpl.nasa.gov; accessed 12/12/2013), using only those associated with the highest level of quality at a spatial resolution of 4 km. Chlorophyll *a* concentrations were derived from satellite remote sensing data collected from the Sea-Viewing Wide Field-of-View Sensor (http://oceancolor.gsfc.nasa.gov; accessed 12/12/2013) using level-3 processed data. ArcMap (http://www.esri.com/software/arcgis) was used to average the variables over each LME, which were then standardized by dividing annual values by the overall mean. Historical fishing pressure was measured as the probability of the ecosystem to be sustainably fished (P_{sust}) based on the total removal of secondary production compared with reference levels derived from ecosystem models (Coll *et al.* 2008).

Results

Drivers of production

Within the majority of Large Marine Ecosystems (36 of the 47 considered), fisheries production varied as a function of bottom-up (environmental) and top-down (fishing) forcing. For 18 of these regions, the most parsimonious model contained all explanatory variables (i.e. sea surface temperature, chlorophyll *a* and fishing effort); however, for 12 regions, the inclusion of sea surface temperature (SST) reduced model fit and only chlorophyll *a* (ChlA) and fishing effort were retained, whilst for six regions, fishing effort and SST were retained and ChlA dropped.

In general, top-down drivers (fishing) had the most widespread effect on production, proving the most important correlate of commercial landings within 16 LMEs (Table 1). Of the bottom-up forces, ChlA was of greatest importance with 12 regions and SST within 8; however, for 11 LMEs, no variable proved to be of greater significance (Table 1). There was a particularly striking spatial dimension to the findings; production within southern, low-latitude LMEs was generally best explained by changes in fishing effort, whilst ChlA was of greater importance within mid-latitude regions and SST within northern, high-latitude LMEs (Fig 1; Table 1). However, there were a number of exceptions to this pattern; the yield within LMEs associated with Eastern Boundary upwelling currents was primarily correlated with ChlA, irrespective of the latitude of the LME. Furthermore, fishing effort proved to be the most important factor in a number of LMEs (e.g. the Newfoundland Shelf) not found at lower latitudes (Fig 1).

Table 1 Dominant form of trophic forcing within 47 Large Marine Ecosystems based on correlation analysis of interacting trophic levels together with the principal factor driving changes in the regions fisheries yield (*c*).

Bottom-up		Top-down		Inconclusive	
LME	*c*	LME	*c*	LME	*c*
Agulhas Current	ChlA	Caribbean Sea	Effort	Celtic-Biscay Shelf	–
Arabian Sea	ChlA	East Brazil Shelf	Effort	Gulf of Mexico	–
Bay of Bengal	ChlA	E.C Australia	Effort	Iceland Shelf	–
Benguela Current	ChlA	Gulf of Thailand	Effort	Mediterranean Sea	–
California Current	ChlA	Newfoundland Shelf	Effort	North Brazil	–
Canary Current	ChlA	New Zealand	Effort	Norwegian Sea	–
East Bering Sea	SST	North Australia	Effort	Red Sea	–
Gulf of Alaska	SST	N.E Australia	Effort	Sea of Japan	–
Gulf of California	ChlA	N.W Australia	Effort	Southeast U.S	–
Guinea Current	ChlA	Okhotsk Sea	Effort	Somali Current	–
Greenland Shelf	SST	Patagonian Shelf	Effort	Scotian Shelf	–
Humboldt Current	ChlA	P. C American	Effort		
Iberian Coastal	SST	S.W Australia	Effort		
Indonesian Sea	ChlA	S.E Australia	Effort		
Kuroshio Current	ChlA	W.C Australia	Effort		
Northeast US	SST	Sulu-Celebes Sea	Effort		
Oyashio Current	SST				
South Brazil Shelf	ChlA				
North Sea	SST				
West Greenland	SST				

LME, Large Marine Ecosystems; SST, sea surface temperature.

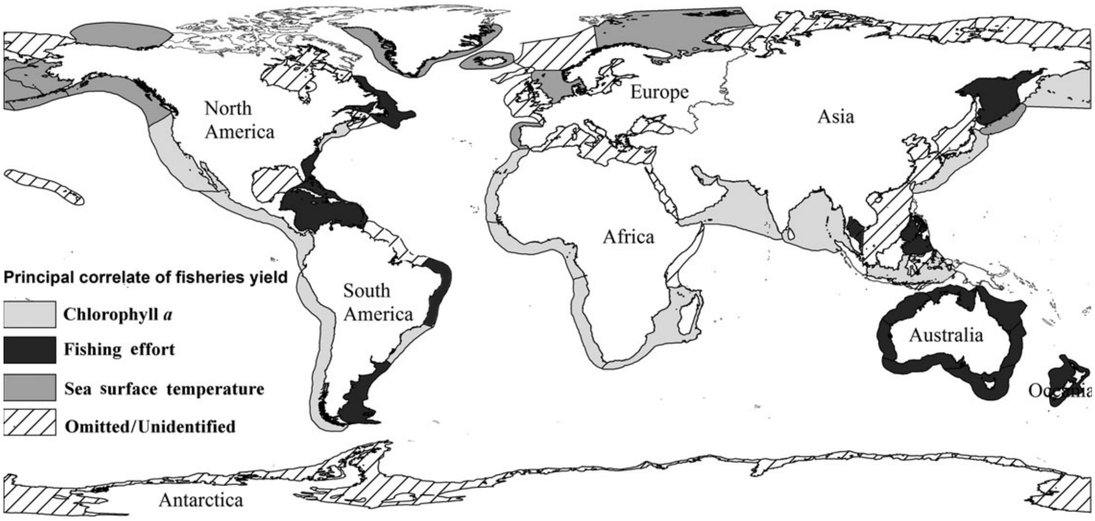

Figure 1 The geographical distribution of the correlates of fisheries yield within Large Marine Ecosystems.

Factors influencing the relative importance of top-down or bottom-up forces

Grouping LMEs according to their prominent driver of production (top-down or bottom-up) revealed significant differences in chlorophyll *a* concentrations (two-tailed *t*-test, $t_{46} = 3.17$, $P = 0.002$); the average maximum length of the fish landed within the regions ($t_{46} = 2.91$, $P = 0.004$); and the probability of the ecosystems being sustainably fished ($t_{46} = 4.79$, $P = 0.002$) between groupings. Bottom-up forcing predomi-

Table 2 Full model and MAM from multiple regression of predictors of trophic forcing coded as a binomial variable: bottom-up (0), top-down (1). Full model: AIC = 63.98 and minimum adequate model AIC = 52.38.

	Full model			MAM		
Predictor	Coefficient	SE	*P*	Coefficient	SE	*P*
ChlA	−0.815	0.063	**0.043**	–	–	–
L_{max}	−1.218	0.041	**0.031**	−0.068	0.029	**0.022**
P_{sust}	1.642	0.035	**0.028**	0.072	0.031	**0.019**
SST	−0.020	0.057	0.722	–	–	–

AIC, Akaike's information criterion; MAM, minimum adequate model. Bold indicates $P < 0.05$.

nates in relatively productive regions in which the average size of the species landed is small and the regions had a comparatively low probability of being sustainably fished (Table 1). However, no difference was found in the average sea surface temperatures between the groups ($t_{46} = 1.43$, $P = 0.100$).

The result obtained from the multiple regression analysis support the findings outlined above; with sea surface temperature found to be the only non-significant predictor from the range considered. However, the minimum adequate model showed that a model containing the average size of the species landed and the probability of the ecosystem being sustainably fished provided the best fit to the data; omitting a regions productivity as a predictor (Table 2).

Discussion

This is the first attempt to model the relationship between fisheries production and environmental and anthropogenic drivers on a global scale; thus, the results obtained provide unique insight into the relative importance of 'bottom-up' (resource) and 'top-down' (fishing) mechanisms.

Within the majority of Large Marine Ecosystems (LME), models that contained a combination of top-down and bottom-up drivers proved to be the most informative in explaining variation in fisheries landings, complimenting the findings of Chassot *et al.* (2010) and Friedland *et al.* (2012) by highlighting that the relationship between fisheries yield and primary production is more complex than had been previously suggested (Nixon *et al.* 1986; Ware and Thomson 2005; Chassot *et al.* 2007). The inherent complexity of marine ecosystems may suggest that this is an intuitive conclusion; nevertheless, in most cases, the explicit goal of researchers has been to determine the primacy of a single driver type, be it bottom-up or top-down, rather than giving a balanced view to each (Planque *et al.* 2010). However, the novel methodology used within this study, that is, determining the drivers of production *within* a number of regions rather than analysing mean values *across* regions, provides clear and compelling evidence that dichotomous approaches are often too simplistic.

Whilst it is clear from our results that both fisheries and environmental drivers shape production, the relative importance of each was found to vary across ecosystems, whereas fishing effort was the most informative correlate of landings within many LMEs, within other environmental factors (sea surface temperature or chlorophyll *a*) proved to be of greater importance. In a similar analysis, albeit considering different correlates, Fu *et al.* (2012) explored the drivers of marine fish productivity within 13 Northern Hemisphere ecosystems and found largely analogous results, that is, that the relative importance of the individual drivers varies spatially, a result they linked to contextual factors and 'system specific' properties. Nevertheless, their focus upon a single geographical region and ecosystem type made it difficult to infer the generality of these results or determine the specific contextual factors. Consequently, the principal aim of this study was to compare the drivers of fisheries production among a diverse range of ecosystems, with different climates and fishing histories, such that the factors underlying their relative strength could be elucidated.

The importance of context

Of the factors considered, the probability of an LME being sustainably fished proved most important in determining whether bottom-up or top-down factors were of greater importance as drivers of production: environmental drivers were found to be more informative correlates of landings within relatively unsustainably fished regions. In addition, bottom-up forcing was also found to be of greater importance within comparatively productive regions, together with those in which relatively small-bodied fish species are landed; however, these three properties are likely correlated. Due to the global nature of this study (a requirement in order to elucidate the general patterns we have described), it is not possible to formulate a detailed, mechanistic understanding of these findings; nevertheless, we now outline a number of plausible explanations based upon the results of previous investigations.

Regions in which bottom-up drivers predominated

Commercial fisheries are generally size selective, targeting large, long-lived and slow-growing species before moving onto (Pauly 1998) or supplementing their catch with (Essington *et al.* 2006) less valuable, low-trophic-level fisheries as their original target species become depleted. There is growing evidence that decades of size-selective harvesting have significantly impacted exploited populations, altering their structure, function and dynamics and their sensitivity to environmental forcing. For example, within heavily fished regions, the selective removal of larger, older individuals has been shown to result in age-truncated or juvenescent populations that are more sensitive to changes in the climate, hypothesized to relate to reduction in their capacity to 'buffer' unfavourable conditions or survive successive years of poor recruitment (Hsieh *et al.* 2006; Anderson *et al.* 2008). Furthermore, as a consequence of the overfishing of large predators, whole ecosystems have been shown to have undergone restructuring (Frank *et al.* 2011), transitioning from complex, diverse systems to relatively simple ecosystems, in which the food webs are shorter and simpler (dominated by planktivorous forage fishes and macro-invertebrates) and the communities less resilient to environmental perturbations (Pauly and Maclean 2003).

Whilst the aforementioned factors likely contribute to the prevalence of bottom-up forcing within North Atlantic LMEs [some of the most heavily fished regions in the world (Christensen *et al.* 2003)], within other ecosystems, the food webs are naturally simple and the fish stocks inherently sensitive to bottom-up forcing. This is particularly true of LMEs located along the eastern boundaries of the Pacific and Atlantic Ocean basin, in which catch predominately consists of small plankton-feeding fish, such as sardine (*Sardinops sagax*, Scombridae) and anchovy (*Engraulis encrasicolus*, Engraulidae), which are highly abundant in these areas due to the intense upwelling of cold, nutrient-laden waters into the coastal zone. Landings of these species are notoriously variable, exhibiting pronounced fluctuations, often spanning several orders of magnitude, over interannual and multidecadal time scales. It is widely accepted that bottom-up, climate-driven forcing is responsible for this variation, supported by the detection of synchronies in sardine and anchovy abundances across large parts of the Pacific (Humboldt Current, Benguela Current, California Current and Kuroshio Current LMEs) in relation to changes in sea surface temperature (Chavez *et al.* 2003), together with the analysis of sedimentary records from the Santa Barbara Basin demonstrating similar fluctuations over the two millennia before the development of commercial fisheries (Baumgartner *et al.* 1992).

Regions in which top-down drivers predominated

In contrast, changes in fishing effort best explained variance in commercial landings within the majority of tropical and southern Pacific and Atlantic LMEs considered. The relatively low productivity of these regions and their resultant inability to support high-yield fisheries (Caddy *et al.* 1998) means that they remained comparatively underexploited by industrialized fishing fleets for a relatively long period of time (Swartz *et al.* 2010). Consequently, whilst the effects of overfishing were detectable upon ecosystems within the North Atlantic and Northern European LMEs as early as the 1950s, the impact of fishing fleets within these regions was comparatively small (Coll *et al.* 2008). Furthermore, whilst fisheries within the North Atlantic largely developed through a pattern of sequential collapse and replacement (i.e. moving from high to low-trophic-level species as the former become depleted), within southern latitude and tropical regions, fisheries predominately followed a pattern of sequential addition (i.e. supplementing high-trophic-level fisheries with lower-trophic-level fisheries (Essington *et al.* 2006)), resulting in a larger diversity of species being landed, with a greater component of large pelagic species; thereby diminishing the sensitivity of production to changes in environmental conditions.

Moreover, at present, fish stocks within the majority of these regions are considered to be relatively well managed (Mora *et al.* 2009); in particular, those within New Zealand and Australia, where management practices such as individual user rights (ITQs) are well developed and widespread and a relatively small proportion of the stocks are classed as overfished (Beddington *et al.* 2007). In previous studies, it has been shown that the degree of linearity between fishing effort and yield is influenced by the intensity of historical fishing pressure; over-exploited fish stocks have an increasingly nonlinear relationship compared with those managed in a sustainable manner, in which catch per unit effort can approach linearity (e.g. Paloheimo and Dickie 1964; Jennings & Polunin 1995). Therefore, unlike the majority of fisheries within upwelling and temperate regions, which are close to or beyond the top of their multispecies yield curve, and the effects of environmental changes predominate, changes in production within these LME arise predominately through effort-controlled stock management.

Regions in which the drivers of production were inconclusive

There were a number of LMEs for which the dominant factor driving variability in its yield could not be identified. There are a number of possible reasons for this; for example, LMEs such as the Gulf of Thailand and the Somalia Coastal Current are known to have unreliable catch statistics (Duda and Sherman 2005), which leads to inaccurate measures of yield. Furthermore, there is always the possibility that the yield within a system is influenced by factors not considered here, for example wind strength (Mann 1993) or mesozooplankton productivity (Friedland *et al.* 2012), and factors shown to influence yield but for which data were not available. Additionally, the chlorophyll *a* estimates used could potentially result in inaccuracies; we used values derived from the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS), which as one of the most important global observational platforms for oceanic biogeochemistry and the only means of determining phytoplankton chlorophyll concentrations on a basin or global scale (Gregg and Casey 2004; Siegel *et al.* 2013) has been the primary source of ocean chlorophyll for numerous studies (Christensen *et al.* 2003; Ware and Thomson 2005; Jennings *et al.* 2008; Chassot *et al.* 2010; Friedland *et al.* 2012; Fu *et al.* 2012). However, problems still remain to be solved in regard to its accuracy; these include the presence of dissolved organic matter, radiance-absorbing aerosols and suspended sediments within the water column, together with general problems associated with satellite estimates, including clouds, ice and sun glint (Gregg and Casey 2004).

Conclusion

With growing human populations, stagnating global fisheries catch and projected large-scale climatic changes, there is a need to go beyond listing the caveats and difficulties that relate to the complexity of ecosystems and instead make explicit attempts to capture the relative influence of, and linkages among, the key drivers of change. Here, we have developed a first approach showing that despite the complexity of ecological systems, by comparing the mechanisms controlling ecosystem production across a diverse range of ecosystems, it is possible to elucidate a number of generalities and contextual factors that mediate the relative strength of key drivers. As we seek to sustainably manage future fisheries production under a range of climatic scenarios, this is an important realization aiding the development of more parsimonious ecosystem models, facilitating the transition to 'ecosystem-based' fisheries management plans and projecting how the global ocean, particularly fisheries productivity, will change in the future. We propose there is a growing need for fisheries managers and researchers to better understand, and take account of, the relationship between the multitude of factors (both past and present) influencing production rather than attempting to disentangle their effects and address each separately.

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