Università degli Studi della Tuscia di Viterbo

Dipartimento di Ecologia e Sviluppo Economico Sostenibile (DECOS)
Dottorato di Ricerca in "Ecologia e Gestione delle risorse biologiche" - Ciclo XXIII

Co-tutoring
Université Paul Sabatier – Toulouse III – Ecole Doctorale "Sciences Ecologiques, Vétérinaries, Agronomiques et Bioingenieres" (SEVAB)

Trends and processes in large marine ecosystems fisheries

BIO/07

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ABSTRACT

This study aimed at exploring the dynamics of large marine ecosystems (LMEs) fisheries and the relationships between catches and potential drivers, taking into account both ecological and economic processes. Data analyses were based on fisheries landings time series provided by the Sea Around Us Project (SAUP) and time series of environmental and economic variables from different sources. Artificial neural networks (ANNs) have been extensively applied both for modeling and data analysis purposes.

A general introduction is provided in Chapter I, where the state-of-the-art in modern fisheries science is described, together with a general framework within which the aims and scopes of the thesis are presented.

In Chapter II the relationship between primary productivity (PP) and fish yield was investigated through PP estimates based on satellite observations and reported fisheries landings from 14 selected LMEs. Correspondence analysis performed on yield data outlined the role played by different trophic levels (TLs) in LMEs catches. PP temporal variability was significantly and positively correlated to average trophic level of catches (TLc) so that high yields in less variable ecosystems were characterized by low TLc. The percentage primary productivity required to sustain catches (%PPR) and TLc were used to assess fisheries impact on ecosystems and the PP model choice emerged as a critical step affecting the assessment of exploitation levels. A more conservative estimation of PP could contribute to a more precautionary approach to fisheries management where high levels of exploitation are more easily attained (Conti & Scardi, 2010).

In Chapter III the regional dynamics of industrial fisheries within the LMEs boundaries were investigated by means of an historical-descriptive approach. An unsupervised artificial neural network (Self Organizing Map, SOM) was proposed as a tool for analyzing changes in composition of fisheries landings over five decades in 51 LMEs. From the analysis of LMEs fishing histories a broad distinction emerged between two main types of fisheries, based on different exploitation strategies: (1) pelagic dominated landings showed stable or cyclic compositions, mainly driven by intrinsic oscillation in exploited populations of target species and are located in LMEs sharing specific features (e.g. productive regimes, upwelling) and (2) trawl fisheries seemed to be more affected by economic drivers (e.g. investments in fishing gears and new technologies), and tended to cluster in the northern hemisphere, where fishing pressures and investments have been historically higher. It could be further

suggested that northern hemisphere LMEs are also generally characterized by wider continental shelves, which represent a critical feature for demersal exploitation.

In Chapter IV fisheries yields and landings composition by functional groups were predicted for 51 LMEs by means of an artificial neural network. Input variables selected for the two models described both ecological and economic features of each LME, and no assumptions on inter-variables relationships were made. The neural network provided accurate estimates of total fisheries yields and catches composition, overcoming the restrictive assumptions imposed by linear models. New insights into underlying processes governing fisheries harvests were provided by the sensitivity analysis carried out on the two models. Both economic and ecological predictors were strictly linked to fisheries landings. Catches composition seemed to be influenced by intrinsic ecosystems dynamics, while total yields seemed to be mainly driven by latitude and factors related to the economy of the fishing countries.

General conclusions and future perspectives are provided in Chapter V.

RESUMÉ

Cette étude visait à explorer la dynamique de la pêche et les relations entre les captures et les variables qui les déterminent dans les Large Marine Ecosystems (LMEs), en tenant compte à la fois des processus écologiques et économiques. Les analyses des données ont été basées sur les séries historiques des débarquements de la pêche industrielle fournies par le Sea Around Us Project (SAUP) et sur les séries temporelles des variables environnementales et économiques provenant de sources différentes. Les réseaux neuronales artificiels (ANNs) ont été largement appliqués à la fois à des fins de modélisation et d'analyse des données.

Dans le chapitre I une introduction générale est donnée, où l'état de l'art dans la moderne science de la pêche est décrite, et les objectifs et les champs d'application de la thèse sont présentés.

Dans le chapitre II la relation entre la productivité primaire (PP) et le rendement de la pêche a été étudiée par des estimations de PP basées sur les observations satellitaires et les données de pêche dans 14 LMEs sélectionnés. L'analyse des correspondances effectuée sur les données de rendement a souligné le rôle joué par les différents niveaux trophiques (TLs) dans les captures. La variabilité temporelle de la PP est significativement et positivement corrélée au niveau trophique moyen des captures (TLc), de sorte que des rendements élevés dans les écosystèmes moins variables sont caractérisés par un TLc plus bas. La productivité primaire requise pour soutenir les captures (% PPR) et le TLc ont été utilisés pour évaluer l'impact de la pêche sur les écosystèmes ; le choix du modèle d’estimation de la PP a émergé comme une étape cruciale qui peut affecter l'évaluation du niveau d'exploitation de l’écosystème. Une estimation conservatrice de la PP pourrait contribuer à une plus prudente approche gestionnelle, où des niveaux élevés d'exploitation sont plus facilement atteints (Conti & Scardi, 2010).

Dans le chapitre III, la dynamique régionale de la pêche industrielle dans les limites des LMEs a été étudiée au moyen d'une approche historico-descriptive.

Dans cette étude, les réseaux de neurones artificiels non-supervisée (Self Organizing Maps, SOMs) ont été proposés comme un outil d'analyse des changements dans la composition des débarquements de la pêche. Les séries temporelles utilisées regardaient les captures dans 51 LMEs, durant la période 1950-2004. De l'analyse des différentes « histoires » de pêche dans les LMEs, une grande distinction apparue entre deux principaux types de pêche, qui se basent sur différentes stratégies d'exploitation: (1) les débarquements dominés par les poissons pélagiques montrent compositions stables ou cycliques,

déterminées principalement par l'oscillation intrinsèque des populations exploitées , et on les retrouve dans les LMEs qui partagent des caractéristiques spécifiques (par exemple, les régimes de production ou de upwelling) ; (2) les débarquements dominés par les demersaux semblent être plus affectés par les facteurs économiques (par exemple, les investissements dans les engins de pêche et les nouvelles technologies), et ont tendance à se regrouper dans l'hémisphère nord, où les pressions de pêche et les investissements ont été historiquement plus élevés. On peut aussi souligner que les LMEs dans l'hémisphère nord sont généralement caractérisés par un plus large plateau continental, ce qui représente une caractéristique essentielle pour l'exploitation en eau profonde.

Dans le chapitre IV, les rendements de la pêche et la composition des débarquements par groupes fonctionnels dans les 51 LMEs ont été prévus par un réseau de neurones artificiels. Les variables d'entrée sélectionnés pour les deux modèles décrivent à la fois les caractéristiques écologiques et économiques de chaque LME, et aucune hypothèse sur les relations inter-variables ont été faites. Le réseau neuronal a fourni des estimations précises des rendements totaux de la pêche et de la composition des captures, en surmontant les hypothèses restrictives imposées par les modèles linéaires. Un nouveau regard sur les processus sous-jacents qui régissent les captures de la pêche a été fourni par l'analyse de sensibilité effectuée sur les deux modèles. Les deux prédicteurs, économiques et écologiques, sont étroitement liées à la prévision des débarquements de la pêche : la composition des captures semblait influencée par la dynamique intrinsèque des écosystèmes, alors que les rendements totaux semblait principalement déterminés par la latitude et les facteurs liés à l'économie des pays qui pêchent dans le LME.

Des conclusions générales et perspectives pour des études futures sont décrits dans le chapitre V.

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1. Conti L. & Scardi M (2010). Marine Ecology Progress Series, 410: 233-244.

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CHAPTER I

General introduction

1. RECENT TRENDS IN FISHERIES RESEARCH

'The time has come to look at the future of fisheries through (i) identification and extrapolation of fundamental trends and (ii) development and exploration (with or without computer simulation) of possible futures'. (Pauly et al. 2003)

In 2010, 160 years after fishery science was recognized as a scientific discipline (Jennings et al. 2000), research is still dwelling on modeling the dynamics of fish populations and their responses to environmental and anthropogenic pressures. The spectrum of disciplines involved in fisheries research is still widening, and the integration of abiotic change and biological responses in the ocean is now the main scope of fisheries scientists.

Since the 1990s, fisheries science has experienced a strong impulse towards a holistic approach, which lead to the definition of the "ecosystem approach to fisheries" (EAF) adopted in the FAO Technical Consultation on Ecosystem-based Fisheries Management held in Reykjavik in 2002 (FAO 2003). Most of principles and the conceptual framework of an ecosystem approach to fisheries were already stated in a number of agreements and conventions dealing directly or indirectly with fisheries: the 1982 UN Convention on the Law of the Sea, the 1995 FAO Code of Conduct for Responsible Fisheries and its International Plans of Action (IPOAs), the 1971 Ramsar Convention, the 1992 Convention on Biological Diversity (CBD), including the 1995 Jakarta Mandate on Marine and Coastal Biological Diversity. EAF was defined by Ward et al. (2002) as "an extension of conventional fisheries management recognizing more explicitly the interdependence between human well-being and ecosystem health and the need to maintain ecosystems productivity for present and future generations, e.g. conserving critical habitats, reducing pollution and degradation, minimizing waste, protecting endangered species". The Reykjavik FAO Expert Consultation (FAO 2003) agreed that the "purpose of an ecosystem approach to fisheries is to plan, develop and manage fisheries in a manner that addresses the multiplicity of societal needs and desires, without jeopardizing the options for future generations to benefit from a full range of goods and services provided by marine ecosystems". Therefore, "an ecosystem approach to fisheries strives to balance diverse societal objectives, by taking account of the knowledge and uncertainties about biotic, abiotic and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries". Despite the official schedules and the publication of general guidelines and reference points, it could be said that EAF was already the common framework for most of fisheries scientists, whose concern about industrial fisheries as a part of a global enterprise has been published in a number of papers (e.g. Jackson et al. 2001, Myers & Worm 2003, Pauly & Christensen 1995, Pauly et al. 1998, Watson & Pauly 2001). Decades away from the failure of the single- and multi-species approaches, the ecosystem-based investigation became the consensus framework within which methodological advances and new modeling tools are expressed (e.g. 3D hydrodynamic high-resolution models coupled with biogeochemical and fish models, remote sensing and tagging experiments) (Cury et al. 2008). Nevertheless, it can still be argued that many fisheries failures resulted not from the lack of consideration of ecosystem issues but because of systematic overfishing and destructive harvesting practices for which existing scientific paradigms offered appropriate prescriptive advice (Murawski, 2000). Moreover, the shift towards an ecosystem-orientated approach is still dwelling with the paucity of data and the demands of multiparameterized multispecies models, often resulting in *ad hoc* manipulations of the single-species approach (Beddington et al. 2007).

The shift from local to regional and global studies, allowed by the availability of longer time series and synoptic observations (e.g. remote sensing of the ocean color from satellite platforms, as SeaWiFS), enable scientist to investigate fisheries as components of a global enterprise on its way to undermine its supporting ecosystems (Pauly et al. 2003). Marine capture fisheries and aquaculture produced over 143 million tonnes in 2006, with an estimated first-sale value of US$ 91.2 billions, supplying the world with over 110 million tonnes of food fish (i.e. 16.7 kg per capita, live weight equivalent). Industrial marine fisheries accounted for 64% of the total catches (FAO 2008). In this context, the "giant enterprise" in question is having so severe an impact on its own resources that, if present trends continue, it will collapse in the next decades, and drag down with it many of the species it exploits together with their supporting ecosystems (Pauly et al. 2003, 2005). An understanding of the fishery management process can only come from analyzing the capacity and incentives of the two key stakeholders: the fishing community and the management authority (Beddington et al. 2007).

In order to provide new insights into exploited ecosystem dynamics and, therefore, useful suggestions to decision makers before reaching the "point of no return" for global fishing activities, fisheries science is nowadays experiencing new research strategies, that plunge different types of models, ranging from statistical to dynamical and from simple to complex, into a global change context. This strategy is also referred as "ecosystem oceanography" and aims at relating ecosystem components and their interactions with climate change and exploitation practices (Cury et al. 2008).

2. FISHERIES LANDINGS AS A PROXY FOR ECOSYSTEM STRUCTURE

Fisheries science always had to cope with the (often scarce) quality of datasets on which the studies relied. Deriving from scientific surveys, from landings statistics (officially introduced in the 1970s) or from international databases, fisheries time series have been shown to be severely biased (Watson & Pauly 2001). The intrinsic weakness of catch statistics derive from systematic distortions in landings reporting by single countries, from market demand and from the discarded "by-catch" (about 30% of global landings), which is only one of the components of the illegal, unreported and unregulated (IUU) catches that recently became part of the international fisheries research agenda (Pauly et al. 2002, Pitcher et al. 2003). Itself, the word "landings" has triggered much of the unreliability of fisheries time series, as it defines catches that are retained from catches that are discarded (Agnew et al. 2009), thus providing a strongly selected and underreported fisheries harvest, which may not satisfactorily represent the underlying ecosystem. Illegal and unreported fishing prejudices the managed recovery of the world's oceans from severe fish depletions (Agnew & Barnes 2004, Beddington et al 2007, Sumaila et al. 2006). It is reported that this fraction of total harvests leads to a loss of many billions of dollars of annual economic benefits, creates significant environmental damage through the use of unsustainable fishing practices, provoking wider consequences for food supply (Agnew et al. 2009). Even in the statistics documented for some of those states with appreciable management capacity, what is striking is for how many stocks, the status is uncertain or not determined. In the United States, the stock status of 30% of the 230 major stocks was undetermined in 2006 and the Northeast Atlantic the numbers are even higher (i.e., up to 61%) (Beddington et al. 2007). For most authorities, deriving reliable quantitative assessments of their stocks of major commercial importance is a most challenging scope. Large numbers of small, commercially unimportant stocks present in most areas, usually as by-catch, are often neglected in national statistics, as they cannot realistically be assessed (Beddington et al. 2007). The issue of fisheries data reporting is not trivial and the concern is not only for the resource. The chronic underreporting of the small-scale fishing sector leads to inequitable policy decisions that favor industrial fisheries (that often compete for the same resources), underestimate the economic contribution of small-scale fishing, and jeopardize food security (Jaquet et al. 2010).

Nevertheless, the availability of open-access databases of multi-decadal time series, together with the large scale resolution provided by international research teams, such as the Sea Around Us Project (www.searoundus.org), lead to the unresolved "dilemma" between availability and reliability of fisheries landings time series. Fisheries data may contain ecological information as well as data about harvesting patterns (Blanchard & Boucher 2001) and it is generally considered that there is a certain degree of association between relative species abundance in the landings and in the ecosystem from which they are extracted (Halley & Stergiou, 2005). Moreover, although the usefulness of catch data still remains a matter of debate, the general assumption is that scientific evidence based on data is a prerequisite for policies to protect resources, and to manage the people using them (Jaquet et al. 2010). In most cases, the evidence based on catch-per-unit-effort (cpue) has been considered far more reliable and accurate by the scientific community with respect to studies based on total catches abundances, yet abundance indices based on cpue data are notoriously problematic (e.g., Beverton & Holt 1957, Gulland 1974, Hilborn & Walters 1992, Harley et al. 2001, Walters 2003). Raw cpue is seldom proportional to abundance over the whole exploitation history and the entire geographic range, because many factors affect catch rates and even if cpue is standardized appropriately, the resulting index of relative abundance, in isolation, provides limited information about the effect of fishing (Maunder et al. 2006). Beside these shortcomings, the use of cpue data at large spatial (and long temporal) scales is hindered by the lack of information about fishing effort. At present, the effort measures to which we have access are quite tentative (Gelchu and Pauly 2007) or lacking in resolution (Alder et al. 2007) so that they are actually pointless for modeling purposes (Christensen et al 2009).

The Sea Around Us Project (SAUP) online database (www.searoundus.org) represents today the best available source for world fisheries catches time series. Data come from a variety of sources harmonized into a single dataset representing global catches since 1950, for which capture landings from the Food and Agriculture Organization (FAO) of the United Nations represent the foundation for the global coverage. Furthermore, data from regional organizations such as the International Council for the Exploration of the Sea (ICES) (www.ices.int/fish/statlant.htm), the Northwest

Atlantic Fisheries Organization (NAFO) (www.nafo.ca/) and others, provides a finer spatial catch breakdown for most of the Atlantic and the Mediterranean. Finally, national datasets, such as that from Canada's Department of Fisheries and Oceans (DFO) for Atlantic Canada are also included.

The SAUP database provides time series of fisheries landings with different levels of aggregation. In this thesis, the grouping based on habitat preferences, feeding habits, and maximum size, which define the so-called 'functional groups', was used. This grouping separates fishes by where they live in the water column. Demersal animals that live on the bottom are separated from those that live on the surface (pelagic), and these fish groups are in turn separated according to their maximum length (Lmax) into "small" (Lmax < 30 cm), "medium" (Lmax = 30-89 cm) and "large" (Lmax ≥ 90cm).

SAUP database recognized this three-classes division for most bony fishes functional groups, while only two dimensional classes, namely "small to medium" (Lmax < 90 cm) and "large" (Lmax > 90 cm), are identified for flatfishes and Chondrichthyans. Therefore, SAUP identifies 30 functional groups. The usefulness of this grouping system, besides facilitating ecological studies, is particularly evident when addressing the impacts of fishing gear as different functional groups, as they tend to be impacted and targeted by fishers differently.

In this thesis, 28 amongst 30 functional groups were selected for the analyses, with the exclusion of 'krill' and 'jellyfish' which have no significant reported catches in the selected LMEs used in this thesis (e.g., krill represent a major target species for fisheries in Antarctic waters and in the Southern Ocean, which were excluded from the present analysis).

3. DISENTANGLING THE RELATIVE FORCING FACTORS DRIVING FISHERIES YIELDS AND CATCHES COMPOSITION

For about a century, fisheries science has tried to understand the processes governing the dynamics of fish stocks and to predict sustainable yield levels of exploited marine resources. In spite of the large research effort, the present state of the marine resources is alarming when considering the increasing demand on fisheries products. About the half of world's marine resources are fully exploited (FAO 2007) and another large part of targeted stocks are currently in danger of being overfished (Keyl & Wolff 2008).

The present situation is the result of the interplay of many different factors, of which economic forces, political interests, lack of control and enforcement of fishery regulations, but also great natural variations of fish stock sizes and productivities play a role (Quinn & Deriso 1999, Haddon 2001). Poor yield predictions and unexplained natural stock fluctuations are often assumed to be the result of a variable environment that in most cases has just been considered as unpredictable "environmental noise" (Hilborn & Walters 1992, Quinn & Deriso 1999, Haddon 2001, Jonzén et al. 2001). The missing inclusion of this "noise" in fisheries models has led to wrong estimations of the performance of exploited resources, which has contributed to the present deteriorated state of many marine stocks (Keyl & Wolff 2008). Several studies have been reported on climate change impact on fish production and catch (Bakun 1990, Bakun & Broad 2003, Cury et al, 2008, Hannesson 2007, Klyashtorin 1998, Orlowski 2003, Tian et al. 2003, Yatsu et al. 2008), being climate change in the form of coastal upwelling, atmospheric circulation index and surface water temperature (Biswas et al 2009).

Disentangling the relative effects of the many factors affecting the dynamics of populations has been considered to be the ultimate target of fisheries science (Link et al. 2010, Rouyer et al 2008). While the patterns of variations in fisheries time series are known to result from a complex combination of species and fisheries dynamics, all coupled with environmental forcing, economic indicators have been a long time overseen. Even among the most complex analysis of ecological time series, taking into account nonlinear, nonstationary, aperiodic and noisy signals, the contribution of economic pressures is often ignored (e.g. Rouyer et al 2008). In a recent paper, Chassot et al. (2010), proposed a linear model of fisheries yields, accounting for several covariates that represent major physical and ecological processes within LMEs: primary productivity, ecosystem type, sea surface temperature, ecosystem size, species richness, fishing pressure, mean trophic level and maximum average body length of catches. While fishing pressure is actually stated as part of the input variables, it must be stressed that this information (e.g. fishing effort) is unavailable at the LME scale. The authors actually proposed an index of the overall ecosystem effects of fishing, accounting for differences in fishing pressure, named the mean annual probability of sustainable fishing (Psust) (Libralato et al. 2008; Coll et al. 2008). Lower probabilities of sustainable fishing Psust indicate higher fishing pressures (Coll et al. 2008). Nevertheless, even though Psust may account for fishing pressure on the ecosystem, it still represents the output of a model reconstructing potential influences, while other descriptors are available.

Recent forecasts of future changes in ecosystems structure, functioning and productivity are often embedded into scenarios – sets of coherent, plausible stories designed to address complex questions about uncertain future. The central idea of scenario planning is to consider a variety of possible futures that include many of the important uncertainties in the system rather than to focus on the accurate prediction of a single outcome (Peterson et al. 2003). Reports published by the Intergovernmental Panel on Climate Change (IPCC) and the United Nations Environment Program (UNEP) describe a range of potential futures, which actually represent the new frontier for fisheries (and ecology) research. Most scenarios focus on sea surface temperature (SST), which has been demonstrated to be warming in most of the LMEs of the world, with acceleration in the late 1970s-early 1980s and strong regional variations (Belkin 2009). The effects of a reduction in primary production derived from SST change could have global negative impacts on fisheries catch and exacerbate current trends of overfishing (Chassot *et al.* 2010). Nevertheless, reliable scenario planning needs to take into account both changes in natural dynamics (e.g. SST and primary productivity) and changes in anthropogenic drivers. Global fisheries are currently overcapitalized, resulting in overfishing in many of the world's fisheries (Sumaila et al. 2008). Given that fuel constitutes a significant component of fishing costs, increases in fuel prices are expected to reduce overcapacity and overfishing. While government fuel subsidies to the fishing sector reduce, if not completely negate, this positive aspect of increasing fuel costs (Sumaila et al. 2008), the tight relationship between fishing pressures and the investment potential of national economies force the scientific community to use such "unconventional" predictors in ecological modeling.

4. AIMS AND SCOPES OF THE WORK

This study aimed at exploring the dynamics of LMEs fisheries over a fifty-five years time lapse. The time series of harvests composition by functional groups, provided by the Sea Around Us Project (SAUP) online database, were used to investigate whether landings data provide useful information about the ecosystem's dynamics from which these landings were extracted. Although catches statistics are widely considered as a scarce quality data source – especially when fishing effort is not taken into account (i.e., catches expressed as CPUE) –, the detection of common trends amongst LMEs fisheries may highlight the persistence of significant regional features, which may represent the output of ecological or economic processes embedded in the exploited ecosystems.

Following the EAF paradigm, the relationships between catches and potential drivers, taking into account both ecological and economic descriptors were investigated. In order to cope with the complexity of these data sources and the non-linear interplays between descriptors, in this thesis artificial neural networks (ANNs) have been extensively applied as tools to explore new approaches in modeling and data analysis.

This study aimed at providing new insights into the structure and functioning of large marine ecosystems all over the world, in order to test whether the available time series of fisheries landings represent a reliable data source when addressing management issues at large spatial scale.

Therefore, the main goals of this work were:

1. to investigate the relationship between primary productivity (PP) and fisheries yield through PP estimates based on satellite observations and reported fisheries landings (Chapter II);
2. to detect trends in total yields and to describe variations in catch composition by functional groups over time, through the analysis of change in the harvests time series, from 51 LMEs all over the world, by means of a unsupervised artificial neural network (Chapter III);
3. to model and predict LMEs total fisheries yields and landings composition by functional groups from a set of ecological and economic descriptors by means of a supervised artificial neural network (Chapter IV).

The background for the analysis of these three themes has been provided in this Chapter (Chapter I), while general conclusions and future perspectives arising from the results obtained are briefly stated in Chapter V.

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CHAPTER II

Fisheries yield and primary productivity in large marine ecosystems

1. INTRODUCTION

The relationship between primary productivity (PP) and fisheries yield has been widely demonstrated (e.g. Nixon 1982, 1992, Nixon et al. 1986, Iverson 1990, Nielsen & Richardson 1996, Sommer et al. 2002, Steingrund & Gaard 2005). Nixon (1982, 1992) and Nixon et al. (1986) showed an empirical relationship between annual yields of fish and autotrophic productivity in a selection of sites, both marine and estuarine, on the basis of the 'agricultural model' (i.e. linking marine PP to nutrient input) and of the tropho-dynamic approach (Lindeman 1942). Longer time series and enhanced measurement technologies, together with an improved knowledge of marine food web dynamics, demonstrated that this relationship is not a simple one and often not even linear. Iverson (1990) related nekton production (fish and squids) from offshore areas to the amount of nitrogen incorporated into phytoplankton biomass, the 'new production' being the only type of PP that directly affects fish yields (Nielsen & Richardson 1996). Variations in food web structure have also been linked to different nutrient richness scenarios in oligotrophic, upwelling and temperate seas (Sommer et al. 2002). Two main models have been proposed to describe marine ecosystems dynamics: (1) bottom-up control, where food web components are regulated by either primary producers or the input of limited nutrients (White 1978), and (2) top-down control, where lower food web components are regulated by one or several upper-level predators (Hairston et al. 1960, Fretwell 1977, 1987, Oksanen et al. 1981, Power 1992, Pace et al. 1999, Cury et al. 2001). Several studies pointed out that both systems act locally (e.g. Ware & Thomson 2005, Mueter et al. 2006, Mackinson et al. 2008).

The shift from local to regional and global spatial scales, added to the potential effects of climate change and regime shifts, highlights the complexity that underlies marine food webs. Cyclic and punctual events, both environmental and anthropogenic, influence the structure and functioning of marine ecosystems, hindering the identification of the relative role of each driving force. Landings statistics are the main source of data for these kinds of studies, representing the only spatial and temporal large-scale data sets available for the detection of different sources of variation. Recently, Perry & Schweigert (2008) suggested that these highly aggregated data and large (often global) spatial domains may have played a key role in the identification of the general relationship between

PP and fisheries yields. The primary criticism about large-scale fisheries studies is their reliance on poor quality of data: landings might not correspond to real abundance due to changing market demand or selectivity of fishing gears, together with uncertainties about catch reporting systems. Nevertheless, it is generally considered that there is a certain degree of association between relative abundance in the landings and in the ecosystem from which these landings are extracted (Halley & Stergiou 2005). Furthermore, landings represent the best and only available source for regional and global studies. Substantial advances have been made in PP estimation procedures, reducing at least one of the sources of variation in studies aimed at relating PP and fisheries yield. For a long time, ship-based estimates and chronic undersampling made it difficult to resolve low-frequency spatial and temporal variability, and forced an estimation of global PP based on the extrapolation of sparse (in time and space) measurements (Carr et al. 2006). Satellite observation of ocean color, since the beginning of the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) mission in September 1997, determined the shift from a local snapshot view to synoptic and large-scale images, thereby allowing considerable advances in estimation accuracy on a global perspective. The range of modeling approaches for estimating primary productivity from satellite chlorophyll a (Chl *a*) measurements and modeling performances are summarized in Carr et al. (2006). According to Field et al. (1998), global PP is evenly supported by terrestrial and marine photosynthesis, the latter being conveyed for the most part (up to 90%) towards production at higher trophic levels (TLs), sustaining three-quarters of global fisheries yields (Myers & Worm 2003). The total amount of carbon fixed by autotrophs, mainly phytoplankton, sets the ultimate threshold to the production at higher TLs (Friedrichs et al. 2009) and the possibility of reaching this maximum sustainable production is determined by the structure and functioning of the underlying food web by means of transfer efficiencies (TEs). Typically, 13% of phytoplankton PP is transferred to herbivore mesozooplankton and benthos, while the ‘zooplankton/zoobenthos → fish’ step is characterized by a TE of 10% (Ware 2000). From a more general perspective, ecological efficiency in marine ecosystems ranges from 5 to 20% (Lindeman 1942) depending on the food web structure (i.e. number of trophic levels involved) and decreases with higher trophic levels due to increased respiration (Christensen & Pauly 1993, Trites 2001). The relative importance of carbon pathways in different marine ecosystems reflects both the intrinsic properties of primary producers and physical forcing. In oceanic ecosystems, the bulk of phytoplankton production is conveyed through the herbivory chain that sustains production at higher TLs, which in turn is subjected to industrial harvest (Duarte & Cebrián

1996). Different marine PP estimation algorithms (depth-integrated models and general circulation models [GCMs], coupled with ecosystem or biogeochemical models) converge on a global marine PP annual value of 45 to 50 Gt C yr^{-1} (Carr et al. 2006).

The purpose of the present study was to investigate the relationship between primary productivity and fish yield through satellite observations and reported fisheries landings from 14 selected large marine ecosystems (LMEs). We adopted a double approach for relating PP and fish production: (1) bottom-up, where available PP fixes the threshold for production at higher TLs, and (2) top-down, where the primary production required (PPR) to support production at the exploited level was assessed from landing biomass under the assumption that reported landings effectively reflect total fish production (Pauly & Christensen 1995).

From an ecosystem-based management perspective, PPR provides an estimation of the ecosystem's carrying capacity based on its actual exploitation, and therefore represents a potential guideline for the future. In particular, the relationship between PPR normalized to the PP (%PPR) and the averaged TL of catches (TLc) have been proposed as indicators of ecosystems exploitation level (Tudela 2003, Tudela et al. 2005), as TLc actually reflects the strategy of a fishery in terms of the food web components selected (Pauly et al. 1998, Christensen & Walters 2004).

The purpose of this approach is to provide new insights into ecosystem functioning and to give a contribution to key issues in management strategies. It is within the boundaries of the 66 LMEs that major efforts are presently under way to meet the World Summit on Sustainable Development (WSSD) deadlines, namely: (1) introducing an ecosystem approach to marine resource assessment and management by 2010, and (2) maintaining fish stock maximum sustainable yield levels by 2015. While these standards are still far from being reached, there is a general agreement on the reference space-based ecosystem unit of LMEs, for which a 5-modules strategy of assessment (productivity, fish and fisheries, pollution and ecosystem health, socioeconomics and governance) has been developed (Sherman et al. 2005). In this context, the present paper proposes a focus on the first 2 modules, productivity and fisheries, even though any attempt to better understand ecosystem functioning has important outcomes on all LME strategy components.

2. MATERIALS AND METHODS

Area

Catch and PP data were obtained for 14 out of the 66 LMEs defined by Sherman et al. (2005). Selected LMEs belong to boreal temperate shelves and major upwelling systems (i.e. the Eastern Boundary Currents [EBCs]) (Fig. 1).

LMEs are 'regions of ocean and coastal space that encompass river basins and estuaries and extend out to the seaward boundary of continental shelves and the seaward margins of coastal current systems …, delineated according to continuities in their physical and biological characteristics, including *inter alia*: bathymetry, hydrography, productivity and trophically dependent populations' (Sherman & Duda 1999, p. 18). Their extension ranges from 300000 km^2 (Scotian Shelf) to over 2.5 million km^2 (Humboldt Current). Selected ecosystems are characterized by marked seasonality and by time series that are much more reliable than those from equatorial systems, which are often characterized by highly aggregated reported landings (i.e. miscellaneous fishes or invertebrates). The reason for this scarce reliability of data from equatorial regions is to be found in the particular socio-economic conditions of the developing countries bordering these LMEs, where fisheries landings data have been seldom collected on a routine basis.

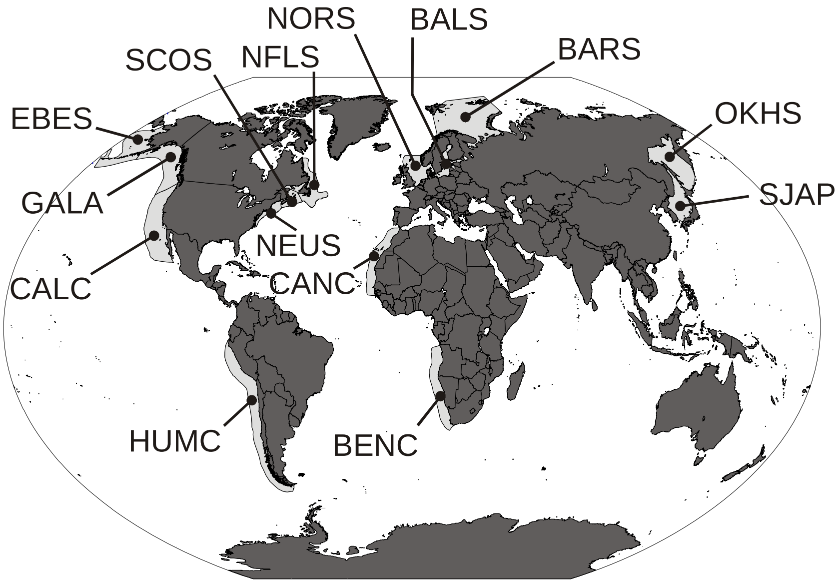


Fig. 1. Map of the Large Marine Ecosystems (LMEs) analyzed.

Table 1. Acronyms and geographical information for each region are reported below the map. Surface areas are expressed in 10^6 km^2 and centroid coordinates as decimal degrees

Complete name	Acronyms	Surface Areas	Longitude	Latitude
Atlantic Ocean				
Barents Sea	BALS	1.874	37.87 E	75.81 N
Baltic Sea	BARS	0.394	19.76 E	58.97 N
North Sea	NORS	0.696	2.71 E	57.40 N
Newfoundland-Labrador Shelf	NFLS	0.681	53.01 W	49.45 N
Northeast US Continental Shelf	NEUS	0.310	70.42 W	41.01 N
Scotian Shelf	SCOS	0.415	61.71 W	46.98 N
Pacific Ocean				
East Bering Sea	EBES	1.187	168.71 W	57.40 N
Gulf of Alaska	GALA	1.475	139.75 W	54.06 N
Okhotsk Sea	OKHS	1.558	148.94 E	53.77 N
Sea of Japan	SJAP	0.987	135.67 E	41.26 N
Eastern Boundary Currents				
Benguela Current	BENC	1.463	12.50 E	21.25 S
California Current	CALC	2.216	122.51 W	33.25 N
Canary Current	CANC	1.125	15.30 W	24.65 N
Humboldt Current	HUMC	2.559	75.30 W	31.96 S

Primary productivity

Our study is based on regional PP estimates obtained from a neural network global model (Scardi 2000, 2001) and from the basic version of the most popular PP model (i.e. Vertically Generalized Production Model, VGPM, Behrenfeld & Falkowski 1997). PP in each LME has been estimated from monthly mean satellite-derived measures of surface Chl *a* concentration from SeaWiFS (Level 3) and related ancillary sea surface temperature (SST) and irradiance data (available at: oceancolor.gsfc.nasa.gov/). PP estimates were extracted from global raster data (latitudinal pixel size = 9.766 km) from January 1998 to December 2002. PP was estimated by means of a depth-integrated model, the Vertically Generalized Production Neural Network (VGPNN) (Scardi 2000, 2001). VGPNN is based on an artificial neural network that performs a generalized nonlinear regression of PP based on surface Chl *a* concentration and other predictive variables (latitude, longitude, day length, mixed layer depth, SST, PB opt, i.e. maximum C fixation rate within a water column, mg C (mg Chl)$^{-1}$ h^{-1} [following Behrenfeld & Falkowski 1997] and photosynthetically active radiation [PAR]). Neural networks have been recently introduced in ecological modeling and their applications are becoming more and more frequent. They do not require an explicit formulation, as they are able to adapt themselves for reproducing complex relationships, provided that enough data are available and that they account for the effects of the most important sources of variation to be modeled. Further details about the specific modeling strategies adopted for developing the VGPNN model can be found in Scardi (2000, 2001), whereas a more general introduction to the modeling applications of artificial neural networks in coastal marine ecosystems can be found in Scardi (2003). A special feature of the VGPNN is that it was calibrated (commonly referred to as ‘trained’) on the basis of a data set in which records with high productivity to biomass (P/B) ratio (depth-integrated primary productivity to biomass in the surface layer ratio) were filtered out. In fact, major distortions in vertically integrated PP may arise when deep chlorophyll (and therefore PP) maxima are associated with low chlorophyll concentrations in the upper layer of the water column. In most cases PP estimates are vertically integrated taking into account samples collected at a few discrete depths. The depth difference between samples is usually not constant, as it increases with depth, and therefore samples are more sparse in the deeper part of the water column. Thus, a deep PP maximum, which is usually confined to a layer much thinner than the depth difference between 2 sampling depths, may be artificially spread on the entire stretch between 2 samples because of the trapezoidal vertical integration. Although this source of bias probably accounts for many cases of high PP values associated with relatively low surface phytoplankton biomass, it has often been overlooked in the development of other models. The exclusion of potentially biased records from the data set that supported the VGPNN development made this model conservative in estimating high PP values. The effects of this feature can be observed by comparing VGPNN PP estimates with those provided by other depth-integrated models. For instance, the estimate for annual global PP obtained from the VGPM (Behrenfeld & Falkowski 1997) is 43.5 Gt C yr^{-1}, while VGPNN provided a lower estimate of 40 Gt C yr^{-1} (Carr et al. 2006). Average values for each LME were computed from monthly global PP raster data. Some missing values at high latitudes, due to reduced day length and cloud cover, were computed by linear interpolation for the Baltic Sea (November to January 1997 and December to January 1999 to 2002), Barents Sea (November to February 1998 to 2002), East Bering Sea (December) and the North Sea (December).

Catches

Yield data were obtained from the Sea Around Us Project (SAUP 2006) catch database, which provides a 50 yr time series of fisheries landings (1950 to 2004) from 66 LMEs around the world, accounting for 83% of the global fisheries yield (Worm et al. 2006). Yield data are available as average annual catches (metric tons) of each taxon (species, genus or family) within each LME. To compare data from different LMEs, catches are expressed as average values per unit surface area (t km^{-2} yr^{-1}). Yield data were also aggregated by TL, following SAUP database TLs attribution. Five TL classes were defined, namely L225 (TL, 2.25 to 2.75), L275 (TL, 2.75 to 3.25), L325 (TL, 3.25 to 3.75), L375 (TL, 3.75 to 4.25) and L425 (TL, 4.25 to 4.75). Species with TL of <2.25 were excluded from the analysis as there are no nektonic species below this threshold—with the exception of *Mugil cephalus* (TL = 2.13) and *Sarpa salpa* (TL = 2.01), whose contribution to the overall fish yield is negligible. When reported, *M. cephalus* was considered as part of L225; Mugilidae (TL = 2.3) were also reported in this group. *S. salpa* was excluded from the analysis as total catches in the Benguela Current (1998 to 2002) were below 2 t. All benthic invertebrates were excluded independently of their TLs.

Multivariate analysis

A correspondence analysis (CA) (Benzecri 1973) was performed on averaged catches per TL class for each LME (t km^{-2} yr^{-1}). PP temporal variability (as the variation coefficient of the average monthly LME PP) and total yield were represented as bubble plots in CA ordinations. PP spatial variability (as the average monthly LME PP variation coefficient) was also taken into account.

Primary production required to sustain catches

Following Pauly & Christensen (1995), PPR to sustain LME catches was computed as:

$$\mathrm{PPR} = (\mathrm{catches}/9) \times 10^{(\mathrm{TL}-1)}$$

Although landings represent only a fraction of the total biomass available in the ecosystem, PPR still represents an indicator of energy TE of the food web. A PPR/PP ratio (%PPR) was assumed as an energetically based fishing pressure index (FPI) to assess yields in relation to intrinsic energetic limits for each LME (Knight & Jiang 2009). The %PPR in combination with TLc was also used to visually assess LME exploitation level (Tudela 2003, Tudela et al. 2005). Moreover, following Shannon et al. (2009), 2 ecosystem indicators were computed from reported catches to highlight fisheries impacts in exploited ecosystems: (1) the fish/invertebrates ratio (F/I) and (2) the demersal fish and chondrichthyans fish/pelagic fish ratio (D/P). For each indicator, the median value over the 5 yr (1998 to 2002) was assumed as a measure for the ‘ecosystem state’ (Shannon et al. 2009). The analysis of these and other indices over a time lapse was proposed by Shannon et al. 2009 as a tool to detect overexploitation effects, as a decrease of TLc, better known as ‘fishing down marine food webs' (Pauly et al. 1998). Under high harvesting pressures, a decline of these indicators is likely to be observed as a signal of top predatory fish removal in overexploited ecosystems, which in turn determines the decrease of TLc. Therefore, F/I and D/P median values are 'snapshots' of the actual LME state, which summarizes catch composition, in terms of fish/invertebrates and pelagic fish/demersal fish dominance in fisheries landings. This status could be related to different productivity regimes and overall total yields.

3. RESULTS

PP estimates and catch trends

Primary productivity

Average PP values estimated by VGPNN and VGPM models during the period from 1998 to 2002 are reported in Table 1. Values for VGPNN estimates ranged from 363 mg C m^{-2} d^{-1} in the Newfoundland-Labrador Shelf up to 1527 mg C m^{-2} d^{-1} in the Baltic Sea. A positive trend (r=0.9636, $p < 0.01$) was observed for North Sea PP estimates, which increased gradually from 786 in 1998 to 851 mg C m^{-2} d^{-1} in 2002. The Canary Current showed the highest average PP spatial variability, while the Baltic Sea was associated with the lowest extreme. On the other hand, temporal variability was the lowest in the Benguela Current, while the highest variability was observed in the Okhotsk Sea. PP temporal variability and spatial variability display opposite patterns, indicating an inverse relationship between these 2 sources of variation, which is even more evident when LME ranks are taken into account (Spearman rank correlation, r_s=–0.6923, $p < 0.01$) (Fig. 2). In fact, spatial heterogeneity is usually lower in ecosystems that are strongly driven by seasonal dynamics, whereas the latter can be completely masked by complex spatial patterns, e.g. ecosystems where physical drivers play a major role. Obviously, spatial and temporal components of PP variability can combine with each other, but only to a limited extent, and therefore an inverse relationship between them emerges as empirical evidence.

Table 2. Average annual PP (mg C m^{-2} d^{-1}) in each LME, estimated for the period 1998-2002 with the VGPNN (i.e. Vertically Generalized Production Neural Network, Scardi 2000, 2001) and VGPM (i.e. Vertically Generalized Production Model, Behrenfeld & Falkowski, 1997) models.

LME	VGPNN	VGPM
Atlantic Ocean		
Baltic Sea	1527	1914
Barents Sea	642	965
North Sea	820	1471
Newfoundland-Labrador Shelf	363	521
Northeast US Continental Shelf	835	1228
Scotian Shelf	549	757
Pacific Ocean	**VGPNN**	**VGPM**
East Bering Sea	446	652
Gulf of Alaska	153	709
Okhotsk Sea	165	671
Sea of Japan	416	628
Eastern Boundary Currents		
Benguela Current	988	1294
California Current	367	628
Canary Current	774	1494
Humboldt Current	629	874

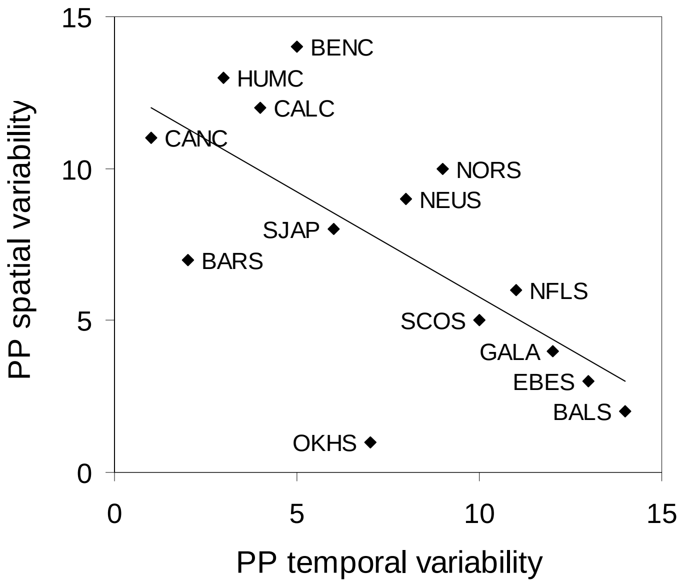


Fig. 2. Temporal vs. spatial variability in PP. The rank correlation between the two is negative and highly significant (Spearman's r = -0.6923 , p < 0.01). See Table 1 for abbreviations.

Fisheries yield

Catch values ranged from 0.32 t km^{-2} yr^{-1} for the California Current LME to 3.93 t km^{-2} yr^{-1} in the Humboldt Current. Total yields exhibited significant trends in 3 LMEs: (1) negative trends were observed for the Okhotsk Sea ($r = -0.9830$, $p < 0.01$) and the Baltic Sea ($r = -0.9471$, $p < 0.05$); (2) a positive trend was observed for the Benguela Current ($r = 0.8813$, $p < 0.05$). Significant trends observed for the Baltic Sea and the Benguela Current were related to a decrease or increase in single TL classes. In particular, the negative trend observed in the Baltic Sea was associated with a decrease in L275 catches, which were mainly represented by small pelagic fishes (sprat *Sprattus sprattus*), while the positive trend in the Benguela Current was associated with an increase in L375 catches, although this class was the less abundant of the two (up to 5% in 2002). In 4 LMEs total catches were dominated by low TL species (L225): in the California Current (41%), the Newfoundland-Labrador Shelf (46%), the Northeast US Continental Shelf (51%) and the Humboldt Current (85%), the latter being the most productive marine fishing ground in the world, where catches are indeed totally represented by Peruvian anchoveta *Engraulis ringens*. The North Sea (59%), the Canary Current (53%) and the Baltic Sea (45%) showed prevalent catches in L275, represented by small pelagic species in the Canary Current and the Baltic Sea (sardine or pilchard *Sardina pilchardus* and sprat, respectively) and by sand eels *Ammodytes* spp. in the North Sea; these are target species of the largest single-taxon fishery in this region. Intermediate TLs, represented by L325, encompassed top-reported species and accounted for almost one-third of the average total catches through selected LMEs. In addition, 6 of the 14 LMEs showed dominant catches in L325 and L375. Finally, none of the 14 LMEs showed average catches dominated by L425, although the Gulf of Alaska exhibited a particularly high proportion of this TL class (around 28%), associated with Pacific cod *Gadus macrocephalus* catches.

Relating PP to fisheries yield

Total fisheries yield and primary productivity

Fisheries yields versus PP, following Nixon (1992) and Nixon et al. (1986), are shown in Fig. 3. LMEs and Nixon’s ecosystems are plotted, together with TE known levels. For each LME, range bars show minimum and maximum annual PP from 1998 to 2002. While values on the PP axis are comparable amongst LMEs (with the Baltic Sea and the Barents Sea showing the highest range, i.e. 85 and 111 g C m^{-2} yr^{-1}, respectively), a greater and more widespread variability is apparent on the yield axis. In other words, fisheries yields can be quite different despite similar ecosystem PP (e.g. Fig. 3; the Humboldt Current, the Okhotsk Sea and the Sea of Japan show considerable differences in total yields and negligible differences in PP). It follows that PP in these systems, although setting the potential for target (and non-target) species, may not represent the main driving force for the harvest, as fisheries yields actually originate from a complex combination of different factors, both biological and industrial (management policies, fishing effort and commercial interests). Thus, PP and fisheries landings could represent input and output variables of a 'black box' into which natural systems dynamics act under the influence of industrial exploitation strategies. Even though these remain known, the efficiency of the complex relationship between PP and landings could be represented by overall TE, which provides a rough measure of the effect of harvesting. The efficiency of this complex relationship is represented by overall TE, which provides a rough measure of the effect of harvesting. Total yields in different LMEs are in fact characterized by different average TLs, so that for any given level of PP, TE may vary according to the combination of exploitation pressures on each TL. While overall TEs in Nixon et al. (1986) ranged from 0.1 to 1%, the estimated values obtained in the present study are smaller (0.01 to 0.3%). However, it must be pointed out that high overall TEs in Nixon et al. (1986) were reported mainly for estuaries and near-shore shelves, with an exception made for the Humboldt Current, which still expressed the highest TE in our data set.

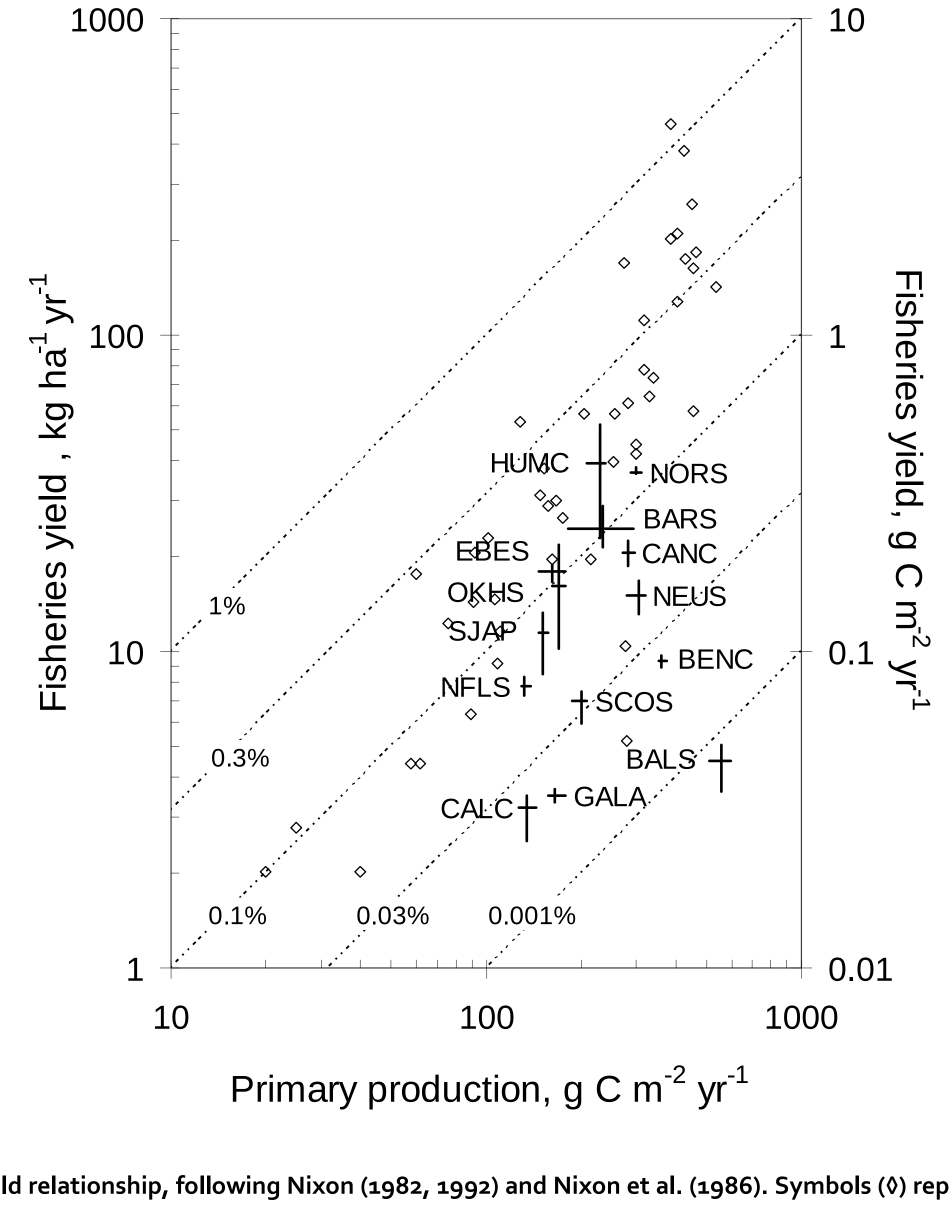


Fig. 3. PP-yield relationship, following Nixon (1982, 1992) and Nixon et al. (1986). Symbols (◊) represent Nixon's ecosystems. Variability in PP (horizontal bars) and total yield (vertical bars) are shown for each LME. Diagonal lines and associated % values show different levels of efficiency in energy transfer from PP to fisheries yield (see 'Results' for details; see Table 1 for abbreviations).

Multivariate analysis

The CA ordination of average catches per TL class for each LME is shown in Fig. 4. Three main features arise from the ordination: (1) the lowest TL class (L225) is isolated from the others and it drives the ordination, (2) the second TL class (L275) is separated from the 3 subsequent TLs and (3) intermediate TLs are close to each other (L325 and L375). The upper TL class (L425) does not appear to contribute in a relevant way to the ordination along the first axis (CA1 in Fig. 4). Moreover, LMEs are associated with different dominant TL classes: in particular, 3 out of 4 EBCs are associated with low TL classes (the Humboldt Current and the California Current with L225 and the Canary Current with L275), while intermediate TLs seem to be associated with temperate shelves and sub-polar ecosystems (e.g. East Bering Sea, Gulf of Alaska, Okhotsk Sea, Scotian Shelf). Demersal-dominated ecosystems (East Bering Sea, Gulf of Alaska, Okhotsk Sea and Newfoundland Labrador Shelf) were located in the negative CA2 semi-plane (Fig. 4), with the only exception being the North Sea, which is associated with L275 catches (see also Fig. 8).

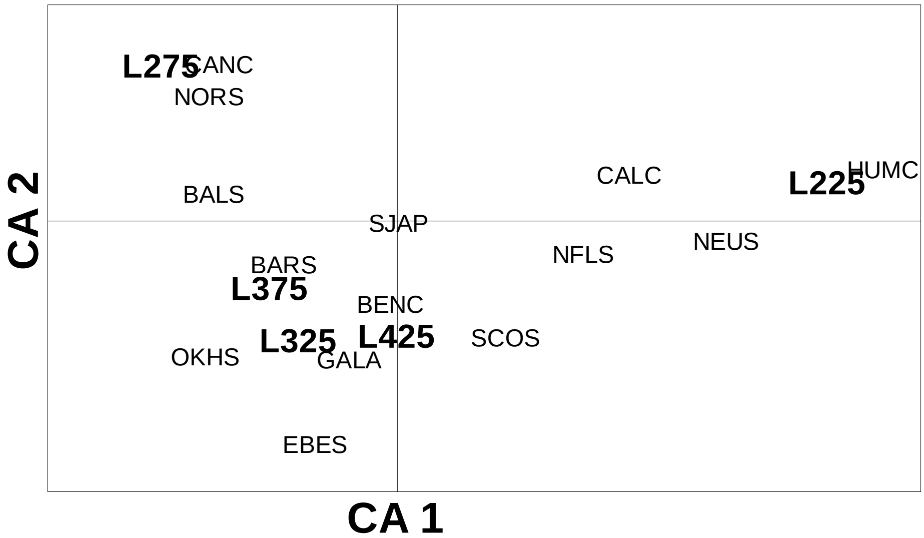
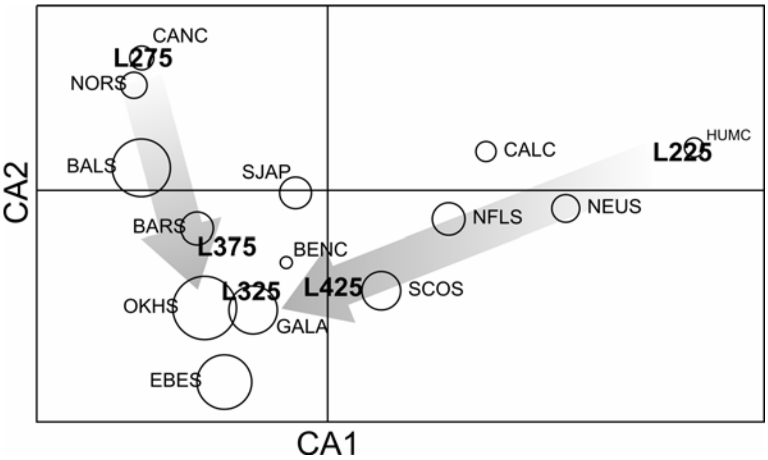


Fig. 4. Correspondence analysis (CA) of LMEs and trophic levels. This ordination shows the role that trophic levels (TLs) play in each LME (see Fig. 1 for abbreviations of LME names).

Information about PP temporal variability and total yields was displayed in the CA ordination plot by turning the plot into 2 bubble plots (Fig. 5, a and b). A general relationship between the PP temporal variability and the composition of catches is apparent: a high PP temporal variability, indicating marked seasonal variations (Fig. 5a), seemed to favor upper and intermediate TLs (L325, L375 and L425), whereas low TL catches (L225 and L275) are associated with much more stable ecosystems (Fig. 5a) and higher yields (Fig 5b). In other words, the fisheries yield under conditions of high PP variability is associated with intermediate TLs (demersal catches) and is generally lower than in more stable fishing grounds, where pelagic-dominated (low TLs) harvests produce the world's highest yields in marine fisheries. Average PP and spatial variability are not presented here as they did not show any clear pattern in association with total yields.

(a)



(b)

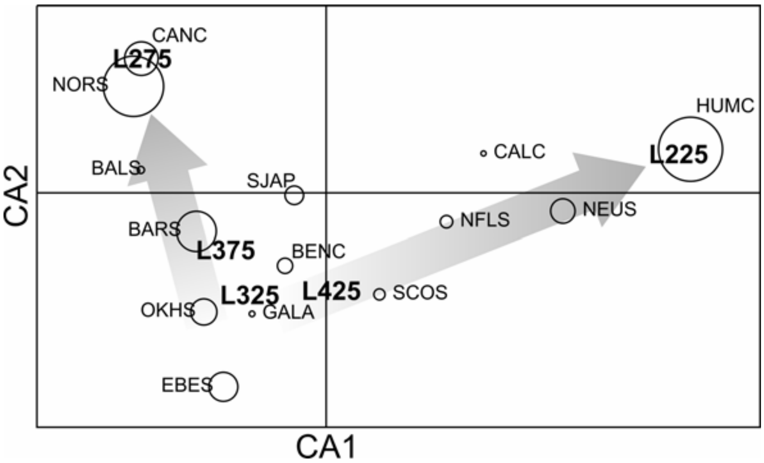


Fig. 5. Correspondence analysis: bubble size represents (a) primary productivity (PP) temporal variability and (b) total fisheries yield. As suggested by the grey arrows, temporal variability is minimum in LMEs where lower TLs, especially L225, play a major role. In contrast, total yield is maximum in these LMEs, as the overall efficiency of energy transfer is negatively correlated to the exploited TL. See Table 1 for abbreviations.

Primary productivity required to sustain total yields

Estimated PP values ranged from 132 to 557 g C m^{-2} yr^{-1}, while PPR values ranged from 15 to 130 g C m^{-2} yr^{-1} (Table 2). In Fig. 6, %PPR (PPR/PP) estimates are plotted against the average TL of catches in a bubble plot, where the bubble size represents the total yields. The highest yields occur in combination with moderate fishing pressures (0.1 < %PPR < 0.5, Fig. 6), especially when the average catch TL is in the intermediate to low range. High fishing pressures (%PPR > 0.5, Fig. 6) are associated with intermediate total yields and high average TL of catches. This condition seems to occur in high-latitude boreal LMEs (>50° N) where the stocks are possibly overexploited. A low fishing pressure (%PPR < 0.1, Fig. 6) is observed only in the Baltic Sea, where fisheries target relatively low TL species and the PP is very high (up to 600 g C m^{-2} yr^{-1} in 2002). Obviously, under these conditions an increase in catches can be, in theory, supported by ecosystem production.

Table 3. Average fisheries annual catches (t km^{-2} yr^{-1}), average trophic level of catches (TLc), PP (g C m^{-2} yr^{-1}), primary production required to sustain catches (PPR, g C m^{-2} yr^{-1}) and PPR/PP ratio (%PPR) for each LME. LMEs are ordered by descending %PPR.

LME	Catches	TL_c	PP	PPR	%PPR
East Bering Sea	1.79	3.59	163	116	0.71
Sea of Japan	1.14	3.40	152	100	0.66
Okhotsk Sea	1.61	3.52	170	99	0.58
Barents Sea	2.43	3.47	234	130	0.55
North Sea	3.69	3.26	299	128	0.43
Newfoundland-Labrador Shelf	0.78	3.21	132	48	0.36
Gulf of Alaska	0.35	3.82	165	52	0.32
Humboldt Current	3.93	2.72	230	71	0.31
Canary Current	2.06	3.23	282	76	0.27
Benguela Current	0.94	3.48	361	89	0.25
Northeast US Continental Shelf	1.50	3.00	305	66	0.22
Scotian Shelf	0.70	3.31	200	42	0.21
California Current	0.32	3.11	134	19	0.14
Baltic Sea	0.45	3.33	557	15	0.05

For ecosystem indicators computed on fisheries landings (Figs. 7 & 8), 2 LMEs, both located in the NW Atlantic Ocean, showed an F/I ratio value of <0: the Newfoundland-Labrador Shelf and Northeast US Continental Shelf fisheries harvest invertebrates rather than fish (Fig. 7). The F/I ratio was not computed for the Barents Sea, as invertebrates represent a negligible portion of total catches in this LME. A linear correlation of the F/I ratio in time (1998 to 2002) showed that the Northeast

US Continental Shelf exhibited a significant negative trend (r = –0.98425, p < 0.01), demonstrating that the dominance of invertebrates in the catch became stronger in this period of time.

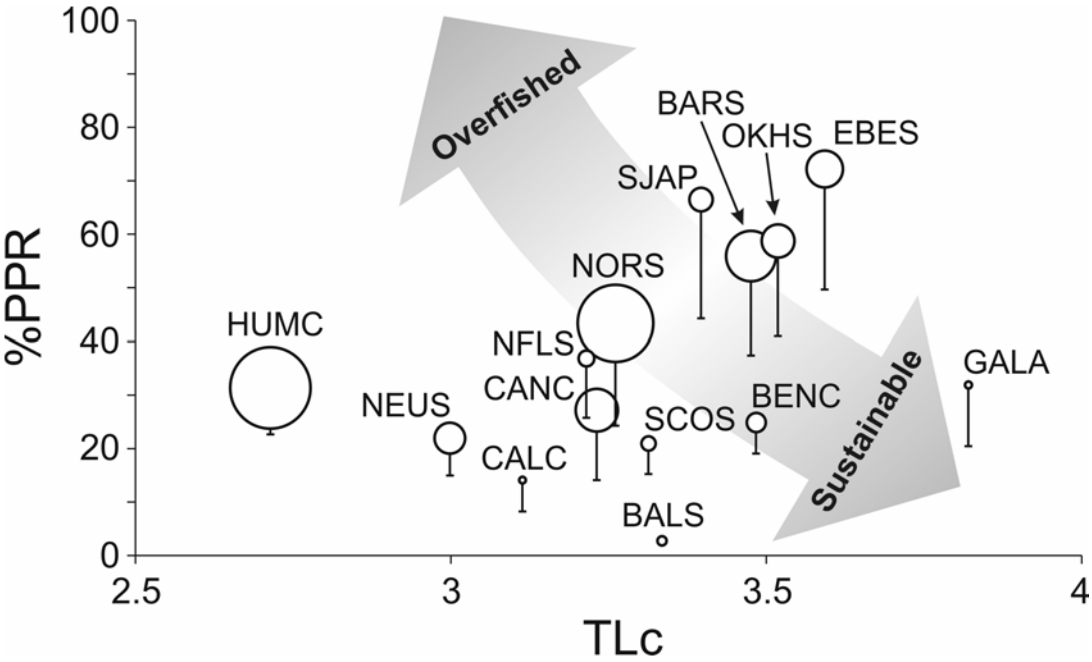


Fig. 6. %PPR versus TLc relationship: %PPR estimates for each LME based on the VGPNN model (Scardi 2000, 2001) are shown, while the lower end of the vertical bars show %PPR according to the VGPM model (Behrenfeld & Falkowski 1997). Vertical bars outline the difference between a %PPR estimate based on VGPNN (bubble) and an estimate provided by the VGPM model, i.e. the effect of uncertainty due to the PP model selection. Bubble size represents LME's total yield. See Table 1 for abbreviations.

In particular, a shift from fish to invertebrate dominance was observed to occur in 2000. An opposite pattern was observed in the Scotian Shelf, where catches from 1998 to 2000 were invertebrate-dominated, while the last 2 years of landings were fish-dominated, although a significant linear trend is missing. The demersal/pelagic composition of fisheries harvests was also assessed through the D/P ratio for LMEs showing a clear dominance in fish catches (Fig. 8). This indicator also provided a rough measure of TLc, with demersal catches showing an overall higher TLc that pelagic ones, especially when pelagic fisheries harvested small and medium-sized species (e.g. anchovies and sardines). The majority of LMEs show pelagic-dominated landings: a strong unevenness in catches was observed in the Baltic Sea and Humboldt Current, where low TL pelagic catches represented almost all landings, but low TLs species were dominant also in the other 3 EBCs (i.e.

the Benguela, Canary and California currents) and in the Barents Sea, Scotian Shelf and Sea of Japan. A significant negative trend in D/P ratio over time was observed in the Barents Sea (r = –0.97594, p < 0.01) and Scotian Shelf (*r*=–0.97949, p < 0.01), demonstrating an increase in pelagic dominance. Demersal dominance was observed in North Pacific LMEs (Gulf of Alaska, East Bering Sea and Okhotsk Sea) as well as in the North Sea. The latter showed a lower TL, which was associated with a fishing pressure exerted on low to intermediate TLs (L275 in Fig. 4), especially on *Ammodytes*.

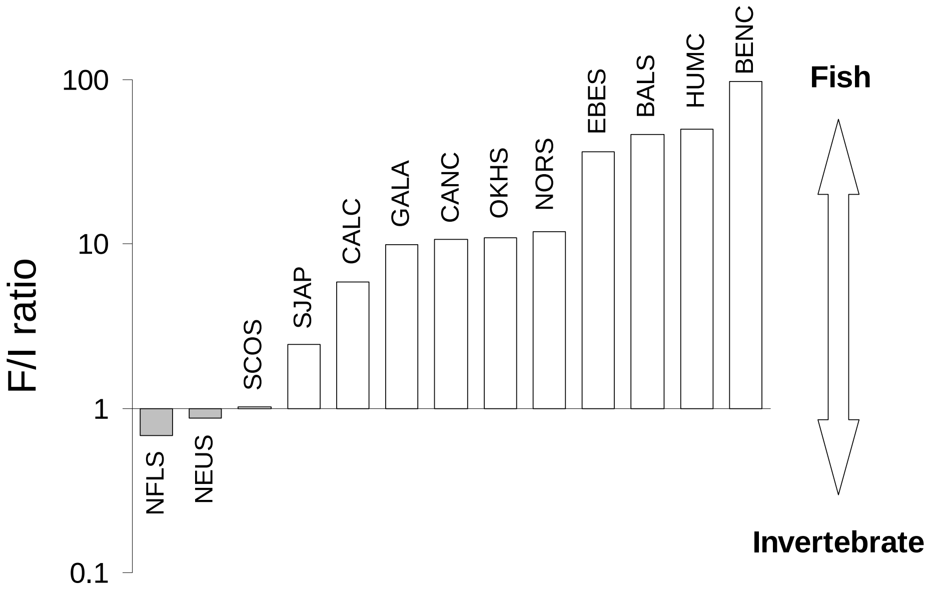


Fig. 7. Average "fish/invertebrates ratio" (F/I) (following Shannon et al. 2009). Only two LMEs, namely NFLS and NEUS, exhibit total fisheries yields dominated by invertebrate species rather than fish species. F/I ratio was not computed for the Barents Sea, as invertebrates represent a negligible portion of the total catches in this LME. See Fig. 1 for abbreviations.

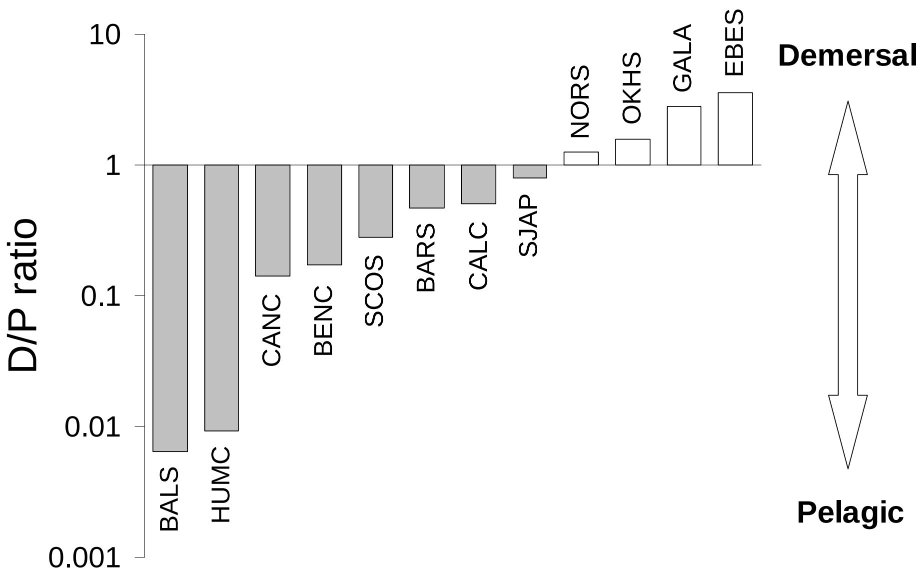


Fig. 8. Average "demersal and chondrichthyans fish/pelagic fish ratio" (D/P) (following Shannon et al. 2009).

4. DISCUSSION

Yield relationship between PP and fisheries

The present study provides new insights into the PP–fisheries relationship, suggesting that total fisheries yields can be linked more to PP temporal variability than to PP average values, as has been proposed in previous studies (e.g. Nixon 1982, 1992, Nixon et al. 1986, Iverson 1990, Nielsen & Richardson 1996, Sommer et al. 2002, Steingrund & Gaard 2005). Moreover, total yields are, in turn, negatively correlated with PP spatial variability as a consequence of the negative correlation between PP spatial and temporal variability. From an ecological perspective it would be reasonable to imagine that fish populations experiencing lower fluctuations in resources availability may profit from regular feeding of larvae and juveniles. This could determine longer reproductive and spawning seasons, which, as a result, may sustain higher yields. At the same time, from a management point of view, it would be only natural to conclude that where seasonal variability is weak, fisheries effort should be organized in a more effective way to obtain higher harvests. Furthermore, the significant relationship between PP temporal variability and TLc (r=0.5604, $p<0.05$) points to a strong correlation between environmental variability and catches composition (Fig. 9). Higher yields are typically obtained when low TLs are harvested in ecosystems that experience stable productive regimes. Under these conditions, catches are typically dominated by pelagic species. Obviously, the role of PP variability in determining fisheries yields should be further investigated when longer time series, especially on the fisheries side, are available. CA shows that intermediate TL classes (L325 and L375) tend to occur simultaneously. This coupling may be governed by intrinsic features of the TL assignment: intermediate TL species may oscillate between slightly definition is more accurate for low TL species (i.e. small pelagic fishes), whose diet is more stable and determined by physiological and morphological characteristics. Nevertheless, co-occurrence of L325 and L375 could also suggest that they share a common feature regarding fishing gear: intermediate TL species are represented mainly by demersal or benthopelagic species, which are usually all targeted by trawls. As indicated previously, intermediate TL species are typical of demersal-dominated catches and are associated with overall lower yields in LMEs characterized by less stable PP conditions.

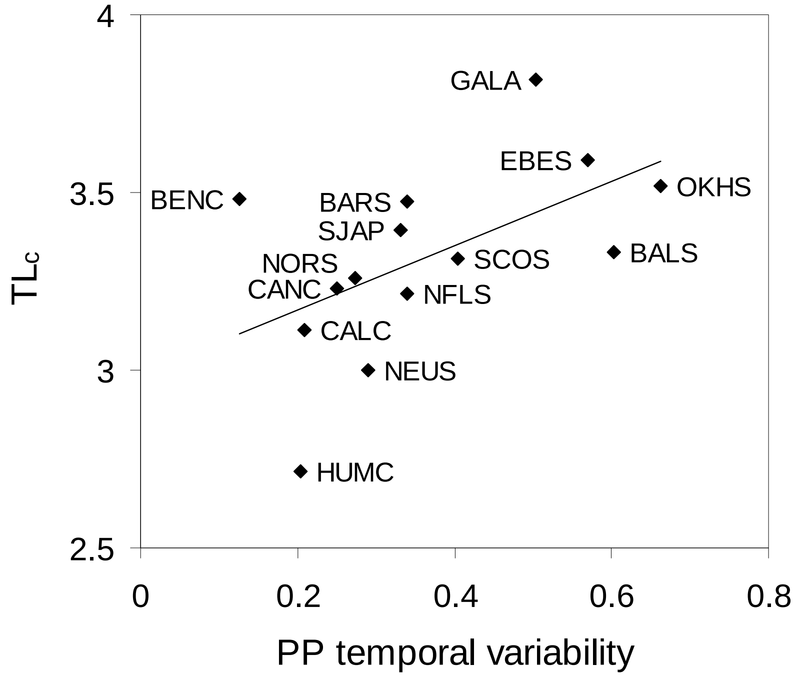


Fig. 9. TLc vs. PP temporal variability. The linear correlation is positive and significant ($r = 0.5604$, $p<0.05$). See Table 1 for abbreviations

PPR and ecosystem transfer efficiencies

Any consideration about PPR is obviously affected by the lack of accuracy in both fisheries and PP data. Uncertainty in these data may lead to widely variable estimates and, in the end, to strikingly different scenarios. PP estimates can be obtained from a number of models, but their range can be as wide as 100%. In the present study, a conservative model (VGPNN, Scardi 2001) was selected, which provides PP estimates close to the lower end of their range. The rationale supporting this choice is that, while other models have been calibrated with PP data that are possibly overestimated because of the artificial spread of PP maxima caused by vertical integration, these records have been filtered out from the VGPNN 'training set' by setting a threshold in the P/B ratio. In addition, although we assume that the overestimation of PP can also affect the VGPM model (Behrenfeld & Falkowski 1997), we compared our results with this model, which is by far the most commonly applied and the most popular template for further developments (Carr et al. 2006). Obviously, the selection of a reference PP model is inherently subjective, as there is no way to prove that any given model is better than others on a global scale (Friedrichs et al. 2009). However, differences between PP models affect the definition of the relative relationships between LMEs only to a limited extent. An estimated 8% of the total aquatic PP is required to sustain global fisheries, although shelf and upwelling ecosystems show markedly higher values ranging around 25% (Pauly & Christensen 1995). Other PPR values were computed to estimate PP requirements of single-species populations such as the Pacific herring *Clupea pallasii* in the NE Pacific Ocean and East Bering Sea (Perry & Schweigert 2008) and North Sea demersal fishes (Jennings et al. 2008). In agreement with previous studies (Pauly & Christensen 1995, Tudela et al. 2005), we obtained high PPR values for temperate shelves, even though absolute LME-specific PPR values were higher than those reported elsewhere. For example, the East Bering Sea %PPR was estimated at 0.7 compared with previously reported values of 0.15 to 0.31 (Trites et al. 1997), and the 0.36 %PPR estimated for the Newfoundland-Labrador Shelf is twice the value of 0.15 reported by Heymans (2004) for an overlapping time interval (1995 to 2000). Upwelling regions show lower PPR values (14 to 30%) in association with a fishing effort that targets lower TLs (mainly small pelagic species), so that a lower carbon fraction is necessary to sustain catches in these LMEs. The Baltic Sea was a unique condition among LMEs, where the highest average PP, determined by semi-enclosed conditions, was associated with catches at the lowest end of the TLs, leading to an extremely small PPR value (<3%). In general, the high %PPRs estimated in the present study are partially attributed to more conservative PP estimates obtained with the VGPNN model, a feature that affects both the assessment of exploitation level and management practices. A relationship between average TL of catch (TLc) and %PPR has been proposed in Tudela (2003) and Tudela et al. (2005) as an indicator of ecosystem fishing impact. Based on the approach of those authors, 2 sets of %PPR–TLc pairs for each LME were plotted (Fig. 6), each obtained with a different PP estimation model (VGPM and VGPNN). The relative location of these 2 blocks in the plot indicates a possible range of variation, which could lead to potentially different management perspectives. Following Knight & Jiang (2009), choosing the VGPM PP estimation model instead of the VGPNN model could lead to different conclusions in terms of exploitation levels. In fact, the threshold of 0.5 FPI indicated by these authors as the limit for an intermediate fishing pressure is not exceeded by LMEs when PP is estimated by VGPM. In contrast, the more conservative estimation of PP obtained with VGPNN determines the shift of high-latitude boreal shelves towards overexploitation (FPI > 0.5). It follows that a more conservative estimation of PP could contribute to a more precautionary approach to fisheries management, where high levels of exploitation are more easily attained. However, although FPI provides a rough measure of fisheries exploitation, it fails to take into account the TL on which fisheries effort is being expressed. The same pressure exerted upon low or high TLs will lead to different exploitation scenarios.

5. CONCLUSIONS

The double bottom-up/top-down approach, borrowed from food web theory, allowed us to better focus on which PP aspect acted as the principal driving control for overall fisheries yields (bottom-up) and to assess carbon budget demands (PPR) for individual fisheries in 14 LMEs (top-down). Although it could be considered a crude approach to dealing with such a complex subject, this approach turned out to be effective in addressing general questions on the dynamics underlying exploited ecosystems on a large scale. After several previous attempts (e.g. Nixon 1982, 1992, Nixon et al. 1986, Iverson 1990, Nielsen & Richardson 1996, Sommer et al. 2002, Steingrund & Gaard 2005) that focused on a limited set of records, mainly represented by direct PP measurements and local fisheries statistics, the availability of new remotely sensed data sets allowed an important scaling up to regional or even global studies. These data have been constantly collected since late 1997 in the framework of the SeaWiFS mission, providing a consistent source of information for improved PP estimates. Further advances are associated with recent comparisons between different

PP models (Carr et al. 2006, Friedrichs et al. 2009), which contribute substantially in obtaining more accurate global PP estimates and a better and more reliable analysis of the process. Nevertheless, some limitations intrinsic to these kinds of studies need to be considered. First, the limited spatial scale (e.g. the limited number of LMEs selected) could hinder a global generalization, although the LMEs considered encompass the bulk of industrial fishing grounds both in the Northern (e.g. temperate shelves like the North Sea, Baltic Sea and NW Atlantic Ocean) and in the Southern Hemisphere (e.g. major upwelling regions like the Humboldt Current). Second, it must be stressed that further information is needed to outline more accurate trends and perspectives: for instance, no information about fishing efforts is available at the same resolution as are yield data, so that landings are actually used as an approximation of actual fish catches. Nevertheless, the limited time lapse considered in our work allowed us to reasonably assume a constant exploitation pressure. Obviously, there are potential sources of error in such an assumption (e.g. moratoria measures). Finally, although we can estimate TEs from an ecological perspective, estimates need to be corrected for external energy budgets. In fact, while the photosynthetic production of organic carbon is supported by solar irradiation, the fisheries harvest is sustained by alternative energy sources (fossil fuels), which guarantee exploitation levels that exceed those supported by natural processes alone. So, even though fishing activities may be considered as a ‘top predation’, these external energy uploads significantly differentiate fishery from natural predation (Trites et al. 1997).

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CHAPTER III

Patterning large marine ecosystems fisheries landings

1. INTRODUCTION

The regional dynamics of industrial fisheries within the Large Marine Ecosystems (LMEs) boundaries were investigated by means of an historical-descriptive approach. This approach is particularly effective when addressing ecological issues, in particular in the domain of fisheries oceanography (Francis & Hare 1994), where reductionism and experimental–predictive methods could be ineffective in dealing with uncertainty and complex interplays.

While historical time series of industrial fisheries catches are available, few reviews have been published up until now, and published papers focused mainly on single species and selected LMEs, often from north Atlantic or north Pacific (e.g. Drinkwater 2009, Rose 2005). In particular, multi-decadal ecological time series have been largely used for the detection of gradual or abrupt changes in ecosystems, such as regime shifts (see Overland et al. 2008 for "regime shifts" definitions), and for the analysis of teleconnections (Stein 1998), i.e. co-variations and synchronies of single species in different hemispheres (e.g. Alheit et al. 2005, Bakun 1998, Fréon et al. 2003, Lluch-Belda et al. 1992, Schwartzlose et al. 1999). Typically, these associations are driven by cyclic or abrupt events, as ENSO (i.e. El Niño Southern Oscillation) and regime shifts themselves, whose effects spread far beyond local influence through known and less known linkages. Shifts in climate regimes can reorganize marine communities and tropho-dynamic relationships and induce changes in the mix of dominating species over decadal time scales (Alheit et al. 2005). Recent findings suggest that overexploitation, and not only climate regime shifts, can promote such long-term changes in marine ecosystems (Cury et al. 2008). Fisheries-induced regime shifts involve not only the species-level, but also entire functional groups. Savenkoff et al. (2007) demonstrated that the Gulf of St. Lawrence ecosystem shifted from a mixed piscivorous groundfish and small-bodied forage species structure to a dominance of low trophic level pelagic species, as a consequence of overfishing removal of large-bodied demersal predators. Other shifts from demersal-dominated to pelagic-dominated ecosystems have also been documented in the Atlantic Ocean and the Baltic Sea (Worm & Myers 2003, Bundy 2005, Frank et al. 2005).

In this study, landings data from the Sea Around Us Project database (available on-line at www.searoundus.org) were used to detect trends in total yields and variations in catch composition by functional groups over time. The temporal and spatial scales covered by this study allowed addressing general issues such as the detection of recurrent patterns and synchronies in fisheries landings. These kind of ordered responses represent the result of change in economic conditions, resources exploitation and fishing pressures dealing with environmental dynamics and climate change over more than fifty years. In this context, emerging patterns could represent the first step towards a better comprehension of complex interplays and synergies between ecosystems and governance.

In order to cope with the complexity of ecological data sets, powerful and flexible tools such as artificial neural networks could play a key role, both in descriptive and predictive analysis, thus providing synthetic and informative insights into large scale dynamics (e.g. Almeida 2002, Laë et al 1999, Lek & Baran 1997, Lek & Guégan 1999, Lek et al 1996). In this study, an unsupervised artificial neural network (Self Organizing Map, SOM)) is proposed as a tool to analyze fisheries landings composition variation over five decades in 51 LMEs all over the world.

2. MATERIALS AND METHODS

Dataset

Fifty-five years (1950-2004) of reported fisheries catches from the world's LMEs were extracted from the SAUP database. 51 LMEs were selected for the analysis, with the exception of LMEs from Polar Oceans, which presented scarce and low differentiated catches (Fig.10, Table 4). A definition of LMEs is given in Chapter II, page 21.

Time series were represented by annual LME-specific catch composition of fisheries harvests by functional groups, as reported by SAUP (Table 5). This level of aggregation was chosen as a closer descriptor of fisheries dynamics at larger spatial scales with respect to a finer taxa resolution (e.g. single species). In other words, the dataset was composed by 2805 records (i.e. 51 LMEs times 55 years), each representing a typical catch profile or "fishery's behavior" in space and time.

Trend analysis of annual total fisheries catches

Trends of regional catches were estimated by linear regression of catch versus year for the period 1950-2004.

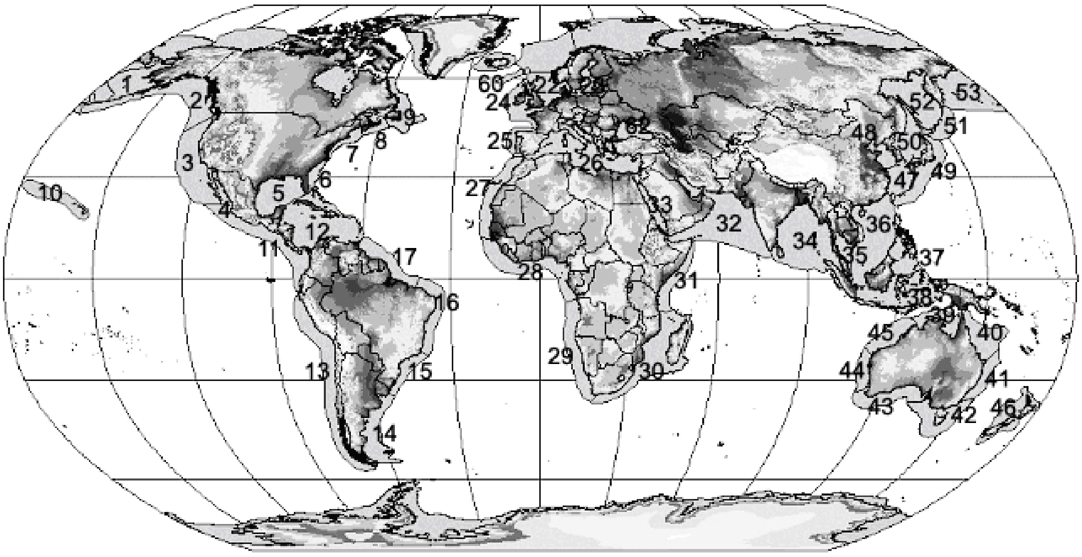


Fig. 10. Map of World's Large Marine Ecosystems. For LMEs legend and description see Table 4.

Catch composition analysis

In order to remove the effect of the trend in catches abundances, the relative contribution of each functional group to total catches was used as a descriptor of fisheries harvests. In particular, the proportions of 13 amongst 28 functional groups (i.e. characterized by >1% of average contribution across LMEs) and a mixed category (i.e. total contribution of the other 14 functional groups reported in the SAUP database, with an average contribution < 1%) were used to train a Self Organizing Map (SOM).

The SOMs are a class of neural networks based on competitive unsupervised learning. Their "neurons" are placed at the nodes of a square or hexagonal lattice that is usually two-dimensional (lower- or higher-dimensional SOMs are seldom used). As they compete with each other to be activated, only one of them can be the winner at any one time. The neurons become selectively tuned to a set of input patterns during the competitive learning and the locations of the tuned neurons become ordered relative to each other in such a way that a meaningful coordinate system emerges from their arrangement (Kohonen 1990). A SOM can be therefore regarded as a map of the input patterns in which the coordinates of the neurons in the lattice are related to their features and similar patterns will be mapped onto neighboring neurons (Fig. 11).

Table 4. The 51 Large Marine Ecosystems (LMEs) analyzed in this study. LMEs identification number, acronym, name, area (km^2), centroid coordinates (decimal degrees) and oceanic basin are reported.

LME Nr.	Acronym	LME name	Area (km^2)	Lat N	Long E	Ocean
1	EBS	East Bering Sea	1397933	57.3	-167.5	Pacific
2	GAL	Gulf of Alaska	1460365	54.3	-139.9	Pacific
3	CAL	California Current	2273942	34.9	-120.4	Pacific
4	GCA	Gulf of California	222713	33.4	-110.4	Pacific
5	GME	Gulf of Mexico	1549163	30.2	-92.9	Atlantic
6	SUS	Southeast US Continental Shelf	319775	33	-81.8	Atlantic
7	NUS	Norteast US Continental Shelf	308656	48.2	-75.8	Atlantic
8	SCS	Scotian Shelf	300258	45.6	-62.1	Atlantic
9	NFL	Newfoundland-Labrador Shelf	898803	51.5	-60.6	Atlantic
10	IPH	Insular Pacific/Hawaiian	982811	23.3	-166.6	Pacific
11	PCA	Pacific Central-American Coastal	1990321	9.1	-90.5	Pacific
12	CAR	Caribbean Sea	3285047	12.9	-75.2	Atlantic
13	HUM	Humboldt Current	2529645	-29.1	-71	Pacific
14	PAT	Patagonian Shelf	1167969	-37.6	-61.5	Atlantic
15	SBR	South Brazil Shelf	567996	-22.5	-48.6	Atlantic
16	EBR	East Brazil Shelf	1079113	-11.3	-45.6	Atlantic
17	NBR	North Brazil Shelf	1058516	1.3	-53	Atlantic
22	NOR	North Sea	698130	54.6	10.7	Atlantic
23	BAL	Baltic Sea	389252	59.6	21.1	Atlantic
24	CBS	Celtic-Biscay Shelf	769121	51.1	-5.1	Atlantic
25	IBE	Iberian Coastal	303958	40.4	-6.1	Atlantic
26	MED	Mediterranean Sea	2561659	36.4	17.7	Atlantic
27	CAN	Canary Current	1141648	23.9	-1.3	Atlantic
28	GUI	Guinea Current	1927373	4.5	3.8	Atlantic
29	BEN	Benguela Current	1436847	-20.9	17.8	Atlantic
30	AGU	Agulhas Current	2632932	-22.1	34.9	Indian
31	SCC	Somali Coastal Current	843937	0.6	38.7	Indian
32	ARA	Arabian Sea	3945355	28.4	51.7	Indian
33	RED	Red Sea	462210	18.5	31.9	Indian
34	BBE	Bay of Bengal	3679296	25	90.1	Indian
35	THA	Gulf of Thailand	395780	8.4	102.2	Pacific
36	SCH	South China Sea	3183503	17.2	105.5	Pacific
37	SUL	Sulu-Celebes Sea	1017861	7.8	121.4	Pacific
38	IND	Indonesian Sea	2275957	-3.9	119.9	Pacific
39	NAS	North Australian Shelf	782956	-17.8	133.8	Pacific
40	NEA	Northeast Australian Shelf	1284441	-18	149.8	Pacific
41	ECA	East Central Australian Shelf	654158	-28.6	149.4	Pacific
42	SEA	Southeast Australian Shelf	1192306	-40.5	143.2	Pacific
43	SWA	Southwest Australian Shelf	1052046	-31.6	126	Indian
44	WCA	West Central Australian Shelf	545539	-26.9	118.6	Indian
45	NWA	Northwest Australian Shelf	915060	-18	118.9	Indian
46	NZS	New Zealand Shelf	967616	-40.7	172.8	Pacific
47	ECH	East China Sea	780554	37.4	105.3	Pacific
48	YEL	Yellow Sea	440387	41.7	110.1	Pacific
49	KUR	Kuroshio Current	1322524	32.4	133.5	Pacific
50	SJA	Sea of Japan	997858	43.6	134	Pacific
51	OYA	Oyashio Current	532831	46	150.4	Pacific
52	OKH	Okhotsk Sea	1570523	54.5	146.4	Pacific
53	WBS	West Bering Sea	2170639	58.2	174.4	Pacific
60	FAR	Faroe Plateau	150558	60.4	-11.5	Atlantic
62	BLA	Black Sea	461958	43.8	39.8	Atlantic

Table 5. The 28 functional groups used for the analysis. From Sea Around Us Project (www.searoundus.org)

Functional group	Size (Lmax)
Vertebrates	
Bathydemersals	Large (> 90 cm)
	Medium (30-89 cm)
	Small < 30 sm
Bathypelagics	Large (> 90 cm)
	Medium (30-89 cm)
	Small < 30 sm
Benthopelagics	Large (> 90 cm)
	Medium (30-89 cm)
	Small < 30 sm
Demersals	Large (> 90 cm)
	Medium (30-89 cm)
	Small < 30 sm
Flatfishes	Large (> 90 cm)
	Small to medium (< 90 cm)
Pelagics	Large (> 90 cm)
	Medium (30-89 cm)
	Small < 30 sm
Reef Associated Fishes	Large (> 90 cm)
	Medium (30-89 cm)
	Small < 30 sm
Rays	Large (> 90 cm)
	Small to medium (< 90 cm)
Sharks	Large (> 90 cm)
	Small to medium (< 90 cm)
Invertebrates	
Cephalopods	
Crustaceans (nectonic)	
Crustaceans (bethonic)	
Other demersal Invertebrates	

The essential elements and parameters of the algorithm are:

- a continuous input space of activation patterns that are generated in accordance with a certain probability distribution;
- a topology of the network in the form of a lattice of neurons, which defines a discrete output space;
- a time-varying neighborhood function $h(t)$ that is defined around a winning neuron and shrinks during the learning phase;
- a learning rate $\eta(t,r)$ that starts at an initial value η_0 and then decreases gradually with time t, but never goes exactly to zero.

There are three basic steps involved in the application of the algorithm after initialization: sampling, similarity matching, and updating. These three steps are repeated until formation of the feature map has completed. The algorithm is summarized as follows:

1. **Initialization**. Choose random values for the initial weight vectors $\mathbf{w}_i(0)$. The only restriction here is that the $\mathbf{w}_i$ (0) be different for i = 1, 2, …, n, where n is the number of neurons in the lattice. It may be desirable to keep a small magnitude of the weights. Another way of initializing the algorithm is to randomly select the weight vectors from the available set of input vectors;
2. **Sampling**. Draw a sample **x** from the input space with a certain probability. The vector **x** represents the activation pattern that is applied to the lattice. The dimension of vector is equal to the dimension of the weight vectors $\mathbf{w}_i$;
3. **Similarity Matching**. Find the best-matching (winning) neuron (Best Matching Unit, BMU) at time step t by using a minimum-distance (usually Euclidean) criterion;
4. **Updating**. Adjust the synaptic weight vectors of all neurons by using the update formula

   $$w_i(t+1)= w_i(t)+ \eta(t, h(t))\ \eta\ [x(t)- w_i(t)]$$

   where $\eta(t, h(t))$ is the learning rate parameter, and $h(t)$ is the neighborhood function centred around the winning neuron; both $\eta(t, h(t))$ and $h(t)$ are varied dynamically during learning phase;
5. **Continuation**. Go back to step 2 until no noticeable changes in the feature map are observed.

The training procedure can be carried out once more, starting with a smaller learning rate and smaller (or even null) radius of the training neighborhood. This second training phase is usually referred to as the fine tuning phase. More details about SOM training can be obtained from several different sources (e.g. Kohonen 1982, 1995, Lippman 1987, Hecht-Nielsen 1990, Zurada 1992). The SOMPAK package, a very classic implementation of SOMs, was developed by Teuvo Kohonen and his co-workers and is now available from the web site http://www.cis.hut.fi/research/ som-research/nnrc-programs.shtml. SOMs have been successfully applied to a broad spectrum of problems and applications to ecology are no exception, because they are not sensitive to some of the problems that often affect ecological data, hindering more conventional methods (non-linear relationships between variables, non-normal distribution of data, etc.). In fact, it can be viewed as a non-linear extension of the Principal Component Analysis (Ritter et al. 1992) or, as a hybrid between clustering and ordination techniques.

By means of a SOM, the 2805 records (i.e. LME/year) were classified into an output map of 63 units (i.e. 7 x 9 hexagons), each representing a virtual vector corresponding to a catch composition profile, to which a different number of observations was assigned. The SOM dimension was chosen in order to avoid empty units and preserving clear patterns in variables distributions.

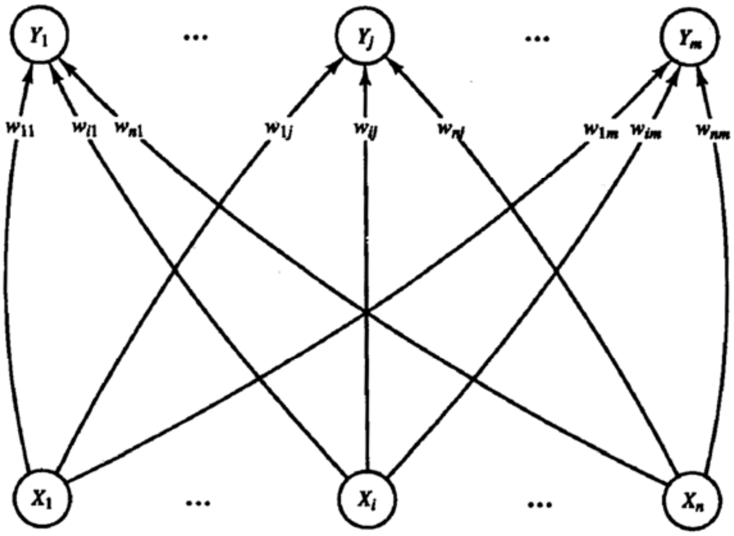


Fig. 11. Structure of a SOM: the input layer (X) is connected to the feature map (Y) and each connection is associated to a weight (w). From L. V. Fausett (1994) Fundamentals of Neural Networks: Architectures, Algorithms, and Applications, Prentice Hall, Englewood Cliffs, NJ, xvi+460 pp

The overall evolution of each regional fishery over the time range was captured by LME-specific temporal tracks drawn on the map, i.e. broken lines connecting the cells in which 1950 to 2004 observations for each LME fell. In order to point out recurrent patterns, a hierarchical classification (UPGMA algorithm) of these LMEs' trajectories was performed, based on the hexagon distance between the relative positions of the LMEs' observation for the same year. The "elbow (or knee) method" was used to determine the optimal partition, which was comprised of 5 clusters.

Mantel's test

Mantel's tests were performed between: (1) distance matrices derived from catches abundances (Bray-Curtis distance) or catches proportions (Euclidean distance) and geographic (and latitudinal) distance between LMEs' centroids. The Mantel's statistics time series was analyzed by linear correlation to detect significant trends. Geographic and latitude distances between LMEs' were computed by means of the rdist.earth function in R.

3. RESULTS AND DISCUSSION

Trend analysis of annual total fisheries catches

A general and widespread positive trend was observed amongst the LMEs when time series of total abundances were analyzed (Fig. 12). 6 LMEs did not show any significant trend (i.e. the US continental shelf LMEs, the Scotian Shelf, the Insular Pacific/Hawaiian, the North Sea, the Iberian Coastal and the Agulhas Current) while Newfoundland-Labrador Shelf showed a negative significant trend ($r = -0.5453$, $p < 0.01$) (Fig 13).

The increase in total fisheries yields represents the direct effect of the corresponding increase in fishing effort driven by growing market demand and determined by the availability of improved technologies for navigation and fishing activities from 1950 onwards. Fishing vessels became able to reach more distant fishing grounds and more and more performing in harvesting marine resources. The reported catch increases were greatest in the 1960s, when the traditional fishing grounds of the North Atlantic and North Pacific became fully exploited and new fisheries opened at lower latitudes and in the Southern Hemisphere (Watson & Pauly 2001). The opposite negative trend showed by total catches landed in the Newfoundland-Labrador Shelf is to be related to a governance "disturbance", as landings in this ecosystem have been for a long time dominated by Atlantic cod (*Gadus morhua*) catches, until the overexploitation of the stocks was interrupted by a "cod moratorium" enacted by the Canadian government in 1992. It followed a drastic reduction of total landings which lead to the negative trend observed, before the fishery was reorganized to target different species (e.g. mainly, demersal invertebrates).

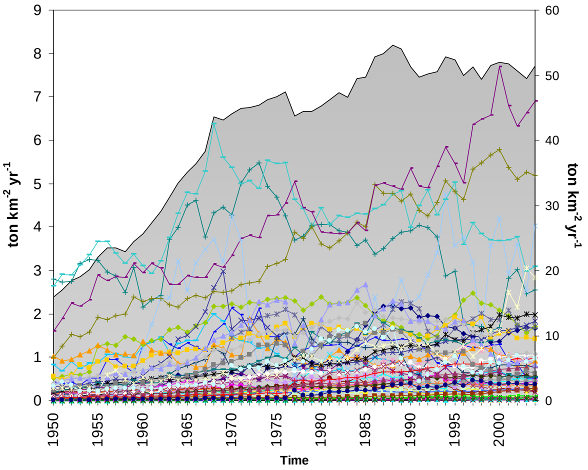


Fig. 12 Trends of total catches in the 51 LMEs from 1950 to 2004. Global catches trend is shown in shaded grey.

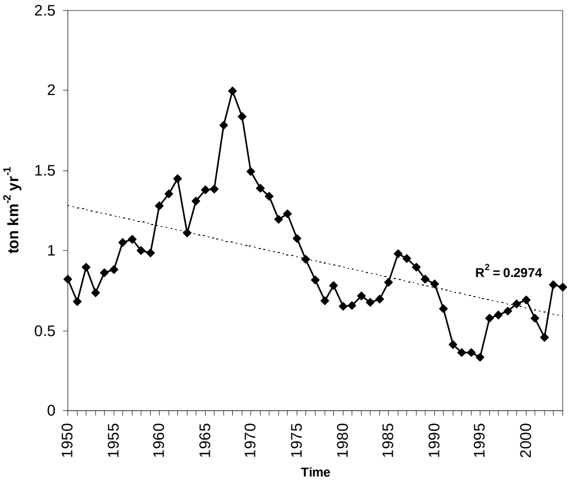


Fig. 13 Total yields in Newfoundland-Labrador Shelf (LME 9) from 1950 to 2004. The negative trend observed (r = -0.5453, p < 0.01) was related to the collapse of the demersal fishery targeting Atlantic cod *Gadus morhua.*

Stability versus Variability in LMEs

Regarding the evolution of landings composition over time, it could be observed that LMEs can be roughly divided into “stable” and “unstable”, the first being those ecosystem which experienced a very little change in landings composition over time, while the latter include LMEs which experienced even radical restructuring of fisheries harvests composition, with linear or cyclic patterns (Fig. 14). In particular, LMEs from North Atlantic and North Pacific showed the most variable patterns, while ecosystems from the Indian Ocean (e.g. LMEs 30 to 34 and 43 to 45) showed very little if any variation (Fig. 14). Amongst the northern temperate ecosystems, the Mediterranean Sea (LME 26) stands out for its stability.

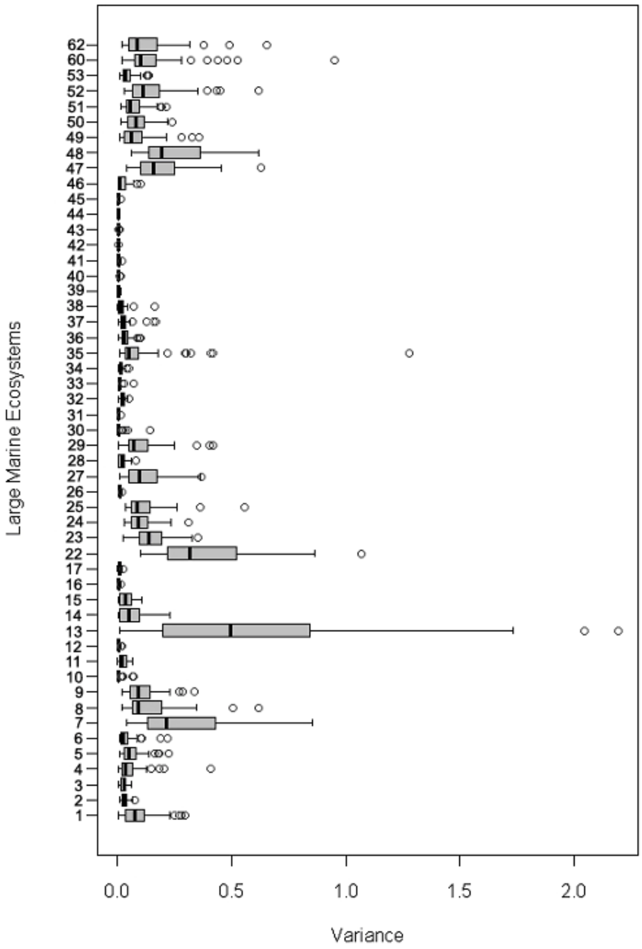


Fig. 14. Box plot showing the distribution of the 54 variances of the differences in catch composition between subsequent years. See Table 4 for LMEs legend.

Catches composition analysis

Self Organizing Map (SOM)

As landings time series were biased by the widespread increase in total yields from 1950 to 2004, change in fisheries catches composition was better described by variation in functional groups' proportions rather than by variation in abundances. The SOM trained on the relative contribution of 14 functional groups to total annual catches in each LME is shown in Fig. 15. The number of observations assigned to each Best Matching Unit (BMU) ranged from 7 (unit 3,4, i.e. unit in line x and column y) to 108 (unit 5,2). The absence of empty units showed that each BMU represents a real harvests composition, which was then associated with a number of real observations. No "virtual" profiles where thus represented on the map. Each unit in the SOM indeed represent a typical combination of the 14 variables, which could be visualized as a histogram representing the relative contribution of each functional group to total catches (Fig. 16). The least represented profile (see unit 3,4) was associated with the Humboldt Current catches from 1950 to 1956. The histogram showed a mixed composition of large and small pelagics, where the mixed category (i.e."Other") was also well represented. The most frequent profile (see unit 5,2) was associated with the time series from Guinea Current and Sulu-Celebes Sea, together with catches from Canary Current (1970 – 1971), East China Sea (1987 – 1989) and Kuroshio Current (roughly from the end of 1970s until 1993). This BMU represented a catch profile dominated by medium pelagic harvests.

The structure of the SOM depends on the parceling of the continuous variation of the input variables in the original data set; the resulting discrete set of variation for each functional group is shown in Fig. 17. The comparison of these patterns allows understanding the relative contribution of each variable to the SOM, and provides a straightforward way to identify those variables which are less determinant (Fig. 17). Regarding these maps, a distinction between regular and irregular patterns of distribution of the different functional groups was observed. Functional groups showed highest and lowest values occuring in units that were located in well-defined SOM regions (e.g. large benthopelagics in the upper right corner and small pelagics in the upper left corner), while other groups showed a more irregular pattern, in which extreme values did not occur in SOM units that were close to each other (e.g. cephalopods, crustaceans and small flatfishes). The complex structure of the SOM was influenced by regular and strong patterns, as those represented by large benthopelagics, medium pelagics and small pelagics. The modulation of the relative dominance of these functional groups in total catches influenced the LMEs displacements onto the map, i.e. the temporal evolution of catch composition in each LME from 1950 to 2004, represented as a broken line on the SOM. The other groups exerted a local (in space or time) influence as they were relevant only in a small number of observations. These less represented groups were often associated with mixed catches profiles, whereas the most fished functional groups tended to dominate reported landings, representing the bulk of total catches.

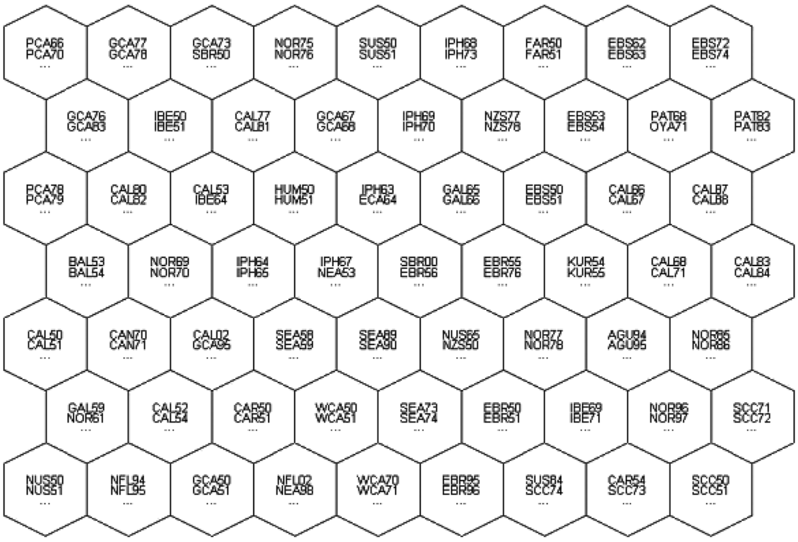


Fig. 15. Self Organizing Map. Only the first two labels are shown in each unit.

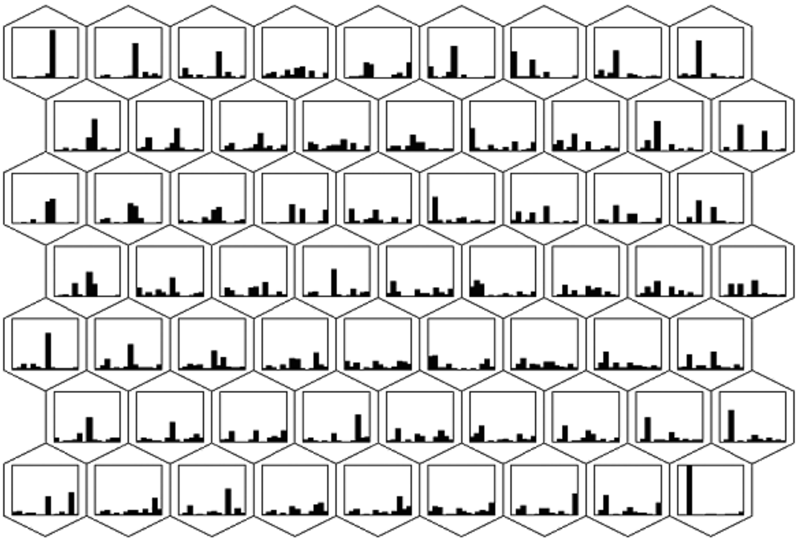
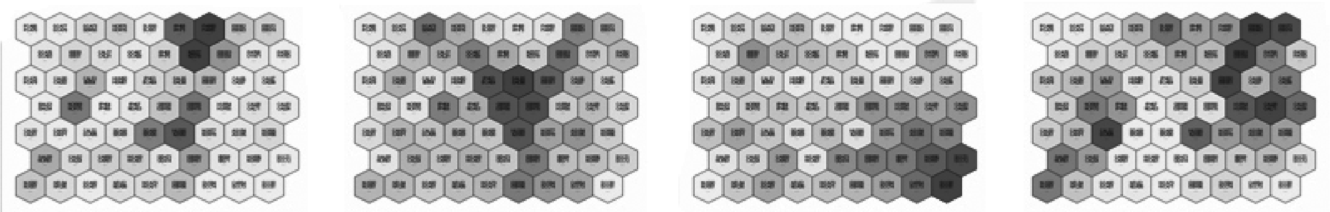
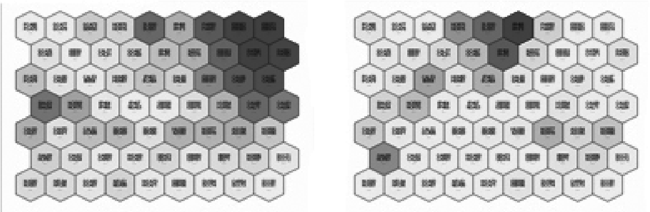


Fig. 16. Self Organizing Map. The relative abundance of the 14 functional groups is shown in each SOM unit.

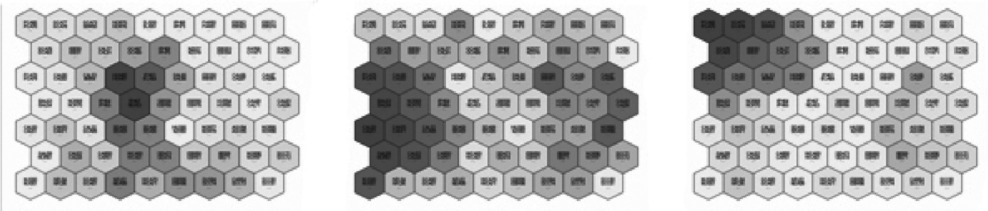
Fig. 17. Self Organizing Map. The weight of input variables are shown in grey scale.



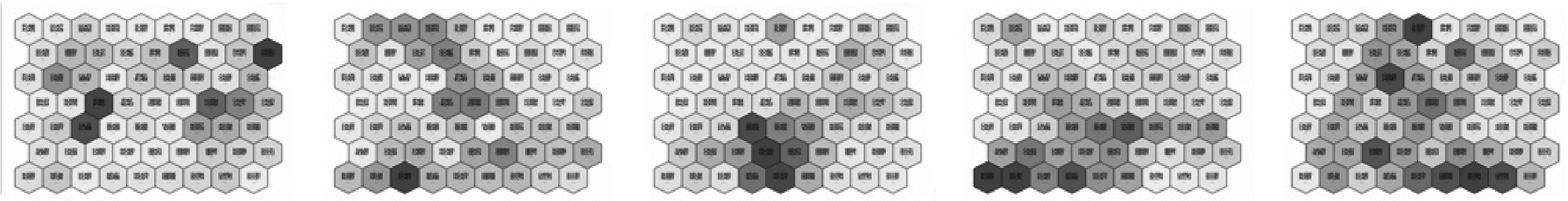
1 - Large demersals 2 - Medium demersals 3 - Small demersals 4 - Small flatfishes



5 - Large benthopelagics 6 - Medium benthopelagics



7 - Large pelagics 8 - Medium pelagics 9 - Small pelagics



10 - Cephalopods 11 - Crustaceans (nectonic) 12 - Crustaceans (reptantia) 13 - Demersal Invertebrates 14 - Other

Fishery tracks: temporal variation of LMEs' catches profiles

As previously described, the evolution of the regional fisheries was described by LME-specific temporal tracks drawn on the SOM. From a hierarchical classification of these 51 "fishery tracks", 5 clusters were identified (Fig. 18, Table 6). A description of the main features for each cluster is given below. The frequency of occurrence of each cluster has been plotted on the SOM to visualize the region of the map where the LMEs time series classified in each cluster tended to converge (Fig. 20, a-e). A better comprehension of the main features described for each cluster could be attained through the comparison of the maps showed in Fig 17, with those in Fig. 20.

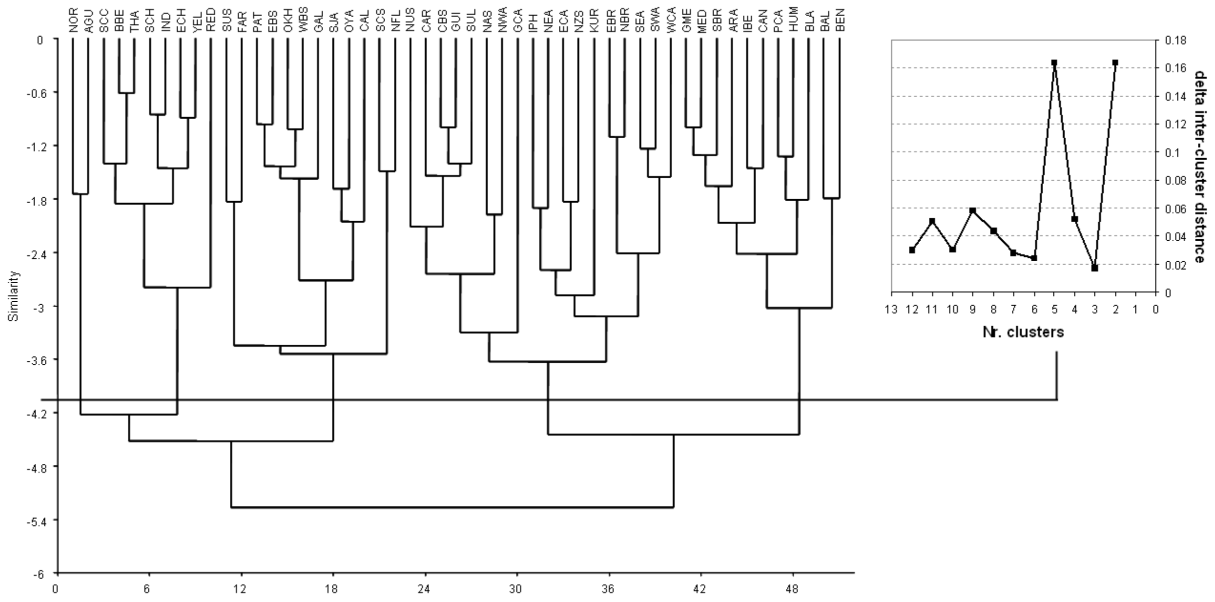


Fig. 18. Hierarchical classification (UPGMA) of SOM units. Five clusters were identified following the "elbow method" shown beside the dendrogram.

Table 6. LMEs' cluster membership as a result of the classification analysis. For abbreviations see Table 1. The classification tree is shown in Fig. 18.

Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
IPH	SUS	GME	SCC	NOR
NEA	FAR	MED	BBE	AGU
ECA	PAT	SBR	THA	
NZS	EBS	ARA	SCH	
KUR	OKH	IBE	IND	
EBR	WBS	CAN	ECH	
NBR	GAL	PCA	YEL	
SEA	JAP	HUM	RED	
SWA	OYA	BLA		
WCA	CAL	BAL		
NUS	SCS	BEN		
CAR	NFL			
CBS				
GUI				
SUL				
NAS				
NWA				
GCA				

Cluster 1 - Mixed catches

This cluster was the largest one, encompassing 18 LMEs. These regions were probably the less characterized with respect to other LMEs classified in other clusters and for this reason they have been grouped together. Nonetheless, it could be observed that a number of LMEs classified in this cluster shared common fisheries profiles in which low trophic level species, as those encompassed in medium pelagics and demersal invertebrates functional groups, were well represented (Fig. 20a).

Cluster 2 - Demersal, benthopelagics and invertebrates

This cluster regrouped 12 LMEs from Northern Hemisphere, both from the Pacific and the Atlantic Ocean, and the Patagonian Shelf. These LMEs showed homogeneous patterns in catch composition variation over time, where harvests were broadly characterized by bottom functional groups, as benthopelagics and demersals (Fig. 20b). In particular, the two currents' systems (i.e. the Oyashio Current and the California Current) showed the most variable patterns amongst the LMEs in this cluster. The Californian Eastern Boundary Current, characterized by periodic strengthening of coastal upwelling linked to climatic teleconnections (Bakun 1990), showed cyclic oscillations between pelagic [Californian anchovy (*Engraulis mordax*) and South American pilchard (*Sardinops sagax*)] and demersal (North Pacific hake, *Merluccius productus*) catches, while landings from the Oyashio Current, characterized by cold sub-polar nutrient rich waters, were dominated by South American pilchard and Pacific saury (*Cololabis saira*) at the beginning of the series (up until early 1960s) and then turned into a mixed pelagic and benthopelagics (i.e. Alaska pollack, *Theragra chalchogramma*) fisheries with more damped oscillations with respect to its eastern Pacific counterpart. As for the other western Pacific LMEs (i.e. Okhotsk Sea, Sea of Japan), they also experienced a common trend from medium pelagics dominated landings to large benthopelagics catches. A similar pattern was observed for the Faeroe Plateau, where catches boosted up at the beginning of the 1970s, when medium benthopelagics (i.e. Blue whiting *Micromesistius potassou*) became the dominant fraction of total harvests.

Cluster 2 encompassed a “Canadian sub-cluster”, which would stand alone if a partition of 8 clusters would have been chosen, in which two Northwest Atlantic LMEs (Newfoundland-Labrador Shelf and Scotian Shelf) showed a general restructuring of fishery landings from typical demersal and large benthopelagic dominated harvests to medium pelagics and demersal invertebrates catches (the temporal evolution of fisheries catches composition in the Scotian Shelf is shown in Fig. 19.

As already mentioned, these ecosystems experienced a quite abrupt (and well documented) change in the 1990s, when mixed demersal catches were totally replaced by medium pelagics and demersal invertebrates. In particular, while the Scotian Shelf ecosystem showed mixed demersal and pelagic catches since the 1970s, and the shift to pelagic and invertebrates landings was observed in 1994, the Newfoundland-Labrador Shelf was characterized by demersal dominated landings until 1992, when demersal fishes were replaced by invertebrates.

The collapse of six of seven cod stocks ranging from southern Labrador to the Scotian Shelf induced Canadian institution to impose the bans of unspecified duration on commercial exploitation in 1992 and 1993 (Myers et al. 1997). Cod had been the main target species of Newfoundland fishery since 1500s, but in 1992, after almost five centuries of exploitation, the stock collapsed leading to the disruption of Canadian fishing industry (Hutchings & Myers 1994). After the “cod moratorium” imposed by the Canadian government in 1992, fishing vessels and gears were converted towards new low-TL target species, mainly represented by demersal invertebrates [e.g. Northern shrimp

(*Pandalus borealis*), Atlantic sea scallop (*Placopecten magellanicus*), Snow crab (*Chionoecetes opilio*), ocean quahog (*Arctica islandica*) and Atlantic lobster (*Homarus americanus*)]. Nevertheless, the scarcity of landings derived from these new target species, together with the lower market value of these species compared with Atlantic cod, obliged the government to refund fishers with welfare payments (Hutchings & Myers 1994).

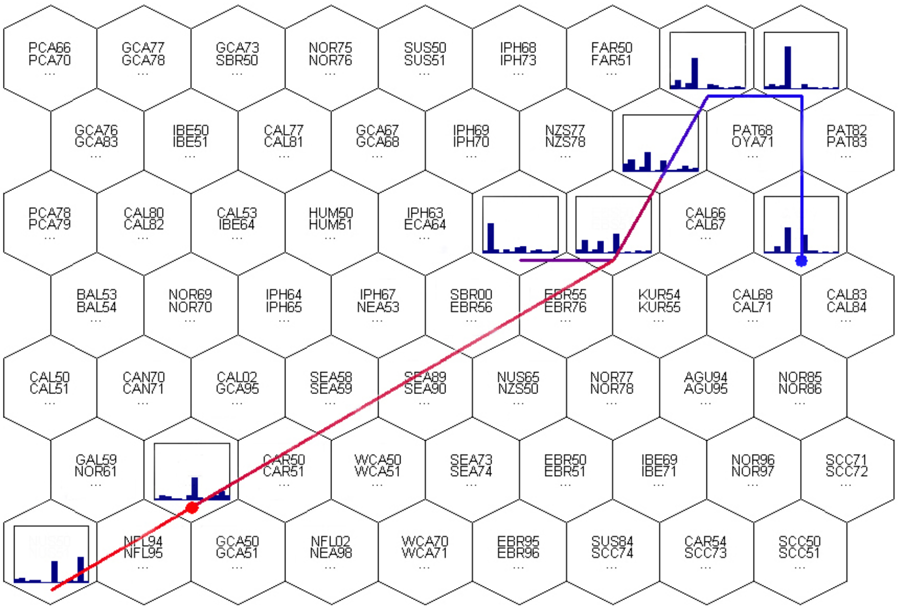


Fig. 19. Self Organizing Map. The temporal evolution of fisheries catches composition in the Scotian Shelf is shown on the SOM, from 1950 (blue dot) until 2004 (red dot). Catches composition in terms of functional groups are shown as histograms inside each unit.

From a tropho-dynamic perspective, the fisheries tracks exhibited by these LMEs could represent an example of the “fishing down marine food webs” trend (Pauly et al. 1998), i.e. decline of the average trophic levels of catches (TLc) over time, even though in these LMEs such a trend was forced by management measures rather than by autonomous reorganization of the fishing fleet.

The Southeast US Continental Shelf was also included in this cluster, although its fishery exhibited a quite unique evolution of catches composition over time, where demersal invertebrates, together with lobsters and shrimps played a major role. At last, only one Southern Hemisphere’s ecosystem was classified in cluster 2: the Patagonian Shelf. This south Atlantic LME has been characterized by large demersal dominated landings until the beginning of the 1980s, when cephalopods captures became an important component of total landings up until 2003.

Cluster 3 - Small and medium pelagics

This cluster is composed by eleven LMEs which share the common feature of landings represented mainly by small and medium pelagics (Fig. 20c). LMEs encompassed in this cluster could be subdivided in three main subgroups: (1) enclosed and semi-enclosed basins (i.e. Baltic Sea, Black Sea and Mediterranean Sea), (2) upwelling ecosystems [i.e. three Eastern Boundary Currents (Humboldt Current, Canary Current and Benguela Current), Arabian Sea, South Brazil Shelf, Iberian Coastal and Pacific Central-American Coastal) and (3) enriched basins (Gulf of Mexico). With the exception of the oligotrophic Mediterranean Sea, LMEs classified in Cluster 3 are moderately to highly productive ecosystems, even though nutrient availability is triggered by different processes in upwelling regions and enclosed basins, where human induced eutrophication, river runoff and lack of rapid exchange with adjacent oceans play a major role (NOAA 2002, Hullenberg 1986, Caddy 1993, Garibaldi & Limongelli 2003).

From an industrial perspective, small and medium pelagic species represent the most abundant catches in world’s fisheries. It has been suggested that these low trophic (and low economically valuable) species are more abundant and heavily exploited in those ecosystems in which primary productivity experiences low temporal (seasonal or intra-annual) variability (Conti & Scardi 2010).

Cluster 4 - Small demersals

This cluster encompassed LMEs from Indian Ocean and Southwest Pacific, which shared the common feature of catches time series dominated by small demersal harvests (Fig. 20d). Going deeper in taxonomic resolution, it could be observed that these LMEs actually showed a large amount of reported landings in the “mixed group” category. The low-resolved catch composition of these ecosystems is related to the low taxa resolution of tropical and subtropical fisheries, where mixed categories (e.g. “Marine fishes not identified”) often represent the bulk of reported landings.

Cluster 5: From medium pelagics to small and mixed demersals

Cluster 5 was the least represented class, which encompassed only two LMEs: the North Sea and the Agulhas Current (Fig. 20e). Although these ecosystems showed self-evident differences in their geographic location and main features (e.g. hydrology, bathymetry, productivity, etc.), they shared a common trend in landings composition, in which pelagics represented the dominant fraction in total landings in the first half of the time series (e.g. up until the mid 1970s), while demersals became predominant in more recent years.

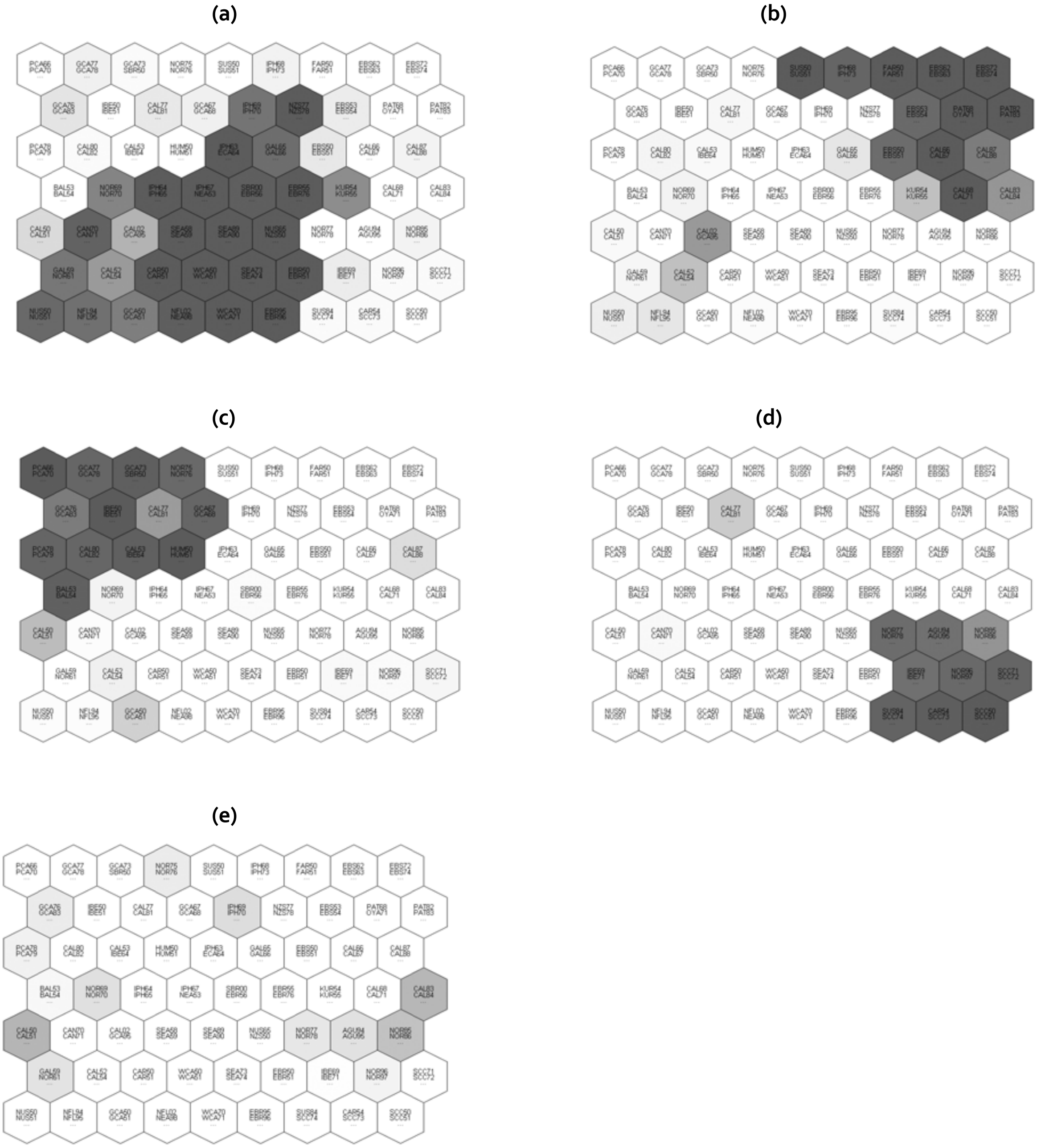


Fig. 20. Self Organizing Map. Proportions of observations belonging to the 5 clusters (a-e) are shown in grayscale.

Mantel's test

The time series of Mantel's statistics values resulting from the comparison of geographic distance matrix and annual distance matrices (Bray-Curtis distance) of fisheries catches by functional groups (ton km^{-2} yr^{-1}) is shown in Fig. 21. A negative trend was observed for this relationship when total abundances were taken into account ($r = -0.4442$, $p < 0.01$). On the contrary, Mantel's statistic between the geographic distance matrix and the annual distance matrices (Euclidean distance) of fisheries catches composition (i.e. percentage contribution of each functional group to total catches) showed no significant relationship. It could be observed that, when addressing catches data by means Bray-Curtis distance, the negative trend observed in the Mantel's statistics time series between catches' profiles and geographic distances between LMEs could be interpreted as a general homogenization of catches profiles across LMEs over time. This trend could be explained as a response to increasing in fishing pressures and market globalization. On the contrary, when functional groups' proportions were taken into account, no trend was detected, demonstrating that catches composition generally remained unchanged over time, showing thus a regional pattern only.

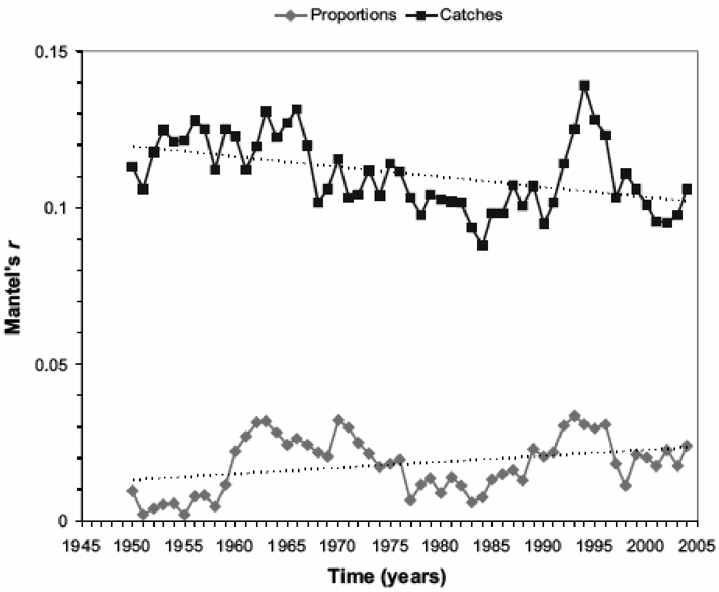


Fig. 21 Mantel's statistics trend between the geographic distance matrix (i.e., distance between LMEs centroids) and annual distance matrices of fisheries catches composition by functional groups.

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5. CONCLUSIONS

Analyzing the temporal variation of fifty-one multivariate time series has been a challenging objective. We aimed at describing the variation both in time and space of fisheries harvests composition in the selected ecosystems, in order to detect potential recurrent patterns. As previously stated, while synchronies in catches trends of e.g. small pelagics species have been described in a number of published papers, the results obtained in this study provide a significant insight into the last fifty-years fisheries strategies at a global scale. It has been demonstrated that the range of variation in LMEs fisheries catches composition by functional groups presented some discontinuities, which enable to distinguish five clusters, each representing a distinct "fishing behavior". In particular, from the historical analysis of these harvests temporal tracks, a broad distinction between two major approaches to fisheries emerged. On one side, fisheries which rely on small and medium pelagics production tend to exhibit stable compositions or cyclic behaviors in catches composition. This pattern has been related to intrinsic features of targeted species populations, which typically exhibit a "wasp-waist" control resulting in cyclic outburst of the exploited small pelagic stocks. Moreover, it has been observed that the LMEs characterized by this type of landings also share common productive features (i.e., upwelling regimes or enriched basins), which easily sustain species at low trophic levels. It follows that pelagic dominated landings are located in those regions which present specific features despite their geographical location.

On the other hand, a trawl fisheries cluster was identified, where harvests were dominated by demersal resources. From the geographical localization of the LMEs encompassed in this second category it seemed that this cluster was more affected by economic drivers (e.g. investments in fishing gears and new technologies) rather than environmental features. In fact, the eleven LMEs tended to concentrate in the Northern Hemisphere, where fishing pressures and investments have been historically higher. It could be further suggested that Northern Hemisphere LMEs are also generally characterized by wider continental shelves, which represent a critical feature for demersal exploitation. Every except the landings profiles encompassed in these two groups represented mixed and low-resolved harvests, which are also characterized by lower total yields with respect to demersal or, especially, pelagic dominated catches.

From a management perspective, the patterning of LMEs fishing histories proposed in this study actually open new scenarios for the decision-makers. The control strategies enacted for purse seine (pelagic) and trawl (demersal) fisheries must rely on different approaches, yet with the same objective. Pelagic fisheries management addresses a resource which is strictly dependent on natural dynamics, therefore long time series of both landings and environmental descriptors are needed in order to effectively control fishing pressures. As for trawl fisheries, which have already demonstrated to be a "dangerous", but still economically fundamental, field for fishery managers, as e.g. the Canadian cod moratorium demonstrated, a regional-multinational approach aiming at reducing the pressures on this multi-species resource could actually represent a better approach. Moreover, the fact that the largest cluster identified encompassed fishing histories based on mixed catches highlighted, once more, the mandatory need for a better resolution of landings data, in order to capture significant trends and to provide useful indications to the policy makers.

The analysis of regional fisheries harvests variation over fifty-five years actually represents the first step towards the challenging scope of disentangling the relative influence of environmental and economical forcing on exploited ecosystems. While few attempts proposed new insights into specific relationships, e.g. between total yields and primary productivity (Conti & Scardi 2010) or SST (Biswas et al. 2008) there is still a lack of comprehension of other dynamics. In this context, long-term multi-decadal studies capture more and more spatio-temporal structures and natural phenomena, thus providing the best way to disentangling anthropogenic and natural biological signals (Edwards et al. 2010).

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CHAPTER IV

Ecosystem functioning, fisheries yields and landings composition

1. INTRODUCTION

Capture fisheries and aquaculture supplied the world with about 110 million tonnes of food fish in 2006, providing an apparent per capita supply of 16.7 kg. Capture fisheries accounted for the 84% of the total amount (92 million tonnes), with an estimated first-sale value of US$ 91.2 billion, comprising about 82 million tonnes from marine waters and a record 10 million tonnes from inland waters (FAO 2008). Marine ecosystems constitute "social-ecological systems", including natural and human components which are highly interconnected and interactive. Traditionally, these two sub-systems have been studied independently by different disciplines (Barange et al. 2010), leading to a disastrous compartmentalization resulting in a generalized failure of marine resources management measures. Mangel (1997) depicted the rationale on which the conventional approach to fisheries management was based '*Since fishing pressure can be managed but the environment cannot, the default assumption in fisheries models has been to assume that the changes are due to fishing pressure. Thus, we use models without systematic environmental changes and leave the challenge of realistically considering environmental change for the next generation*'. The missing inclusion of this "environmental noise" in fisheries models has led to wrong estimations of the performance of exploited resources. The intrinsic weakness of this approach to fisheries research forced scientists and decision makers to respond with a turnaround towards an ecosystem-based management, aiming at bridging the gap between the human impacts (e.g. fishing pressure) and the intrinsic dynamics of commercially exploited ecosystem, including climate and trophic interactions. This is consistent with international agreements, as expressed through the Johannesburg and Reykjavik Declarations, and supported by the UN Food and Agricultural Organization through the Code of Conduct for Responsible Fisheries (FAO 2003). Ecosystem approach to fisheries (EAF) is not meant to replace stock assessments, rather to provide a context for the assessments and the criteria with which to choose Total Allowable Catches (TACs) (Christensen & Pauly 2004). Nevertheless, disentangling the relative effects of these factors still remain the major and most challenging goal of fisheries science, hindered by the fact that such effects are not simply additive, but rather do interact (Rouyeur et al. 2008). A wide range of models have been developed for the assessment of marine resources. Tropho-dynamics models that aggregate organisms into functional groups (e.g. Ecopath with Ecosim, EwE) have been used to simulate the effects of environmental change on biomass and productivity of ecosystem components (Christensen & Walters 2004, 2005, Christensen et al. 2005). The modeling possibilities introduced by the EwE approach, ranging from ecosystems snap-shots (e.g. mass-balance models) to time- and spatial-resolved studies (e.g. Ecosim and Ecospace), ensured the success and widespread use of these tools in recent fisheries research (e.g. Ainsworth et al. 2008, Bundy 2005, Coll et al. 2010, Freire et al. 2008, Guénette et al. 2008, Morissette et al. 2009, Zhang & Cheng 2007). Nevertheless, although a growing amount of time series for different ecosystem components and environmental factors is now available, modeling efforts often collide with the reliability of these data sets, particularly when addressing fisheries landings records. Known this, today's fisheries science aims at (1) identification and extrapolation of fundamental trends, and (2) development and exploration (with or without computer simulation) of possible futures (Pauly et al. 2003). The historical analysis of landings statistics provided new insights into local and global trends, pointing out that beside the general increase of world's catches over time, different regional "fishing histories" can be identified (Conti et al., in prep), while the forecast of potential fisheries yields, under a changing environment, still remains a challenging goal for both scientists and decision makers. While estimates of fish production depend on primary production magnitude, food chains length and transfer efficiency (Jennings et al. 2001), prediction of future yields has to cope with at least two levels of ambiguity (1) the adaptation of fishermen, fishing industry and communities dependent on fish supplies to yields variability and (2) the limited control exerted on the exploited systems by adjusting catching activity (Brander 2007). In this context, regional and local predictions may be more reliable than global forecasts. Moreover, using aggregated catches (e.g. as functional groups) instead of species lists may account for functional substitutions that always occur.

In this study fisheries yields and landings composition by functional groups are predicted for 51 Large Marine Ecosystems (LMEs) by means of an artificial neural network. Input variables selected for the two models describe both ecological and economic features of each LME, and no assumption on inter-variables relationships was made.

2. MATERIALS AND METHODS

Spatial and temporal scale

Large Marine Ecosystems time series of fisheries catches composition by functional groups were extracted from the Sea Around Us Project database (1998-2004). In this study, a selection of 51 LMEs was used, encompassing world's LMEs excluding those from polar Oceans (see Fig. 10, Table 1 in Chapter II). The definition of LME is given in Chapter II, page 21.

Artificial Neural Networks (ANNs)

What are Neural Networks?

Neural networks (NNs) or, according to a more precise definition, artificial neural networks (ANNs) have been defined in many different ways, although none of these definitions has been universally accepted. According to Haykin (1994) "*A neural network is a massively parallel distributed processor that has a natural propensity for storing experiential knowledge and making it available for use. It resembles the brain in two respects: (1) knowledge is acquired by the network through a learning process and (2) interneuron connection strengths known as synaptic weights are used to store the knowledge*".

In general, an ANN can be regarded as a network of simple units that operate on data either stored locally or received via the connections to other units. This kind of structure is somewhat related to the nervous systems of living organisms, and the development of ANNs has been influenced by the idea that artificial systems could mimic the activity of their biological counterpart. It is worth noting that nowadays, even though most ANNs are commonly regarded as mere computational tools, many terms in the NN jargon express this conceptual relationship.

For instance, an ANN learns from examples presented during a training procedure when the synaptic weights associated to the connections between neurons are optimized. Such a training procedure is usually based on rules that define the way the weights of the connections are adjusted when the examples, i.e., the data, are passed to the network.

Several practical applications of the ANNs involve some form of supervised learning. In other words, learning is based on training data that include values for both the predictive variables and for the variables to be predicted. When the training phase is successfully completed, input values can be passed to the ANN, which returns output values that approximate the desired outputs. These ANNs are very effective in solving nonlinear regression problems, but they are also very useful for classification and pattern recognition. The most common supervised ANN is the Multilayer Perceptron (MLP), whereas the error back-propagation is by far the most common training algorithm for those ANNs. Therefore, the majority of the real world ANN applications is based on the combination of the two, and we often refer to this combination as an error back-propagation ANN (or EBP ANN).

MLPs can be modified in several different ways when dynamic systems are to be modeled. Since the previous state of system is a very important source of information in deterministic modeling, it can be taken into account using recurrent ANNs (Pineda 1987). These ANNs use some form of feedback control based on output values or hidden layer synaptic weights from a previous state of the system to enhance their ability to model dynamic systems. Other ANNs are able to learn without supervision, i.e., they are able to adjust their weights according to the data sets used for training. The most common unsupervised ANN is the Self Organizing Map (SOM), which is usually applied to classification or ordination problems.

From a computational point of view, ANN applications are usually very intensive. As in the case of other empirical modeling tools, the quality of the results depends on the amount and quality of available data. However, ANNs require two independent data sets for learning and validation when they are used as generalized regression tools. Obviously, a third, independent data set is still needed for testing the results of the NN model and for comparing them to those provided by other models. As for the need for an independent test data set, it should be stressed that this is not a special requirement for ANNs, even though many modelers tend to overlook it when using conventional regression tools.

Neural network applications to ecological modeling or, more in general, to ecology are quite recent. In fact, the first references about the potential use of neural networks cannot be found in ecological literature before the early 90s (e.g. Colasanti 1991). However, only a few years later, while Edwards and Morse (1995) were pointing out that ANNs could have played an important role in computer-aided biodiversity research, the first ecological applications appeared. They were developed in very different fields and involved very different tasks, such as classifying benthic community data (Chon et al. 1996), predicting various parameters in brown trout management (Baran et al. 1996, Lek et al. 1996b), modeling spatial dynamics of fish (Giske et al. 1998), predicting phytoplankton production

(Scardi 1996, Recknagel et al. 1997), predicting fish diversity (Guégan et al. 1998), predicting production:biomass (P:B) ratio of animal populations (Brey et al. 1996), etc.

The majority of the earlier ANN ecological applications aimed at showing that ANNs performed better than conventional modeling methods. Therefore their focus was mainly on the comparison between ANNs and other methods. Recently, however, the use of ANNs in ecological applications has become more common, even though the majority of the ecologists is still not familiar with these tools. In particular, it is interesting to notice that ANN applications are much more abundant in terrestrial and freshwater ecology than in marine ecology.

From a general point of view, however, the context of ecological modeling is quite different from that of other NN applications, as data sets and knowledge are often very limited with respect to the complexity of the real processes. This implies that relationships between variables are only partly known and understood and that they are usually studied by analyzing correlations rather than by defining causal pathways in a deterministic framework. As Lek et al. (1996a) pointed out, ANNs are very effective in modeling such relationships by "learning" the underlying processes - which are often highly non-linear - independently of the modeler's knowledge. Of course, good results can only be obtained when enough data are available and a correct procedure has been used for "training" the model. A quick, but comprehensive introduction to the use of ANNs in ecological modeling applications can be found in Lek & Guégan (1999).

While most of the existing ANN applications deal with steady-state modeling, other types of ANN applications are emerging, as those based on Self Organising Maps (SOMs) and recurrent ANNs. SOMs have been recently used both to ordinate and to classify ecological data (Giraudel & Lek 2001), whereas recurrent ANNs, which proved to be very effective in modeling time series and dynamic systems (Recknagel 2001), have been successfully applied to model phytoplankton dynamics in freshwater ecosystems (e.g. Jeong et al. 2001, Walter et al. 2001).

Multilayer Perceptrons (MLPs)

Multilayer perceptrons (MLPs) are Artificial Neural Networks (ANNs) that consist of three or more (but usually no more than four) layers of units. In particular, all the MLPs have one input layer (i) and one output layer (o), whereas they can have one or more hidden layers (h). Very often, however, there is only one hidden layer, as shown in the example in fig. xx. Units in the hidden and output layer receive the outputs of the units in the previous layer (input and hidden, respectively), whereas units in the input layer obviously receive inputs from the user.

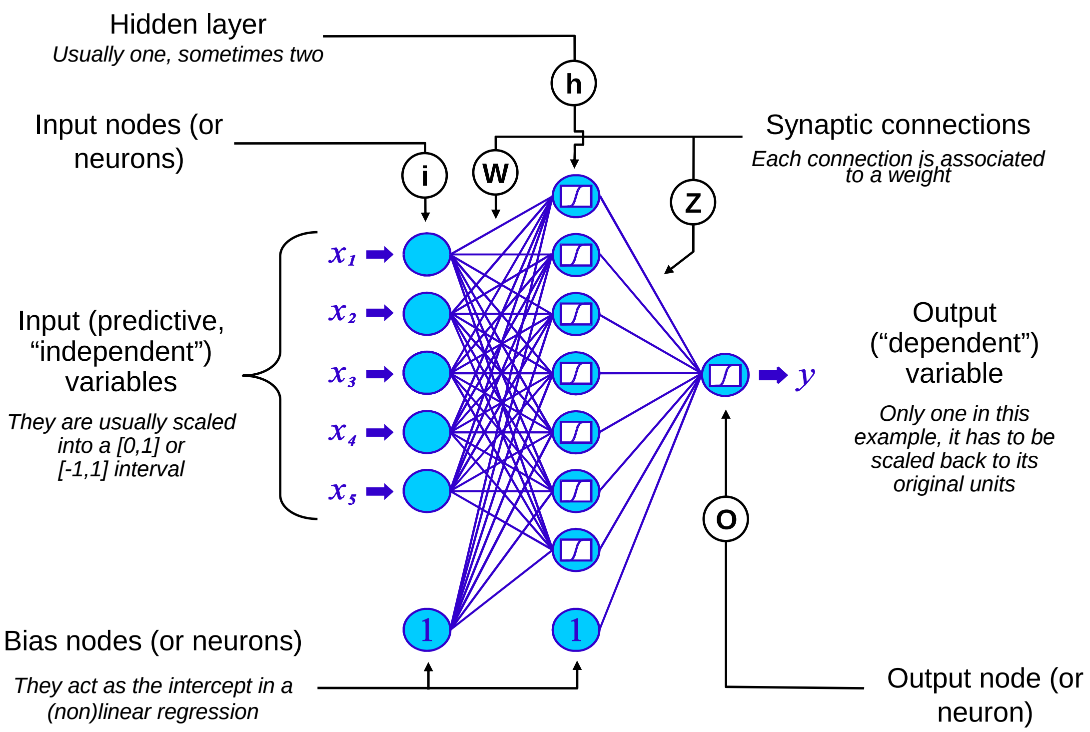


Fig. 22. Structure of a Multilayer Perceptron.

The connections between units are associated to coefficients (W and Z in Fig. 22), often called synaptic weights because of the obvious analogies with real neurons, that are iteratively adjusted during the training process, i.e. as long as their changes allow obtaining output values that are closer to the expected ones.

The MLP in Fig. 22 has three units in the input layer, five units in the hidden layer and a single output unit. Therefore, its structure can be summarized as 3-5-1. Additional units with a constant output (usually 1), called bias units, are also shown in the input and hidden layers. Their role in MLPs is very similar to that of the constant term in multiple regression, i.e. they allow to shift the origin of the space defined by the input variables.

Each unit in hidden and output layers passes the sum of its inputs to an activation function, i.e., a differentiable function that returns the output from that unit. Several functions can be used as activation functions, but the most common choice is the sigmoid function (see equation 2, this chapter).

Error Back Propagation (EBP)

While MLPs are certainly the most popular ANNs, the Error Back-Propagation (EBP) is by far the most common MLP training algorithm. Obviously, a MLP works at its best if all its synaptic weights have been properly tuned, and the EBP algorithm is a way to compute and optimize these weights. It involves four steps: (1) the network is initialized by assigning random values to its synaptic weights; (2) a training pattern is passed to the MLP input layer and propagated through the network to compute an output value for each output unit; (3) computed outputs are compared with the expected outputs; (4) a backward pass through the network is performed, changing the synaptic weights on the basis of the observed output errors. Steps 2 through 4 are iterated for each pattern in the training set, then the network performance is checked (usually on the basis of a mean squared error criterion) and a new set of training patterns is submitted to the network (i.e. a new epoch is started), if further optimization is needed.

Focusing on the most common case, i.e. on MLPs with a single hidden layer, the first step in the forward propagation calculations involves the computation of the weighted sums of input values that are passed to the hidden layer:

$$h_k = \sum_{j=1}^{n_i+1} i_j w_{jk} \qquad (k = 1, \ldots, n_h)$$

where *ij* are the MLP inputs (included the bias unit, that is always equal to 1) and w_{jk} are the weights of the connections between input and hidden layers. To compute the outputs from the hidden layer, these weighted sums are passed to the activation function, except the one for the bias unit that is forced to have an output equal to 1:

$$h_k = f(h_k)$$

$$h_{n_h+1} = 1$$

Then, the network outputs are computed in the same way:

$$o_l = \sum_{k=1}^{n_h+1} h_k z_{kl} \qquad (l = 1, \ldots, n_o)$$

$$o_l = f(o_l)$$

After the forward propagation, the estimated outputs o_l are compared with the expected outputs y_l and a mean square error *E* for the current pattern is computed as:

$$E = \frac{1}{n_o}\sum_{l=1}^{n_o}(y_l - o_l)^2$$

Then, in the back-propagation step, all the synaptic weights are adjusted to follow a gradient descent on the error surface. Therefore, for the connections between hidden and output layers, the weights *zkl* are changed into:

$$z_{kl} = z_{kl} + \eta\delta_l^o h_k \qquad (k = 1,\ldots,n_h + 1;\ l = 1,\ldots,n_o)$$

where η is a constant (learning rate) and:

$$\delta_l^o = (y_l - o_l)\cdot f'(o_l) = (y_l - o_l)\cdot o_l(1 - o_l)$$

The weights w_{jk} of the connections between hidden and input layer are also adjusted:

$$w_{jk} = w_{jk} + \eta\delta_k^h i_j \qquad (k = 1,\ldots,n_h + 1;\ j = 1,\ldots,n_i + 1)$$

where are computed as:

$$\delta_k^h = f'(h_k)\cdot\sum_{l=1}^{n_o}\delta_l^o z_{kl} = h_k(1 - h_k)\cdot\sum_{l=1}^{n_o}\delta_l^o z_{kl}$$

At the beginning of the training procedure the MLP weights are randomly initialized and the available data are divided into three sets for training, validation, and testing, respectively. The training data are then passed to the MLP to compute the output values. The deviations of those output values from the expected ones (i.e. from the observed data) in the training set are used in order to tune the error back-propagation (i.e. the learning procedure), whereas the deviations from the validation set are used as a criterion for stopping the learning procedure. In other words, as long as a MLP keeps improving with respect to the validation set, the learning phase can be continued and the training data can be submitted to the MLP again. The training is iterated until a given condition is met: minimization of the mean square error is usually involved, but other criteria can also be used.

It has to be stressed, however, that the weights adjustment process does not always return the same result, because many non-deterministic factors (e.g. different starting values of the synaptic weights) affect the network training. This means that the trajectory of the gradient descent on the error surface is often attracted by local minima. Therefore, repeating the learning procedure as many times as possible is usually a good practice.

Provided that enough data are available for training, that the activation functions of the hidden layer units are non-linear and that the number of the units in the hidden layer(s) is large enough, a MLP is able to approximate any non-linear function (Hornik et al. 1989).

Models structure

In this study, two MLPs were developed to model fisheries harvests abundances and composition, with a 8-7-1 and 8-7-5 architecture, respectively. Further adjustments of these structures, and the consequent outputs modifications, are presented in the Results section.

Input variables

Annual primary productivity (PP)

Annual primary productivity (PP) in each LME was estimated on SeaWiFS images by means of the Vertically Generalized Production Neural Network (Scardi 2000, 2001, Carr et al. 2006).

Average trophic level of catches (TLc)

Time series of average trophic level of catches were extracted from the Sea Around Us Project database. TLc can be used as a descriptor of the fisheries positioning along the food web (Chassot et al. 2010).

Average maximum length of catches (Lmax)

Time series of average maximum length of catches were extracted from the Sea Around Us Project database. Is has been demonstrated that Lmax could be used as a surrogate for the intrinsic growth rate of increase of the fish community (Denney et al. 2002).

Species richness (SR)

The number of fishes (Osteichthyes and Chondrichthyes) at the species level for each LME was computed from the Sea Around Us Project LMEs fished species lists.

Bathymetry (% platform)

LMEs bathymetry was derived from the ETOPO1 Global Relief Model, a 1 arc-minute global relief model of Earth's surface that integrates land topography and ocean bathymetry, available on-line at http://www.ngdc.noaa.gov/mgg/global/global.html. LMEs bedrock topography was extracted by means of ArcGIS software and a platform (depth<200m)/non-platform (depth>200m) ratio was computed. The percentage of platform was used as a proxy of potential exploitable surface, which in turn may influence the demersal/pelagic dominance of harvests.

Sea surface temperature (SST)

Monthly mean sea surface temperature (°C) time series were downloaded from NOAA Earth System Research Laboratory on-line database, as a 2°x2° global grid. A regional interpolation function was elaborated to extract annual LME-specific time series.

Weighted gross domestic product (GDP)

Time series of gross domestic product for world's countries, [i.e. GDP per capita, PPP (constant 2007 international $)], were extracted from the statistical tables of 2009 Human Development Report (UNEP 2009). Missing years were estimated by linear interpolation. For each LME, average annual GDP was estimated on the GDP of fishing countries weighted on annual reported catches (ton yr^{-1}). Catches per fishing country for each LME were extracted from the Sea Around Us Project database.

Oil Price (Oil)

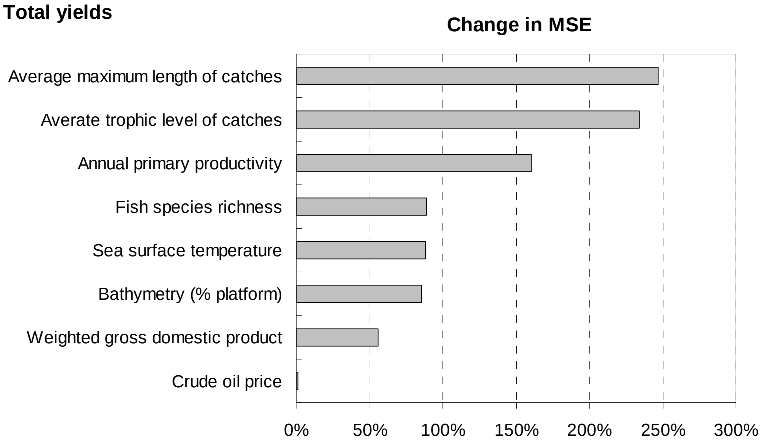
World crude oil price ($ per barrel) time series were downloaded from the Energy Information Administration database, available on-line at http://tonto.eia.doe.gov/dnav/pet/pet_pri_wco_k_w.htm. Fuel constitutes a substantial component of the cost of fishing, which reaches up to 60% in cases such as the commercial fisheries of Hong Kong. Given that many world fisheries are overfished, and that fuel makes up a substantial component of fishing costs, an obvious questions is whether the recent, sharp increase in fuel prices have influenced fishing pressures, reducing the profitability of this activity (Sumaila et al. 2008).

3. RESULTS

The models presented in this section were obtained as the result of a refining step-by-step procedure, aimed at improving modeling performance through different neural networks architectures. At the beginning, two models based on 8 input variables were trained to predict both total yields and catches composition. Although both models performed fairly well (R^2=0.8026 and R^2=0.6735, respectively), a sensitivity analysis was carried out to assess the effect of small changes in input variables. The results of this analysis provided useful insights into the neural network model, and helped to elucidate the underlying processes, i.e. the relative importance of the predictive variables to total yields and catches composition forecasts. In the sensitivity analysis, the mean square error

(MSE) of the neural network output is expected to increase as a larger amount of white noise is added to the selected input variable. The MSE variations that were observed after a 50% of white noise addition are shown in Fig. 23. It could be observed that crude oil price was non influential in both models, suggesting a scarce predictive power of this variable, and the possibility of improving model performance by removing this predictor. The resulting simplified architectures were tested and models outputs are presented below. Regarding catches composition prediction, a further refinement of the ANN's was proposed, in order to cope with the scarce performance of the 7-7-5 architecture for the mixed category (e.g. "Other", R^2=0.2608). Both ANNs were tested on an independent subset of 13 LMEs (n=91 observations) previously excluded from the 1998-2004 dataset.

(a) Total yields



(b) Landings composition

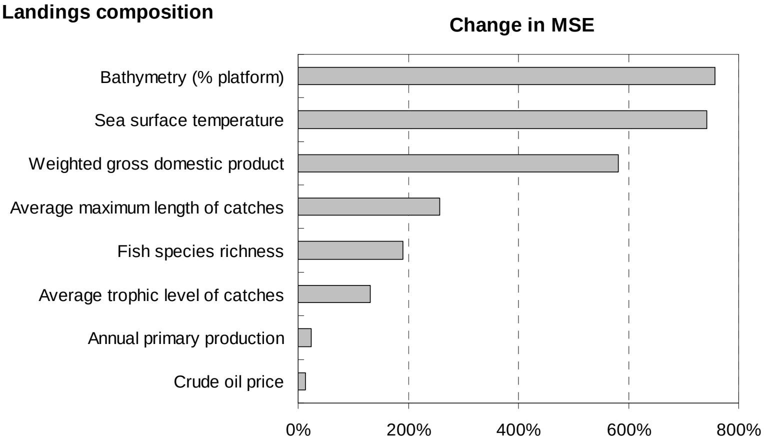


Fig. 23. Percentage variation of the mean square error of the neural network output after the addition of 50% white noise. (a) Sensitivity analysis of the 8-7-1 network predicting total yields and (b) Sensitivity analysis for the 8-7-5 network predicting catches composition by functional groups. The input variables are ranked according to their sensitivity.

Modeling total yields

The 7-7-1 neural network performed well on the test set (R^2=0.8815), and its accuracy improved with respect to the 8-7-1 architecture encompassing crude oil price as a predictive variable (R^2=0.8026) (Fig. 24).

From the sensitivity analysis carried out on the dataset it was observed that sea surface temperature was by far the most influential variable amongst the neural network inputs. Weighted gross domestic product and bedrock topography, i.e. described by the %platform, played a lower but still significant role (Fig. 25). Unexpectedly, average annual primary productivity was virtually non influential in total fisheries yields. With respect to the 8-7-1 model, the relationships between input and output variables are stricter in this second version of the model, where changes in MSE relative to a same amount of input noise are up to double and a half higher than those reported in the 8-7-1 network.

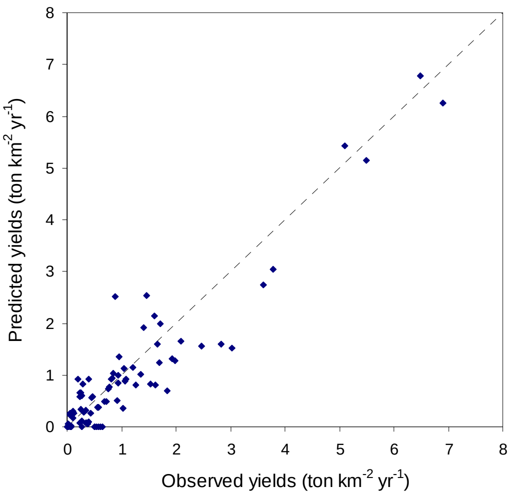


Fig. 24. Scatter plot of the neural network outputs versus observed values for the 7-7-1 model. The overall agreement between observed and predicted values is good (R^2 = 0.8815)

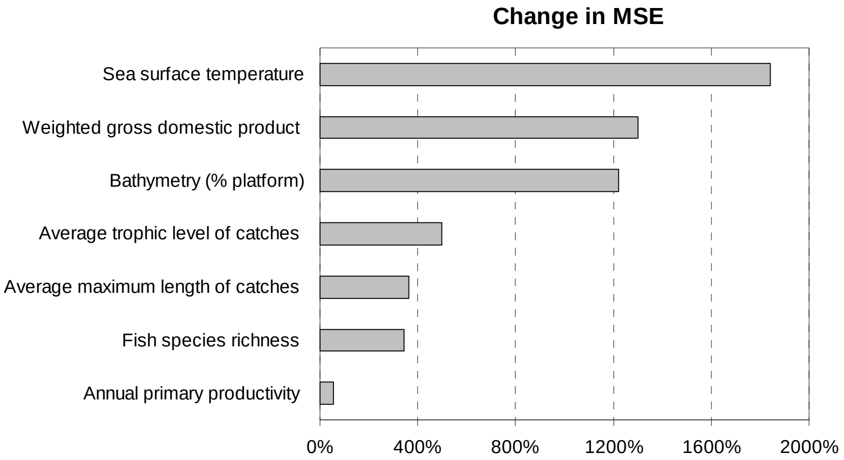


Fig. 25. Percentage variation of the mean square error of the 7-7-1 neural network output after the addition of 50% white noise. The input variables are ranked according to their sensitivity.

Modeling landings composition

The 7-7-4 model overall performance was good (R^2=0.8336) and significantly improved with the removal of the mixed category from the output [e.g. a previous version with a 7-7-5 architecture was tested (R^2=0.6735)]. A plot of observed and predicted values for the 4 functional groups describing catch composition (e.g. pelagics, demersals, benthopelagics and invertebrates) is shown in Fig. 26. It could be observed that fish groups (e.g. pelagics, demersal and benthopelagics) predictions were substantially more accurate than invertebrates forecast, whose prediction worsened with respect to the 7-7-5 model (e.g. from R^2=0.7467 to R^2=0.6696).

The sensitivity analysis performed on the 7-7-4 network showed that the average maximum length of catches was the most influential input for the catches composition forecast, followed by the average trophic level of catches (Fig. 27).

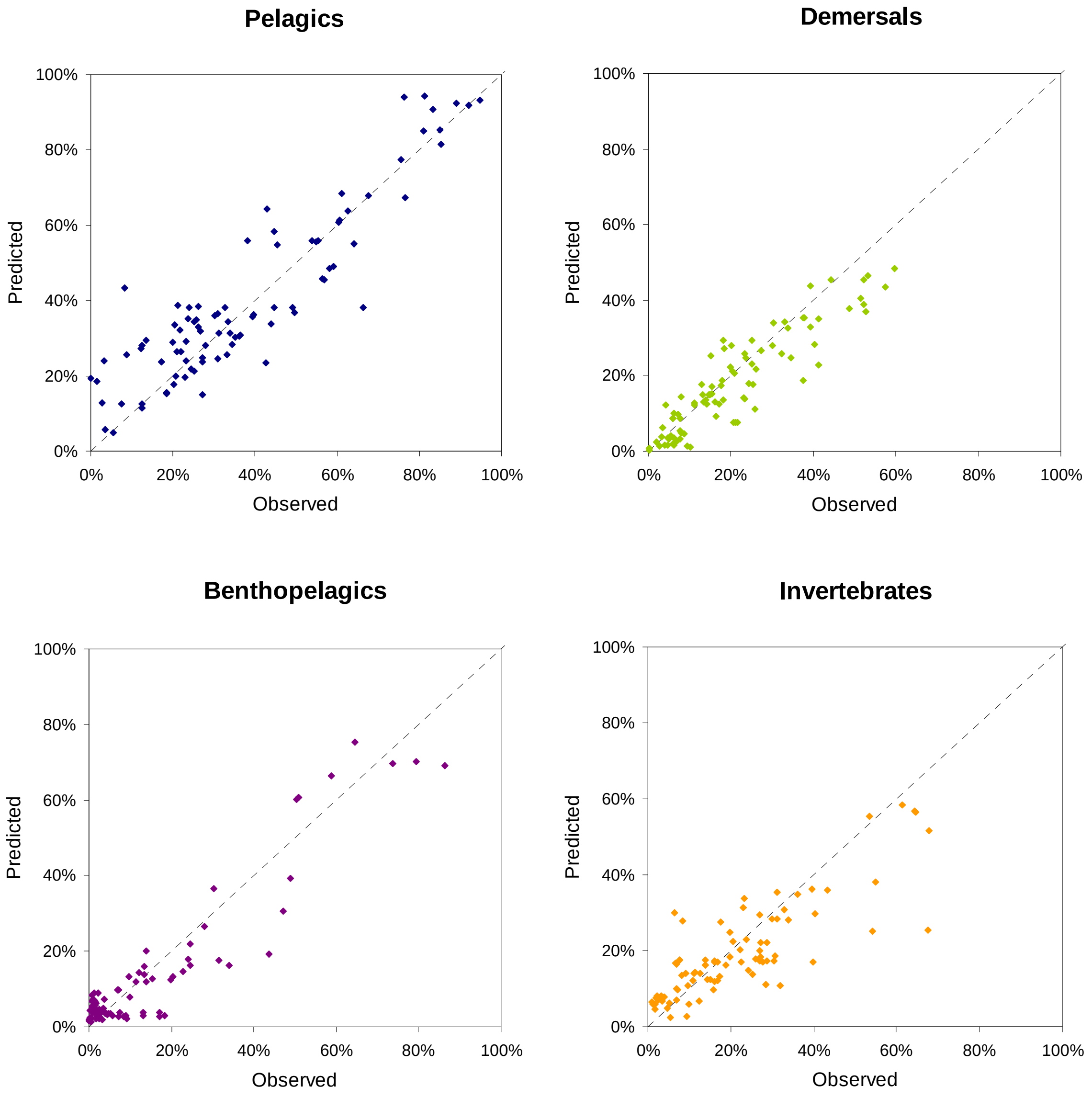


Fig. 26. Scatter plots of the neural network outputs versus observed values for the 7-7-4 model. The overall agreement between observed and predicted values is good (R^2 = 0.8336). Single outputs, i.e. functional groups are predicted with different accuracies: (1) pelagics, R^2=0.8242, (2) demersals, R^2=0.8262, (3) benthopelagics, R^2=0.8742, (4) invertebrates, R^2=0.6696.

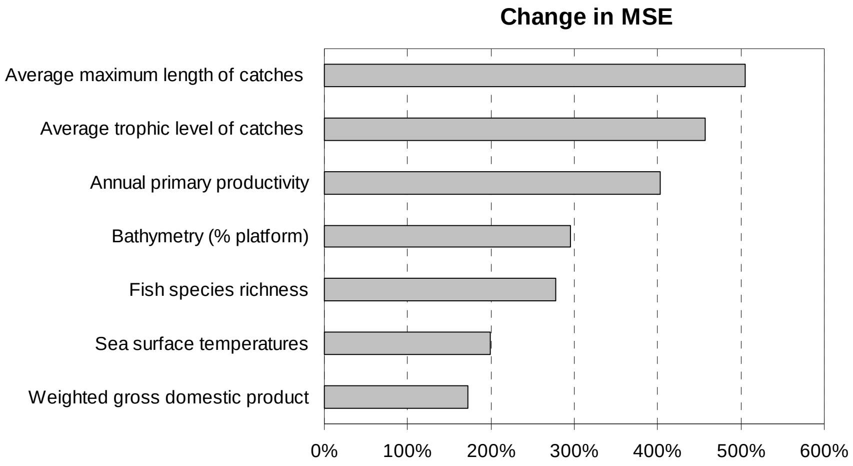


Fig. 27. Percentage variation of the mean square error of the 7-7-4 neural network output after the addition of 50% white noise. The input variables are ranked according to their sensitivity.

4. DISCUSSION

The neural network models provided accurate estimates of total fisheries yields and catches composition overcoming the restrictive assumptions imposed by linear models. The results obtained with these two models proved that this approach is particularly effective in dealing with nonlinear relationships between variables, as it has been demonstrated in a number of applications (e.g., Scardi 1996, Guégan et al 1998). Splitting quantitative and qualitative predictions, i.e. between total yields and catches composition by broad functional groups classes, allowed to provide new insights into the underlying processes governing fisheries harvests. In particular, from the sensitivity analysis carried out on the two models it emerged that total yields seemed to be mostly influenced by SST, weighted gross domestic product and bathymetry. This result is apparently in contrast with what has a long time been stated, i.e. that primary productivity is the principal driver of total fisheries yields. Nevertheless, the neural network output for total yields did not deny the yield-PP relationship at the LME scale (which has been described in published papers as e.g., Chassot et al. 2010, Conti & Scardi 2010), rather it demonstrated that PP does not play as the major driver in total yields control. The overwhelming influence of *sensu lato* economic input variables showed that, although the quantity of future fish production depends on changes in primary productivity and on the proportion which is transferred through the marine ecosystem to human consumption, economic pressures probably act on exploited ecosystems at a higher magnitude with respect to environmental variability. Link et al. (2010) outlined that the dominant drivers in a range of ecosystems (i.e., encompassing upwelling, high-latitude, temperate, and tropical marine ecosystems, covering a range of low- to highly productive areas) are human-related, usually to fishing, but also more generally to human development. In this context, it must be stressed that the short time series used to train the model actually describe a "steady-state" scenario in which SST could be interpreted as a proxy for LMEs latitude, rather than a climatic forcing factor affecting fisheries landings. Moreover, the bedrock topography, described by the percentage of platform depths, actually provides a measure of the "harvestable surface" for trawling fisheries and it is latitude-correlated i.e. the most extended platforms are concentrated in the northern hemisphere. As for the gross domestic product of fishing countries, it is probably the predictor that is most directly correlated to fishing pressures, if we assume that developed economies are potentially more capable of higher investments in economic activities, e.g. fishing. Therefore, the results obtained from the yield prediction model confirm the most recent findings in terms of driving forces acting on fisheries harvests, demonstrating that economic descriptors must be taken into account in the forecast of future fisheries yields.

On the other hand, a different scenario emerged from the sensitivity analysis performed on the neural network modeling catches composition. The estimates provided by this second network were indeed strongly influenced by average maximum length of harvested species which, in turn, could be used as a surrogate for the intrinsic growth rate of increase of the fish community (Denney et al. 2002). This predictor, together with the average trophic level of catches (TLc), i.e. the position of the fisheries along the food web (Froese & Pauly 2009) and primary productivity describe the intrinsic functioning of the exploited fob web. In other words, at the LMEs scale, the relative contribution of different functional groups (e.g. pelagics, demersal, benthopelagics and invertebrates) to total catches depends on the underlying ecosystem structure rather that on selective harvest pressures.

5. CONCLUSIONS

Disentangling and understanding the effects of economic and environmental pressures in LMEs fisheries is a major aim in the international science agenda, for which the 5-module approach to LMEs management proposed by NOAA clearly states the guidelines. Productivity, fish and fisheries, pollution and ecosystem health, socioeconomics, and governance represent the broad fields for which advances in technology now allows cost-effective measuring of the changing states of LMEs. In this context, the results obtained in this study highlighted the need to examine simultaneously a broad suite of ecosystem drivers, as it has already stated in a number of modeling and empirical studies (Link et al. 2002, Fulton et al. 2004, 2005, Frank et al. 2007, Coll et al. 2008a, 2009, Shannon et al. 2008, Mackinson et al. 2009), and particularly to take into account both environmental and human drivers.

Models and computer simulations are fundamental tools to cope with complexity of exploited ecosystems and the accuracy of their predictions is constrained by the uncertainties embedded in the predictors' time series and by the potential non-linear responses at a different organizational levels. Thus, there are trade-offs between model complexity and uncertainty that need to be fully considered in evaluating the predictability of such models (Barange et al. 2010). In this context, artificial neural networks have proved to be a reliable tool, whose applications in fisheries forecasts need to be further investigated. The 7-years time series used to train the neural networks allowed to detect the environmental and economic predictors involved in yields abundances and composition forecasts, while temporal dynamics and low-frequency events, such as regime shifts and multi-decadal changes, were overlooked. Nevertheless, some potential option for future modeling development emerged from this approach: (1) longer time series of input variables may allow disentangling the relative factors affecting fisheries yields abundance and composition in a dynamic perspective, leading to possibly different conclusions with respect to those acting in a "steady state" ecosystem; (2) as SST seemed to drive total fisheries yields, IPCC scenarios may be used to forecast future yields under different conditions.

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CHAPTER V

General discussion, future perspectives and conclusions

This study aimed at exploring the dynamics of LMEs fisheries. A three-step approach was carried out along a trend of increasing complexity, addressing larger/longer spatial/temporal scales. The fisheries landings time series used for this study, which are widely considered a scarce quality data source, actually enabled to detect common trends amongst LMEs fisheries, thus demonstrating that significant features concerning the exploited ecosystems still persist in this low-resolution statistics.

New insights into the structure and functioning of large marine ecosystems all over the world were provided, and significant advances have been made in the description of known and less known relationships. Up until recent years, published studies dealing with the relationships between primary productivity and fisheries yields were based on a limited set of records, which derived from local and regional surveys and direct measurements (e.g. Nixon 1982, 1992, Nixon et al. 1986, Iverson 1990, Nielsen & Richardson 1996, Sommer et al. 2002, Steingrund & Gaard 2005). Today, available open-access time series of fisheries landings, such as those provided by the Sea Around Us Project, represent a new generation of databases, based on the most recent information and refined through a clearly stated methodological approach and large scale interpolations. Beside this, advances in satellite observations and improved modeling of ecological processes provide a range of enhanced global and regional primary productivity estimates. The variability of the outputs provided by available PP models has been evaluated through comparative exercises, which supplied a comprehensive framework facilitating PP model selection (Carr et al. 2006, Friedrichs et al. 2009). In this framework, new insights into relationships between PP and fisheries yields took advantage from improved data quality and larger spatial scales, leading to important progress in the knowledge and comprehension of processes governing this relationship. In particular, a correlation between PP temporal variability and fisheries catches composition was demonstrated, while the PP model choice turned out to be a critical step when management issues are addressed (Chapter II).

While comparative studies surely represent the bulk of ecological research, another promising field of investigation is represented by the long time series now available for different ecosystem components. Fisheries landings records, which date back to 1950s, allow investigating ecosystems changes through their influences on harvested resources. Regional and comparative analysis of fisheries catches time series help understanding the ways in which fisheries activities evolved in different LMEs and how global (and local) change may have influenced the harvest of marine resources. A better knowledge of past and present conditions is crucial in a changing world, where predictions for future scenarios need to be improved in order to provide more and more accurate and reliable forecasts. If short-term previsions are nowadays achievable through a suite of available models, medium and long-term modelling still represents a challenging objective.

In this study, we demonstrated that multi-decadal ecological and fisheries landings time series allowed to: (1) gain new insights into well known relationships (Chapter II), (2) detect recurrent patterns in large scale dynamics (Chapter III) and (3) model exploited ecosystems and predict future trends (Chapter IV). Comparative analysis of fisheries landings time series revealed the presence of recurrent patterns in LMEs fisheries evolutions, which seemed to be related to both geographical or oceanographic (e.g. productive regimes) similar features. It must be stressed that reliability of fisheries landings data for ecological research depends on the aim of the study. While they may be considered as useful proxies for ecosystem structure for basic research, anthropogenic drivers need to be taken into account when addressing management issues. The overwhelming magnitude of economic forcing with respect to environmental variability in the prediction of total fisheries yields highlighted the importance of taking into account a wide spectrum of sources of variation when exploited ecosystems are analyzed. Economic and ecological pressures proved to be comparable at the LME scale, as the first drives total yields and the latter influences catches composition, so that no accurate estimates could derive from accounting only one kind of drivers.

Estimating fisheries yields and composition from easily available descriptors, such as those described in this study, may open new and challenging scenarios for basic and applied research. The availability of ready-to-use time series of predictive variables provides a unique opportunity of testing different suites of predictors, in order to obtain more and more accurate forecasts. Time series of expected change in sea surface temperatures represent the most widespread descriptor for the analysis of marine ecosystems. A first step towards this scenario-based research may be the prediction of total fisheries yields based on the IPCC scenarios.

Fisheries science, from its early development, has always been dwelling with complexity. From the reductionist approach of stock assessment and single population dynamics to the more recent holistic ecosystem approach, modeling advances have triggered fisheries research along a trend of increasing complexity. Improved techniques allow nowadays assessing and predicting the dynamics of exploited ecosystems, where the influences of the synergies between natural variability and human pressures are difficult to disentangle. These effects, which are not simply additive, are proved to be better addressed by means of modern modeling tools, which are able to cope with large data sets and non-linear relationships. In this study, data mining and machine learning has proved to represent the new frontier for fisheries research, in the context of a changing world, where knowledge-based predictions provide the only way to preserve marine – exhaustible – resources.

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APPENDIX A

Publications

Vol. 410: 233–244, 2010
doi: 10.3354/meps08630

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 14

Fisheries yield and primary productivity in large marine ecosystems

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ABSTRACT: Primary productivity (PP) and fisheries yield were analysed in 14 large marine ecosystems (LMEs), which encompassed temperate boreal shelves and the Eastern Boundary Currents (EBCs), from 1998 to 2002. PP was estimated by means of a depth-integrated neural network model based on Sea-viewing Wide Field-of-view Sensor (SeaWiFS) data and aimed at providing conservative PP estimates. Landings records were extracted from the global spatial database provided by the Sea Around Us Project (SAUP). Correspondence analysis performed on yield data outlined the role played by different trophic levels (TLs) in LME catches. PP temporal variability was significantly and positively correlated to average trophic level of catches (TL_c) so that higher yields in less variable ecosystems were characterised by a lower TL_c. From a functional perspective, high PP temporal variability was associated preferentially with demersal fishes and lower yields, while pelagic-dominated catches were harvested in conditions with lower PP variability. Primary production required (PPR) to sustain fisheries in each LME showed that the highest yield occurred in combination with moderate fishing pressure especially when TL_c was intermediate to low. High fishing pressures were associated with intermediate total yields and high TL_c, a condition which seemed to occur in high-latitude boreal LMEs. The %PPR and TL_c were used to assess fisheries impact on ecosystems. PP model choice affects the assessment of exploitation levels, in that a more conservative estimation of PP could contribute to a more precautionary approach to fisheries management where high levels of exploitation are more easily attained.

KEY WORDS: Primary productivity · Fisheries yield · Large marine ecosystems · PPR · Overexploitation

INTRODUCTION

The relationship between primary productivity (PP) and fisheries yield has been widely demonstrated (e.g. Nixon 1982, 1992, Nixon et al. 1986, Iverson 1990, Nielsen & Richardson 1996, Sommer et al. 2002, Steingrund & Gaard 2005). Nixon (1982, 1992) and Nixon et al. (1986) showed an empirical relationship between annual yields of fish and autotrophic productivity in a selection of sites, both marine and estuarine, on the basis of the 'agricultural model' (i.e. linking marine PP to nutrient input) and of the trophodynamic approach (Lindeman 1942). Longer time series and enhanced measurement technologies, together with an improved knowledge of marine food web dynamics, demonstrated that this relationship is not a simple one and often not even linear. Iverson (1990) related nekton production (fish and squids) from offshore areas to the amount of nitrogen incorporated into phytoplankton biomass, the 'new production' being the only type of PP that directly affects fish yields (Nielsen & Richardson 1996). Variations in food web structure have also been linked to different nutrient richness scenarios in oligotrophic, upwelling and temperate seas (Sommer et al. 2002). Two main models have been proposed to describe marine ecosystems dynamics: (1) bottom-up control, where food web components are regulated by either primary producers or the input of limited nutrients (White 1978), and (2) top-down control, where lower food web components are regulated by one or several upper-level predators (Hairston et al. 1960, Fretwell 1977, 1987, Oksanen et al. 1981, Power 1992,

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Pace et al. 1999, Cury et al. 2001). Several studies pointed out that both systems act locally (e.g. Ware & Thomson 2005, Mueter et al. 2006, Mackinson et al. 2008).

The shift from local to regional and global spatial scales, added to the potential effects of climate change and regime shifts, highlights the complexity that underlies marine food webs. Cyclic and punctual events, both environmental and anthropogenic, influence the structure and functioning of marine ecosystems, hindering the identification of the relative role of each driving force. Landings statistics are the main source of data for these kinds of studies, representing the only spatial and temporal large-scale data sets available for the detection of different sources of variation. Recently, Perry & Schweigert (2008) suggested that these highly aggregated data and large (often global) spatial domains may have played a key role in the identification of the general relationship between PP and fisheries yields. The primary criticism about large-scale fisheries studies is their reliance on poor quality of data: landings might not correspond to real abundance due to changing market demand or selectivity of fishing gears, together with uncertainties about catch reporting systems. Nevertheless, it is generally considered that there is a certain degree of association between relative abundance in the landings and in the ecosystem from which these landings are extracted (Halley & Stergiou 2005). Furthermore, landings represent the best and only available source for regional and global studies.

Substantial advances have been made in PP estimation procedures, reducing at least one of the sources of variation in studies aimed at relating PP and fisheries yield. For a long time, ship-based estimates and chronic undersampling made it difficult to resolve low-frequency spatial and temporal variability, and forced an estimation of global PP based on the extrapolation of sparse (in time and space) measurements (Carr et al. 2006). Satellite observation of ocean colour, since the beginning of the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) mission in September 1997, determined the shift from a local snapshot view to synoptic and large-scale images, thereby allowing considerable advances in estimation accuracy on a global perspective. The range of modelling approaches for estimating primary productivity from satellite chlorophyll *a* (chl *a*) measurements and modelling performances are summarised in Carr et al. (2006). According to Field et al. (1998), global PP is evenly supported by terrestrial and marine photosynthesis, the latter being conveyed for the most part (up to 90 %) towards production at higher trophic levels (TLs), sustaining three-quarters of global fisheries yields (Myers & Worm 2003). The total amount of carbon fixed by autotrophs, mainly phytoplankton, sets the ultimate threshold to the production at higher TLs (Friedrichs et al. 2009) and the possibility of reaching this maximum sustainable production is determined by the structure and functioning of the underlying food web by means of transfer efficiencies (TEs). Typically, 13 % of phytoplankton PP is transferred to herbivore mesozooplankton and benthos, while the 'zooplankton/zoobenthos → fish' step is characterised by a TE of 10 % (Ware 2000). From a more general perspective, ecological efficiency in marine ecosystems ranges from 5 to 20 % (Lindeman 1942) depending on the food web structure (i.e. number of trophic levels involved) and decreases with higher trophic levels due to increased respiration (Christensen & Pauly 1993, Trites 2001).

The relative importance of carbon pathways in different marine ecosystems reflects both the intrinsic properties of primary producers and physical forcing. In oceanic ecosystems, the bulk of phytoplankton production is conveyed through the herbivory chain that sustains production at higher TLs, which in turn is subjected to industrial harvest (Duarte & Cebrián 1996). Different marine PP estimation algorithms (depth-integrated models and general circulation models [GCMs], coupled with ecosystem or biogeochemical models) converge on a global marine PP annual value of 45 to 50 Gt C yr^{-1} (Carr et al. 2006).

The purpose of the present study was to investigate the relationship between primary productivity and fish yield through satellite observations and reported fisheries landings from 14 selected large marine ecosystems (LMEs). We adopted a double approach for relating PP and fish production: (1) bottom-up, where available PP fixes the threshold for production at higher TLs, and (2) top-down, where the primary production required (PPR) to support production at the exploited level was assessed from landing biomass under the assumption that reported landings effectively reflect total fish production (Pauly & Christensen 1995).

From an ecosystem-based management perspective, PPR provides an estimation of the ecosystem's carrying capacity based on its actual exploitation, and therefore represents a potential guideline for the future. In particular, the relationship between PPR normalised to the PP (%PPR) and the averaged TL of catches (TL_c) have been proposed as indicators of ecosystems exploitation level (Tudela 2003, Tudela et al. 2005), as TL_c actually reflects the strategy of a fishery in terms of the food web components selected (Pauly et al. 1998, Christensen & Walters 2004).

The purpose of this approach is to provide new insights into ecosystem functioning and to give a contribution to key issues in management strategies. It is within the boundaries of the 66 LMEs that major efforts are presently under way to meet the World Summit on

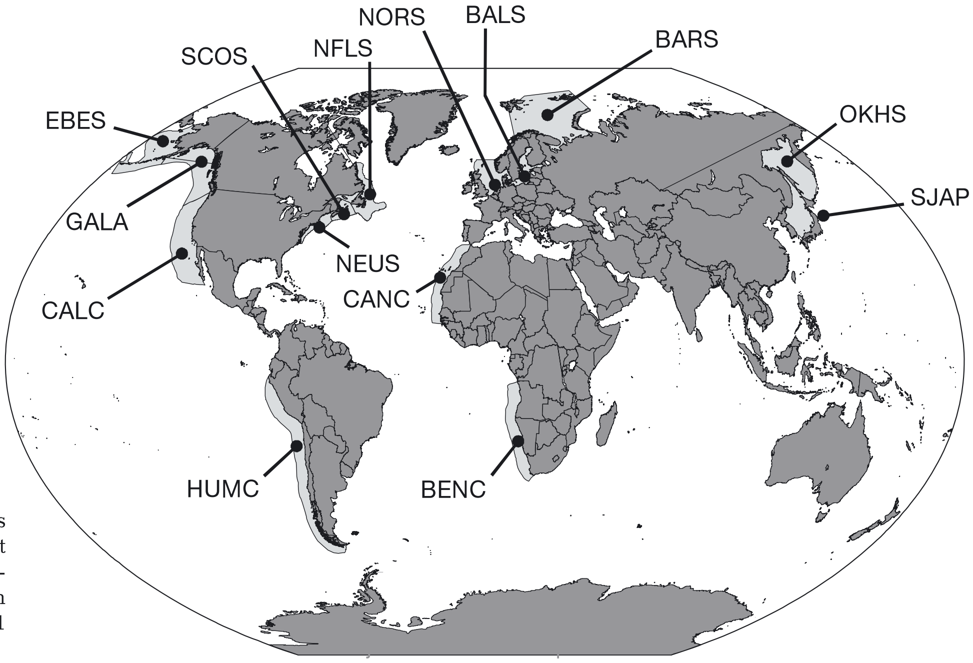

Fig. 1. Large marine ecosystems (LMEs) analyzed in the present study. Abbreviations and geographical information for each region are provided in Table 1

Sustainable Development (WSSD) deadlines, namely: (1) introducing an ecosystem approach to marine resource assessment and management by 2010, and (2) maintaining fish stock maximum sustainable yield levels by 2015. While these standards are still far from being reached, there is a general agreement on the reference space-based ecosystem unit of LMEs, for which a 5-modules strategy of assessment (productivity, fish and fisheries, pollution and ecosystem health, socioeconomics and governance) has been developed (Sherman et al. 2005). In this context, the present paper proposes a focus on the first 2 modules, productivity and fisheries, even though any attempt to better understand ecosystem functioning has important outcomes on all LME strategy components.

Table 1. Acronyms and geographical information for each LME mapped in Fig. 1. Surface areas are expressed in 10^6 km^2 and centroid coordinates as decimal degrees

Complete name	Abbrev.	Surface area	Longitude	Latitude
Atlantic Ocean				
Barents Sea	BALS	1.874	37.87 E	75.81 N
Baltic Sea	BARS	0.394	19.76 E	58.97 N
North Sea	NORS	0.696	2.71 E	57.40 N
Newfoundland-Labrador Shelf	NFLS	0.681	53.01 W	49.45 N
Northeastern US Continental Shelf	NEUS	0.310	70.42 W	41.01 N
Scotian Shelf	SCOS	0.415	61.71 W	46.98 N
Pacific Ocean				
East Bering Sea	EBES	1.187	168.71 W	57.40 N
Gulf of Alaska	GALA	1.475	139.75 W	54.06 N
Okhotsk Sea	OKHS	1.558	148.94 E	53.77 N
Sea of Japan	SJAP	0.987	135.67 E	41.26 N
Eastern Boundary Currents				
Benguela Current	BENC	1.463	12.50 E	21.25 S
California Current	CALC	2.216	122.51 W	33.25 N
Canary Current	CANC	1.125	15.30 W	24.65 N
Humboldt Current	HUMC	2.559	75.30 W	31.96 S

MATERIALS AND METHODS

Area. Catch and PP data were obtained for 14 out of the 66 LMEs defined by Sherman et al. (2005). Selected LMEs belong to boreal temperate shelves and major upwelling systems (i.e. the Eastern Boundary Currents [EBCs]) (Fig. 1, Table 1). LMEs are 'regions of ocean and coastal space that encompass river basins and estuaries and extend out to the seaward boundary of continental shelves and the seaward margins of coastal current systems ..., delineated according to continuities in their physical and biological characteristics, including inter alia: bathymetry, hydrography, productivity and trophically dependent populations' (Sherman & Duda 1999, p. 18). Their extension ranges from 300 000 km^2 (Scotian Shelf) to over 2.5 million km^2 (Humboldt Current). Selected ecosystems are characterised by marked seasonality and by time series that are much more reliable than those from equatorial systems, which are often characterised by highly aggregated reported landings (i.e. miscellaneous fishes or invertebrates). The reason for this scarce reliability of data from equatorial regions is to be found in the particular socio-economic conditions of the developing countries bordering these LMEs, where fisheries landings data have been seldom collected on a routine basis.

Primary productivity. Our study is based on regional PP estimates obtained from a neural network global model (Scardi 2000, 2001) and from the basic version of the most popular PP model (i.e. Vertically Generalized Production Model, VGPM, Behrenfeld & Falkowski 1997). PP in each LME has been estimated from monthly mean satellite-derived measures of surface chl *a* concentration from SeaWiFS (Level 3) and related ancillary sea surface temperature (SST) and irradiance data (available at: oceancolor.gsfc.nasa.gov/). PP estimates were extracted from global raster data (latitudinal pixel size = 9.766 km) from January 1998 to December 2002. PP was estimated by means of a depth-integrated model, the Vertically Generalized Production Neural Network (VGPNN) (Scardi 2000, 2001). VGPNN is based on an artificial neural network that performs a generalised nonlinear regression of PP based on surface chl *a* concentration and other predictive variables (latitude, longitude, day length, mixed-layer depth, SST, P^B_{opt}, i.e. maximum C fixation rate within a water column, mg C (mg chl)$^{-1}$ h^{-1} [following Behrenfeld & Falkowski 1997] and photosynthetically active radiation [PAR]). Neural networks have been recently introduced in ecological modelling and their applications are becoming more and more frequent. They do not require an explicit formulation, as they are able to adapt themselves for reproducing complex relationships, provided that enough data are available and that they account for the effects of the most important sources of variation to be modelled. Further details about the specific modelling strategies adopted for developing the VGPNN model can be found in Scardi (2000, 2001), whereas a more general introduction to the modelling applications of artificial neural networks in coastal marine ecosystems can be found in Scardi (2003).

A special feature of the VGPNN is that it was calibrated (commonly referred to as 'trained') on the basis of a data set in which records with high productivity to biomass (P/B) ratio (depth-integrated primary productivity to biomass in the surface layer ratio) were filtered out. In fact, major distortions in vertically integrated PP may arise when deep chlorophyll (and therefore PP) maxima are associated with low chlorophyll concentrations in the upper layer of the water column. In most cases PP estimates are vertically integrated taking into account samples collected at a few discrete depths. The depth difference between samples is usually not constant, as it increases with depth, and therefore samples are more sparse in the deeper part of the water column. Thus, a deep PP maximum, which is usually confined to a layer much thinner than the depth difference between 2 sampling depths, may be artificially spread on the entire stretch between 2 samples because of the trapezoidal vertical integration. Although this source of bias probably accounts for many cases of high PP values associated with relatively low surface phytoplankton biomass, it has often been overlooked in the development of other models. The exclusion of potentially biased records from the data set that supported the VGPNN development made this model conservative in estimating high PP values.

The effects of this feature can be observed by comparing VGPNN PP estimates with those provided by other depth-integrated models. For instance, the estimate for annual global PP obtained from the VGPM (Behrenfeld & Falkowski 1997) is 43.5 Gt C yr^{-1}, while VGPNN provided a lower estimate of 40 Gt C yr^{-1} (Carr et al. 2006).

Average values for each LME were computed from monthly global PP raster data. Some missing values at high latitudes, due to reduced day length and cloud cover, were computed by linear interpolation for the Baltic Sea (November to January 1997 and December to January 1999 to 2002), Barents Sea (November to February 1998 to 2002), East Bering Sea (December) and the North Sea (December).

Catches. Yield data were obtained from the Sea Around Us Project (SAUP 2006) catch database, which provides a 50 yr time series of fisheries landings (1950 to 2004) from 66 LMEs around the world, accounting for 83% of the global fisheries yield (Worm et al. 2006). Yield data are available as average annual catches (metric tons) of each taxon (species, genus or family) within each LME. To compare data from different LMEs, catches are expressed as average values per unit surface area (t km^{-2} yr^{-1}).

Yield data were also aggregated by TL, following SAUP database TLs attribution. Five TL classes were defined, namely L225 (TL, 2.25 to 2.75), L275 (TL, 2.75 to 3.25), L325 (TL, 3.25 to 3.75), L375 (TL, 3.75 to 4.25) and L425 (TL, 4.25 to 4.75). Species with TL of <2.25 were excluded from the analysis as there are no nektonic species below this threshold — with the exception of *Mugil cephalus* (TL = 2.13) and *Sarpa salpa* (TL = 2.01), whose contribution to the overall fish yield is negligible. When reported, *M. cephalus* was considered as part of L225; Mugilidae (TL = 2.3) were also reported in this group. *S. salpa* was excluded from the analysis as total catches in the Benguela Current (1998 to 2002) were below 2 t. All benthic invertebrates were excluded independently of their TLs.

Multivariate analysis. A correspondence analysis (CA) (Benzecri 1973) was performed on averaged catches per TL class for each LME (t km^{-2} yr^{-1}). PP temporal variability (as the variation coefficient of the average monthly LME PP) and total yield were represented as bubble plots in CA ordinations. PP spatial variability (as the average monthly LME PP variation coefficient) was also taken into account.

Primary production required to sustain catches. Following Pauly & Christensen (1995), PPR to sustain LME catches was computed as:

$$\text{PPR} = (\text{catches}/9) \times 10^{(\text{TL}-1)}$$

Although landings represent only a fraction of the total biomass available in the ecosystem, PPR still represents an indicator of energy TE of the food web. A PPR/PP ratio (%PPR) was assumed as an energetically based fishing pressure index (FPI) to assess yields in relation to intrinsic energetic limits for each LME (Knight & Jiang 2009). The %PPR in combination with TL_c was also used to visually assess LME exploitation level (Tudela 2003, Tudela et al. 2005).

Moreover, following Shannon et al. (2009), 2 ecosystem indicators were computed from reported catches to highlight fisheries impacts in exploited ecosystems: (1) the fish/invertebrates ratio (F/I) and (2) the demersal fish and chondrichthyan fish/pelagic fish ratio (D/P). For each indicator, the median value over the 5 yr (1998 to 2002) was assumed as a measure for the 'ecosystem state' (Shannon et al. 2009). The analysis of these and other indices over a time lapse was proposed by Shannon et al. 2009 as a tool to detect overexploitation effects, as a decrease of TL_c, better known as 'fishing down marine food webs' (Pauly et al. 1998). Under high harvesting pressures, a decline of these indicators is likely to be observed as a signal of top predatory fish removal in overexploited ecosystems, which in turn determines the decrease of TL_c. Therefore, F/I and D/P median values are 'snapshots' of the actual LME state, which summarises catch composition, in terms of fish/invertebrates and pelagic fish/demersal fish dominance in fisheries landings. This status could be related to different productivity regimes and overall total yields.

RESULTS

PP estimates and catch trends

Primary productivity

Average PP values estimated by VGPNN and VGPM models during the period from 1998 to 2002 are reported in Table 2. Values for VGPNN estimates ranged from 363 mg C m^{-2} d^{-1} in the Newfoundland-Labrador Shelf up to 1527 mg C m^{-2} d^{-1} in the Baltic Sea. A positive trend ($r = 0.9636$, $p < 0.01$) was observed for North Sea PP estimates, which increased gradually from 786 in 1998 to 851 mg C m^{-2} d^{-1} in 2002.

Table 2. Average annual primary productivity (mg C m^{-2} d^{-1}) in each LME estimated for the period from 1998 to 2002 with the Vertically Generalized Production Neural Network (VGPNN; Scardi 2000, 2001) and Vertically Generalized Production Model (VGPM; Behrenfeld & Falkowski 1997) models

LME	VGPNN	VGPM
Atlantic Ocean		
Baltic Sea	1527	1914
Barents Sea	642	965
North Sea	820	1471
Newfoundland-Labrador Shelf	363	521
Northeast US Continental Shelf	835	1228
Scotian Shelf	549	757
Pacific Ocean		
East Bering Sea	446	652
Gulf of Alaska	453	709
Okhotsk Sea	465	671
Sea of Japan	416	628
Eastern Boundary Currents		
Benguela Current	988	1294
California Current	367	628
Canary Current	774	1494
Humboldt Current	629	874

The Canary Current showed the highest average PP spatial variability, while the Baltic Sea was associated with the lowest extreme. On the other hand, temporal variability was the lowest in the Benguela Current, while the highest variability was observed in the Okhotsk Sea. PP temporal variability and spatial variability display opposite patterns, indicating an inverse relationship between these 2 sources of variation, which is even more evident when LME ranks are taken into account (Spearman rank correlation, $r_s = -0.6923$, $p < 0.01$) (Fig. 2). In fact, spatial heterogeneity is usually lower in ecosystems that are strongly driven by seasonal dynamics, whereas the latter can be completely masked by complex spatial patterns, e.g. ecosystems where physical drivers play a major role. Obviously, spatial and temporal components of PP variability can combine with each other, but only to a limited extent, and therefore an inverse relationship between them emerges as empirical evidence.

Fisheries yields

Average annual fisheries yields for each of the 14 LMEs in the period 1998 to 2002 are reported in Table 3 ('Catches' column). Catch values ranged from 0.32 t

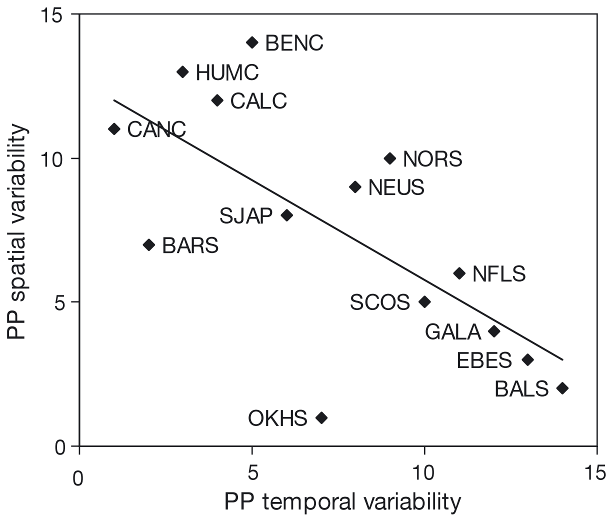

Fig. 2. Temporal versus spatial variability in primary productivity (PP): the rank correlation between the 2 variables is negative and highly significant (Spearman's $r = -0.6923$, $p < 0.01$). See Table 1 for abbreviations

km^{-2} yr^{-1} for the California Current LME to 3.93 t km^{-2} yr^{-1} in the Humboldt Current. Total yields exhibited significant trends in 3 LMEs: (1) negative trends were observed for the Okhotsk Sea ($r = -0.9830$, $p < 0.01$) and the Baltic Sea ($r = -0.9471$, $p < 0.05$); (2) a positive trend was observed for the Benguela Current ($r = 0.8813$, $p < 0.05$). Significant trends observed for the Baltic Sea and the Benguela Current were related to a decrease or increase in single TL classes. In particular, the negative trend observed in the Baltic Sea was associated with a decrease in L275 catches, which were mainly represented by small pelagic fishes (sprat *Sprattus sprattus*), while the positive trend in the Benguela Current was associated with an increase in L375 catches, although this class was the less abundant of the two (up to 5% in 2002).

In 4 LMEs total catches were dominated by low TL species (L225): in the California Current (41%), the Newfoundland-Labrador Shelf (46%), the northeastern US Continental Shelf (51%) and the Humboldt Current (85%), the latter being the most productive marine fishing ground in the world, where catches are indeed totally represented by Peruvian anchoveta *Engraulis ringens*. The North Sea (59%), the Canary Current (53%) and the Baltic Sea (45%) showed prevalent catches in L275, represented by small pelagic species in the Canary Current and the Baltic Sea (sardine or pilchard *Sardina pilchardus* and sprat, respectively) and by sand eels *Ammodytes* spp. in the North Sea; these are target species of the largest single-taxon fishery in this region. Intermediate TLs, represented by L325, encompassed top-reported species and accounted for almost one-third of the average total catches through selected LMEs. In addition, 6 of the 14 LMEs showed dominant catches in L325 and L375. Finally, none of the 14 LMEs showed average catches dominated by L425, although the Gulf of Alaska exhibited a particularly high proportion of this TL class (around 28%), associated with Pacific cod *Gadus macrocephalus* catches.

Relating PP to fisheries yields

Total fisheries yield and primary productivity

Fisheries yields versus PP, following Nixon (1992) and Nixon et al. (1986), are shown in Fig. 3. LMEs and Nixon's ecosystems (Fig. 3) are plotted, together with TE known levels. For each LME, range bars show min-

Table 3. Average fisheries annual catches (t km^{-2} yr^{-1}), average trophic level of catches (TL_c), primary productivity (PP, g C m^{-2} yr^{-1}), primary production required to sustain catches (PPR, g C m^{-2} yr^{-1}) and PPR/PP ratio (%PPR) for each LME. LMEs are ordered by descending %PPR

LME	Catches	TL_c	PP	PPR	%PPR
East Bering Sea	1.79	3.59	163	116	0.71
Sea of Japan	1.14	3.40	152	100	0.66
Okhotsk Sea	1.61	3.52	170	99	0.58
Barents Sea	2.43	3.47	234	130	0.55
North Sea	3.69	3.26	299	128	0.43
Newfoundland-Labrador Shelf	0.78	3.21	132	48	0.36
Gulf of Alaska	0.35	3.82	165	52	0.32
Humboldt Current	3.93	2.72	230	71	0.31
Canary Current	2.06	3.23	282	76	0.27
Benguela Current	0.94	3.48	361	89	0.25
Northeast US Continental Shelf	1.50	3.00	305	66	0.22
Scotian Shelf	0.70	3.31	200	42	0.21
California Current	0.32	3.11	134	19	0.14
Baltic Sea	0.45	3.33	557	15	0.05

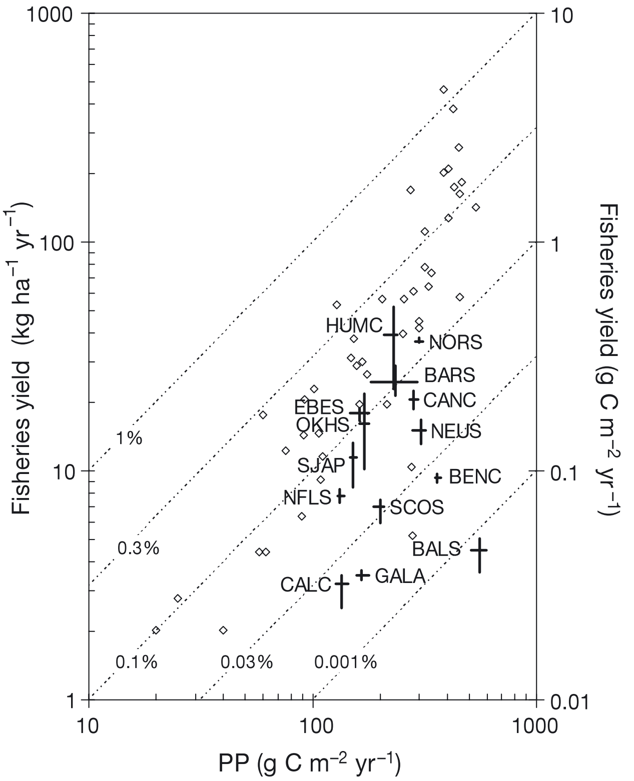

Fig. 3. Relationship between primary productivity (PP) and fisheries yield, following Nixon (1982, 1992) and Nixon et al. (1986). Symbols (◇) represent Nixon's ecosystems. Variability in PP (horizontal bars) and total yield (vertical bars) are shown for each LME. Diagonal lines and associated % values show different levels of efficiency in energy transfer from PP to fisheries yield (see 'Results' for details; see Table 1 for abbreviations)

imum and maximum annual PP from 1998 to 2002. While values on the PP axis are comparable amongst LMEs (with the Baltic Sea and the Barents Sea showing the highest range, i.e. 85 and 111 g C m^{-2} yr^{-1}, respectively), a greater and more widespread variability is apparent on the yield axis. In other words, fisheries yields can be quite different despite similar ecosystem PP (e.g. Fig. 3; the Humboldt Current, the Okhotsk Sea and the Sea of Japan show considerable differences in total yields and negligible differences in PP). It follows that PP in these systems, although setting the potential for target (and non-target) species, may not represent the main driving force for the harvest, as fisheries yields actually originate from a complex combination of different factors, both biological and industrial (management policies, fishing effort and commercial interests). Thus, PP and fisheries landings could represent input and output variables of a 'black box' into which natural systems dynamics act under the influence of industrial exploitation strategies. Even though these remain known, the efficiency of the complex relationship between PP and landings could be represented by overall TE, which provides a rough measure of the effect of harvesting. The efficiency of this complex relationship is represented by overall TE, which provides a rough measure of the effect of harvesting. Total yields in different LMEs are in fact characterised by different average TLs, so that for any given level of PP, TE may vary according to the combination of exploitation pressures on each TL. While overall TEs in Nixon et al. (1986) ranged from 0.1 to 1 %, the estimated values obtained in the present study are smaller (0.01 to 0.3 %). However, it must be pointed out that high overall TEs in Nixon et al. (1986) were reported mainly for estuaries and near-shore shelves, with an exception made for the Humboldt Current, which still expressed the highest TE in our data set.

Multivariate analysis

The CA ordination of average catches per TL class for each LME is shown in Fig. 4. Three main features arise from the ordination: (1) the lowest TL class (L225) is isolated from the others and it drives the ordination, (2) the second TL class (L275) is separated from the 3 subsequent TLs and (3) intermediate TLs are close to each other (L325 and L375). The upper TL class (L425) does not appear to contribute in a relevant way to the ordination along the first axis (CA1 in Fig. 4). Moreover, LMEs are associated with different dominant TL classes: in particular, 3 out of 4 EBCs are associated with low TL classes (the Humboldt Current and the California Current with L225 and the Canary Current with L275), while intermediate TLs seem to be associated with temperate shelves and sub-polar ecosystems (e.g. East Bering Sea, Gulf of Alaska, Okhotsk Sea, Scotian Shelf). Demersal-dominated ecosystems (East Bering Sea, Gulf of Alaska, Okhotsk Sea and New-

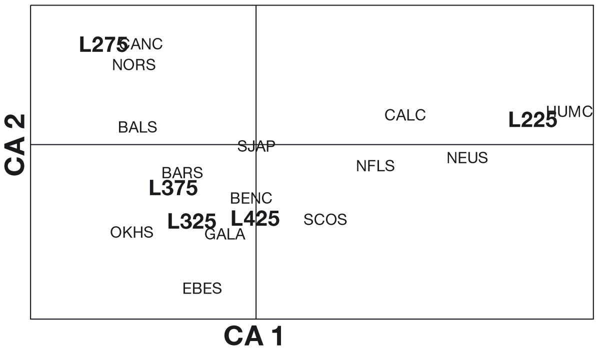

Fig. 4. Correspondence analysis (CA) of LMEs and trophic levels. This ordination shows the role that trophic levels (TLs) play in each LME (see Fig. 1, Table 1 for abbreviations of LME names)

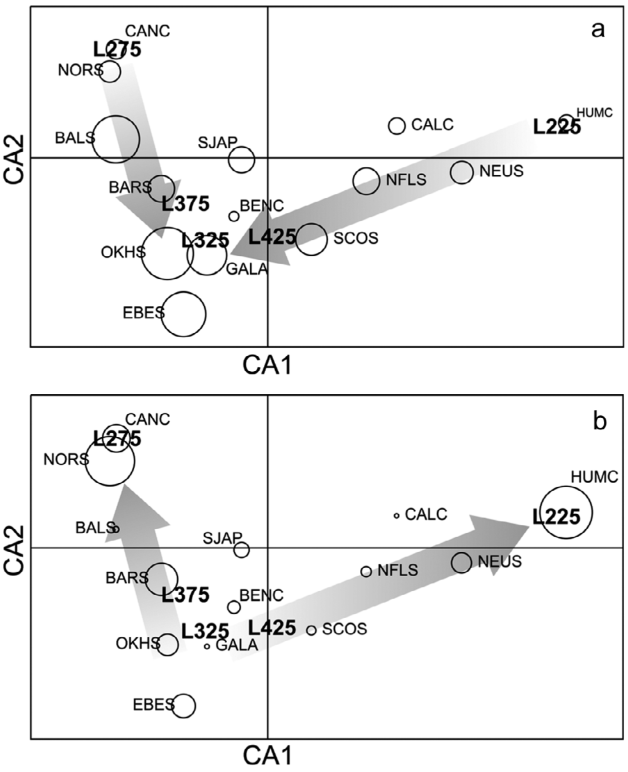

Fig. 5. Correspondence analysis: bubble size represents (a) primary productivity (PP) temporal variability and (b) total fisheries yield. As suggested by the grey arrows, temporal variability is minimum in LMEs where lower TLs, especially L225, play a major role. In contrast, total yield is maximum in these LMEs, as the overall efficiency of energy transfer is negatively correlated to the exploited TL. See Table 1 for abbreviations

foundland Labrador Shelf) were located in the negative CA2 semi-plane (Fig. 4), with the only exception being the North Sea, which is associated with L275 catches (see also Fig. 8).

Information about PP temporal variability and total yields was displayed in the CA ordination plot by turning the plot into 2 bubble plots (Fig. 5a,b). A general relationship between the PP temporal variability and the composition of catches is apparent: a high PP temporal variability, indicating marked seasonal variations (Fig. 5a), seemed to favour upper and intermediate TLs (L325, L375 and L425), whereas low TL catches (L225 and L275) are associated with much more stable ecosystems (Fig. 5a) and higher yields (Fig 5b). In other words, the fisheries yield under conditions of high PP variability is associated with intermediate TLs (demersal catches) and is generally lower than in more stable fishing grounds, where pelagic-dominated (low TLs) harvests produce the world's highest yields in marine fisheries. Average PP and spatial variability are not presented here as they did not show any clear pattern in association with total yields.

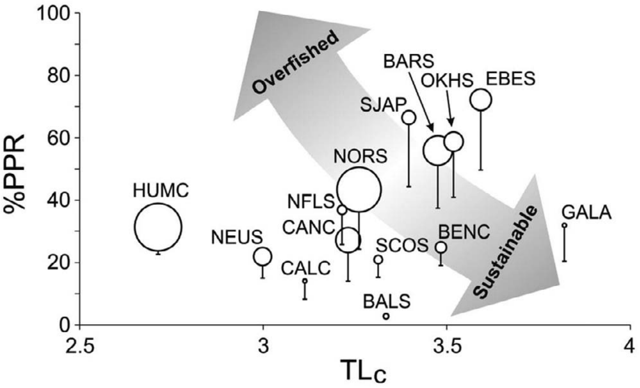

Fig. 6. %PPR versus TL_c relationship: %PPR estimates for each LME based on the VGPNN model (Scardi 2000, 2001) are shown, while the lower end of the vertical bars show %PPR according to the VGPM model (Behrenfeld & Falkowski 1997). Vertical bars outline the difference between a %PPR estimate based on VGPNN (bubble) and an estimate provided by the VGPM model, i.e. the effect of uncertainty due to the PP model selection. Bubble size represents LME's total yield. See Tables 1 & 2 for abbreviations

Primary productivity required to sustain total yields

Estimated PP values ranged from 132 to 557 g C m^{-2} yr^{-1}, while PPR values ranged from 15 to 130 g C m^{-2} yr^{-1} (Table 2). In Fig. 6, %PPR (PPR/PP) estimates are plotted against the average TL of catches in a bubble plot, where the bubble size represents the total yields. The highest yields occur in combination with moderate fishing pressures (0.1 < %PPR < 0.5, Fig. 6), especially when the average catch TL is in the intermediate to low range. High fishing pressures (%PPR > 0.5, Fig. 6) are associated with intermediate total yields and high average TL of catches. This condition seems to occur in high-latitude boreal LMEs (>50° N) where the stocks are possibly overexploited. A low fishing pressure (%PPR < 0.1, Fig. 6) is observed only in the Baltic Sea, where fisheries target relatively low TL species and the PP is very high (up to 600 g C m^{-2} yr^{-1} in 2002). Obviously, under these conditions an increase in catches can be, in theory, supported by ecosystem production.

For ecosystem indicators computed on fisheries landings (Figs. 7 & 8), 2 LMEs, both located in the NW Atlantic Ocean, showed an F/I ratio value of <0: the Newfoundland-Labrador Shelf and northeastern US Continental Shelf fisheries harvest invertebrates rather than fish (Fig. 7). The F/I ratio was not computed for the Barents Sea, as invertebrates represent a negligible portion of total catches in this LME. A linear correlation of the F/I ratio in time (1998 to 2002) showed that the northeastern US Continental Shelf exhibited a significant negative trend ($r = -0.98425$, $p < 0.01$), demonstrating that the dominance of invertebrates in the

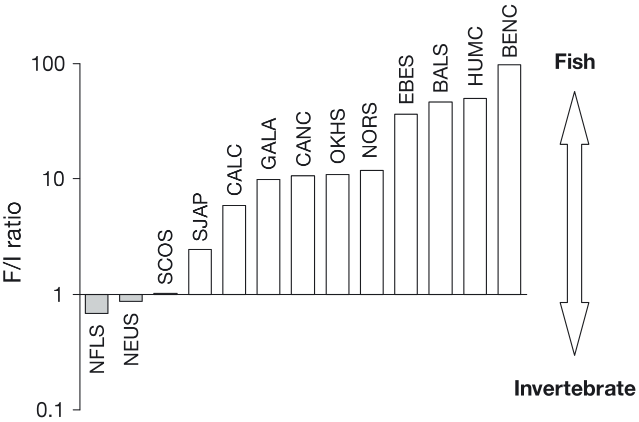

Fig. 7. Average ratio of fish to invertebrates (F/I) following Shannon et al. (2009). Only 2 LMEs, namely NFLS and NEUS, exhibited total fisheries yields dominated by invertebrate species rather than fish species. F/I ratio was not computed for the Barents Sea, as invertebrates represent a negligible portion of the total catches in this LME. See Table 1 for abbreviations

catch became stronger in this period of time. In particular, a shift from fish to invertebrate dominance was observed to occur in 2000. An opposite pattern was observed in the Scotian Shelf, where catches from 1998 to 2000 were invertebrate-dominated, while the last 2 yr of landings were fish-dominated, although a significant linear trend is missing.

The demersal/pelagic composition of fisheries harvests was also assessed through the D/P ratio for LMEs showing a clear dominance in fish catches (Fig. 8). This indicator also provided a rough measure of TL_c, with demersal catches showing an overall higher TL_c than pelagic ones, especially when pelagic fisheries harvested small and medium-sized species (e.g. anchovies and sardines). The majority of LMEs show pelagic-dominated landings: a strong unevenness in catches was observed in the Baltic Sea and Humboldt Current, where low TL pelagic catches represented almost all landings, but low TLs species were dominant also in the other 3 EBCs (i.e. the Benguela, Canary and California currents) and in the Barents Sea, Scotian Shelf and Sea of Japan. A significant negative trend in D/P ratio over time was observed in the Barents Sea (r = –0.97594, p < 0.01) and Scotian Shelf (r = –0.97949, p < 0.01), demonstrating an increase in pelagic dominance. Demersal dominance was observed in North Pacific LMEs (Gulf of Alaska, East Bering Sea and Okhotsk Sea) as well as in the North Sea. The latter showed a lower TL, which was associated with a fishing pressure exerted on low to intermediate TLs (L275 in Fig. 4), especially on *Ammodytes*.

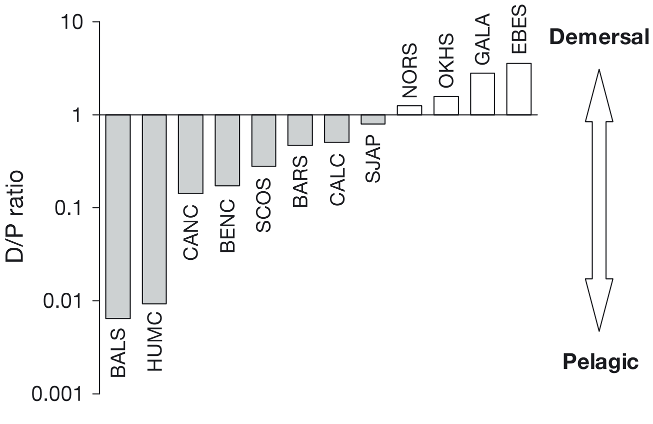

Fig. 8. Average ratio of demersal and chondrichthyans fish to pelagic fish (D/P) following Shannon et al. (2009). See Table 1 for abbreviations

DISCUSSION

Yield relationship between PP and fisheries

The present study provides new insights into the PP–fisheries relationship, suggesting that total fisheries yields can be linked more to PP temporal variability than to PP average values, as has been proposed in previous studies (e.g. Nixon 1982, 1992, Nixon et al. 1986, Iverson 1990, Nielsen & Richardson 1996, Sommer et al. 2002, Steingrund & Gaard 2005). Moreover, total yields are, in turn, negatively correlated with PP spatial variability as a consequence of the negative correlation between PP spatial and temporal variability. From an ecological perspective it would be reasonable to imagine that fish populations experiencing lower fluctuations in resources availability may profit from regular feeding of larvae and juveniles. This could determine longer reproductive and spawning seasons, which, as a result, may sustain higher yields. At the same time, from a management point of view, it would be only natural to conclude that where seasonal variability is weak, fisheries effort should be organized in a more effective way to obtain higher harvests. Furthermore, the significant relationship between PP temporal variability and TL_c ($r = 0.5604$, $p < 0.05$) points to a strong correlation between environmental variability and catches composition (Fig. 9). Higher yields are typically obtained when low TLs are harvested in ecosystems that experience stable productive regimes. Under these conditions, catches are typically dominated by pelagic species. Obviously, the role of PP variability in determining fisheries yields should be further investigated when longer time series, especially on the fisheries side, are available.

CA shows that intermediate TL classes (L325 and L375) tend to occur simultaneously. This coupling may be governed by intrinsic features of the TL assignment: intermediate TL species may oscillate between slightly

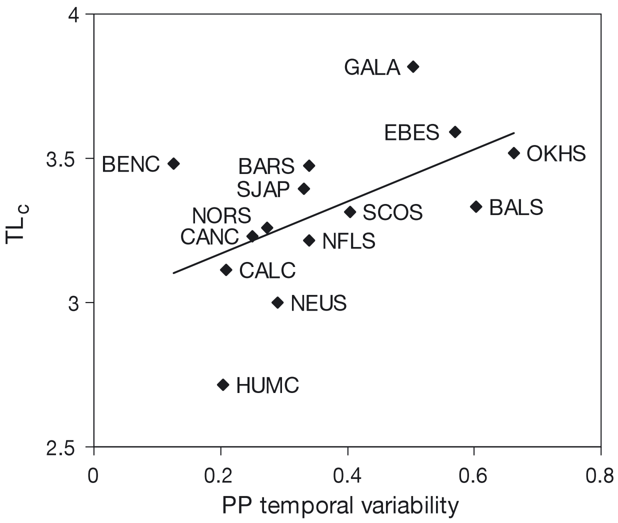

Fig. 9. Average tropihic level of catches (TL_c) versus primary productivity (PP) temporal variability: the linear correlation is positive and significant ($r = 0.5604$, $p < 0.05$). See Table 1 for abbreviations

different TLs due to variable diets; in contrast, TL definition is more accurate for low TL species (i.e. small pelagic fishes), whose diet is more stable and determined by physiological and morphological characteristics. Nevertheless, co-occurrence of L325 and L375 could also suggest that they share a common feature regarding fishing gear: intermediate TL species are represented mainly by demersal or benthopelagic species, which are usually all targeted by trawls. As indicated previously, intermediate TL species are typical of demersal-dominated catches and are associated with overall lower yields in LMEs characterised by less stable PP conditions.

PPR and ecosystem transfer efficiencies

Any consideration about PPR is obviously affected by the lack of accuracy in both fisheries and PP data. Uncertainty in these data may lead to widely variable estimates and, in the end, to strikingly different scenarios. PP estimates can be obtained from a number of models, but their range can be as wide as 100%. In the present study, a conservative model (VGPNN, Scardi 2001) was selected, which provides PP estimates close to the lower end of their range. The rationale supporting this choice is that, while other models have been calibrated with PP data that are possibly overestimated because of the artificial spread of PP maxima caused by vertical integration, these records have been filtered out from the VGPNN 'training set' by setting a threshold in the P/B ratio. In addition, although we assume that the overestimation of PP can also affect the VGPM model (Behrenfeld & Falkowski 1997), we compared our results with this model, which is by far the most commonly applied and the most popular template for further developments (Carr et al. 2006). Obviously, the selection of a reference PP model is inherently subjective, as there is no way to prove that any given model is better than others on a global scale (Friedrichs et al. 2009). However, differences between PP models affect the definition of the relative relationships between LMEs only to a limited extent.

An estimated 8% of the total aquatic PP is required to sustain global fisheries, although shelf and upwelling ecosystems show markedly higher values ranging around 25% (Pauly & Christensen 1995). Other PPR values were computed to estimate PP requirements of single-species populations such as the Pacific herring *Clupea pallasii* in the NE Pacific Ocean and East Bering Sea (Perry & Schweigert 2008) and North Sea demersal fishes (Jennings et al. 2008). In agreement with previous studies (Pauly & Christensen 1995, Tudela et al. 2005), we obtained high PPR values for temperate shelves, even though absolute LME-specific PPR values were higher than those reported elsewhere. For example, the East Bering Sea %PPR was estimated at 0.7 compared with previously reported values of 0.15 to 0.31 (Trites et al. 1997), and the 0.36 %PPR estimated for the Newfoundland-Labrador Shelf is twice the value of 0.15 reported by Heymans (2004) for an overlapping time interval (1995 to 2000).

Upwelling regions show lower PPR values (14 to 30%) in association with a fishing effort that targets lower TLs (mainly small pelagic species), so that a lower carbon fraction is necessary to sustain catches in these LMEs. The Baltic Sea was a unique condition among LMEs, where the highest average PP, determined by semi-enclosed conditions, was associated with catches at the lowest end of the TLs, leading to an extremely small PPR value (<3%).

In general, the high %PPRs estimated in the present study are partially attributed to more conservative PP estimates obtained with the VGPNN model, a feature that affects both the assessment of exploitation level and management practices. A relationship between average TL of catch (TL_c) and %PPR has been proposed in Tudela (2003) and Tudela et al. (2005) as an indicator of ecosystem fishing impact. Based on the approach of those authors, 2 sets of %PPR–TL_c pairs for each LME were plotted (Fig. 6), each obtained with a different PP estimation model (VGPM and VGPNN). The relative location of these 2 blocks in the plot indicates a possible range of variation, which could lead to potentially different management perspectives. Following Knight & Jiang (2009), choosing the VGPM PP estimation model instead of the VGPNN model could lead to different conclusions in terms of exploitation levels. In fact, the threshold of 0.5 FPI indicated by these authors as the limit for an intermediate fishing pressure is not exceeded by LMEs when PP is estimated by VGPM. In contrast, the more conservative estimation of PP obtained with VGPNN determines the shift of high-latitude boreal shelves towards overexploitation (FPI > 0.5). It follows that a more conservative estimation of PP could contribute to a more precautionary approach to fisheries management, where high levels of exploitation are more easily attained. However, although FPI provides a rough measure of fisheries exploitation, it fails to take into account the TL on which fisheries effort is being expressed. The same pressure exerted upon low or high TLs will lead to different exploitation scenarios.

CONCLUSIONS

The double bottom-up/top-down approach, borrowed from food web theory, allowed us to better focus on which PP aspect acted as the principal driving control for overall fisheries yields (bottom-up) and to assess carbon budget demands (PPR) for individual fisheries in 14 LMEs (top-down). Although it could be considered a crude approach to dealing with such a complex subject, this approach turned out to be effective in addressing general questions on the dynamics underlying exploited ecosystems on a large scale.

After several previous attempts (e.g. Nixon 1982, 1992, Nixon et al. 1986, Iverson 1990, Nielsen & Richardson 1996, Sommer et al. 2002, Steingrund & Gaard 2005) that focused on a limited set of records, mainly represented by direct PP measurements and local fisheries statistics, the availability of new remotely sensed data sets allowed an important scaling up to regional or even global studies. These data have been constantly collected since late 1997 in the framework of the SeaWiFS mission, providing a consistent source of information for improved PP estimates. Further advances are associated with recent comparisons between different PP models (Carr et al. 2006, Friedrichs et al. 2009), which contribute substantially in obtaining more accurate global PP estimates and a better and more reliable analysis of the process.

Nevertheless, some limitations intrinsic to these kinds of studies need to be considered. First, the limited spatial scale (e.g. the limited number of LMEs selected) could hinder a global generaliszation, although the LMEs considered encompass the bulk of industrial fishing grounds both in the Northern (e.g. temperate shelves like the North Sea, Baltic Sea and NW Atlantic Ocean) and in the Southern Hemisphere (e.g. major upwelling regions like the Humboldt Current). Second, it must be stressed that further information is needed to outline more accurate trends and perspectives: for instance, no information about fishing efforts is available at the same resolution as are yield data, so that landings are actually used as an approximation of actual fish catches. Nevertheless, the limited time lapse considered in our work allowed us to reasonably assume a constant exploitation pressure. Obviously, there are potential sources of error in such an assumption (e.g. moratoria measures).

Finally, although we can estimate TEs from an ecological perspective, estimates need to be corrected for external energy budgets. In fact, while the photosynthetic production of organic carbon is supported by solar irradiation, the fisheries harvest is sustained by alternative energy sources (fossil fuels), which guarantee exploitation levels that exceed those supported by natural processes alone. So, even though fishing activities may be considered as a 'top predation', these external energy uploads significantly differentiate fishery from natural predation (Trites et al. 1997).

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Editorial responsibility: Kenneth Sherman,
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Submitted: August 31, 2009; Accepted: April 19, 2010
Proofs received from author(s): June 22, 2010