

MAPPING FISHERIES ONTO MARINE ECOSYSTEMS: A PROPOSAL FOR A CONSENSUS APPROACH FOR REGIONAL, OCEANIC AND GLOBAL INTEGRATIONS^{a)}

Daniel Pauly, Villy Christensen, Rainer Froese, Alan Longhurst, Trevor Platt, Shubha Sathyendranath, Kenneth Sherman and Reg Watson

ABSTRACT

Research on ecosystem-based fisheries management, marine biodiversity conservation, and other fields requires appropriate maps of the major natural regions of the oceans, and their ecosystems.

It is proposed here that a classification system proposed by T. Platt and S. Sathyendranath and implemented by A.R. Longhurst, defined largely by physical parameters, and which subdivides the oceans into four 'biomes' and 57 'biogeochemical provinces' (BGCPs), could be merged with the system of 50 Large Marine Ecosystems (LMEs) identified by K. Sherman and colleagues, which would represent subunits of the provinces. This arrangement enhances each of the systems, and renders them mutually compatible. For the LMEs, subprovinces are pragmatically defined to serve as a framework for the management of coastal fisheries, and other purposes, while the BGCPs have rigorous physical definitions, including borders defined by natural features. Moreover, incorporating the 50 defined LMEs into the framework of BGCPs will allow straightforward scaling-up of LME-specific flow estimates (including fisheries catches) up to basin and ocean scales. The combined mapping will allow the computation of GIS-derived properties such as temperature, primary production, etc., and their analysis in relation to fishery catch data for any study area.

A further useful aspect of the proposed scheme is that it will enable us to quantify the EEZ of various countries in terms of the distribution of marine features (e.g., primary production, coral reef areas) which has yet to be straightforwardly^{a)} associated with coastal states.

^{a)} presented as C.M. 2000/T:14 at the Annual Science Conference of the International Council for the Exploration of the Sea.

Applications to shelf, coral reef and oceanic fisheries, and to the mapping of marine biodiversity are briefly discussed.

INTRODUCTION

There is a broad consensus in the scientific community that fisheries management should be ecosystem-based, but very little agreement as to what this means (NRC 1999). Also, there is a need to analyze biodiversity data at larger scales than generally done so far, as demonstrated by, e.g., Sala et al. (2000) for terrestrial and freshwater biomes.

Clearly, when dealing with such complex issues, the first task, as in all science-based approaches to a problem, is to define the object(s) of concern, and to develop a consistent method to show how these objects are interrelated. Here, the objects are the marine ecosystems within which fisheries and biodiversity are to be analyzed, and marine life in general, is embedded.

Fortunately, establishing a consensus on the classification of marine ecosystems may be relatively easy, given the compatibility, so far never elaborated upon, of two classification schemes proposed in recent years. Both of these integrate enormous amount of empirical data, and are sensitive to previous analyses of marine ecology. These two schemes are (1) the global system of 57 'biogeochemical provinces' (BGCPs) developed by Platt and Sathyendranath (1988, 1993), Platt et al. (1991, 1992), Sathyendranath et al. (1989), Sathyendranath and Platt (1993), implemented by Longhurst (1995, 1998), and defined at scales appropriate for understanding physical forcing of ocean primary production and related processes; and (2) the 50 coastal Large Marine Ecosystems (LMEs) gradually defined by Sherman and co-workers (see e.g. Sherman et al. 1990, 1993), whose size and on-shelf location makes them particularly suitable for addressing management issues, notably those pertaining to fisheries on continental shelves, and coastal area management (Sherman and Duda 1999).

After reviewing selected features of these two schemes, we suggest how the partition of ocean regions that they imply can be made mutually compatible. The joint classification which then emerges is presented in form of a spatial hierarchy, and as maps, each emphasizing a key feature of the classification. Overall, the integrated scheme we propose allows explicit consideration of different scales, as discussed e.g. by Levin (1990).

BIOGEOCHEMICAL PROVINCES

This partition of the ocean is derived from a suggestion of Platt and Sathyendranath (1988) for the recognition of natural regions of the ocean, having characteristic physical forcing to which there is a characteristic response of the pelagic ecosystem. These regions were to be dynamic biogeochemical provinces ('dynamic' because their boundaries would respond to annual and seasonal changes in physical forcing, and 'biogeochemical' because within each the biota would respond to those characteristic geochemical processes which determine nutrient delivery to the euphotic zone). This concept has been used to partition both global and basin-scale analyses of primary productivity, though the 'dynamic' boundary aspect of the system remains to be exploited: so far, most applications of the partition have assumed that boundaries between provinces were fixed at locations representing average conditions, though dynamic boundaries have been used for analysis of Arabian Sea productivity.

The central principle in locating boundaries between provinces is that of the critical depth model of Sverdrup (1953), which remains the most useful formulation relating phytoplankton growth to surface illumination, and to the vertical density structure of the water column. It successfully predicts, for example, the timing of the North Atlantic spring bloom. A proposed partition of the North Atlantic into 18 BGCPs (Platt, et al. 1995) was followed by a partition of all oceans and adjacent seas into 57 provinces (Longhurst et al. 1995 and Longhurst, 1998).

The global partition was arrived at by examination of 26,000 archived chlorophyll profiles to determine Gaussian parameters describing the regional/seasonal characteristic profiles, surface chlorophyll from 43,000 grid-points from monthly Coastal Zone Colour Scanner images, and about 23,000 monthly mean mixed layer depths, together with other oceanographic variables. This analysis suggested that a two-level partition would be required adequately to represent regional differences in the expression of the Sverdrup model. The first partition is into a small number of biomes, following the usage of this term by terrestrial ecologists to mean a region of relatively uniform dominant vegetation type, with its associated flora and fauna: grassland, tundra, steppe, humid forest and so on (Golley 1993). Secondly, these biomes are each be partitioned into a number of regional entities, the biogeochemical provinces.

The four biomes (Figure 1) are defined by the dominant oceanographic process that determine the vertical density structure of the water column, which itself is what principally constrains the vertical flux of nutrients from the interior of the ocean.

In the *Polar biome*, vertical density structure is very largely determined by the flux of fresh or low-salinity water derived from ice-melt each spring and which forms a prominent halocline in polar and sub-polar oceans. In oceanographic terms, this occurs in each hemisphere polewards of the Oceanic Polar Front, whose location in each ocean is determined by the characteristic circulation of each. Though looming large on Mercator maps, the Polar biome occupies only about 6% of the ocean's surface.

Between the polar Fronts and the subtropical convergence in each ocean lies the *Westerlies biome*. Here, large seasonal differences in mixed-layer depth are forced by seasonality in surface irradiance and wind stress. Biological processes consequently may have sufficiently strong seasonality so that a spring bloom characterizes the plankton calendar.

Across the equatorial regions, between the boreal and austral subtropical convergences lies the *Trade-wind biome*. Here, the conjunction between low values for the Coriolis parameter, a strong density gradient across the permanent pycnocline and weak seasonality in both wind stress and surface irradiance result in relatively uniform levels of primary production throughout the year.

Upper continental slopes, continental shelves and marginal seas comprise the *Coastal Boundary biome*. This is constrained between the coastline itself and (usually) the oceanographic front characteristically found at the shelf-edge. The single generalization that characterizes this biome is that nutrient flux in the water column is forced by a great variety of processes: coastal upwelling, tidal friction, fresh-water outflow from river mouths, etc. In the partitions discussed above, subdivision of this biome into provinces was not carried as far as might be useful for some purposes. One of the objectives of the present study is to do just that, through the introduction of subprovinces and their identifications with LMEs.

The boundaries between the biomes thus defined certainly vary seasonally and between years, as can readily be inferred from satellite images, and dynamic boundaries that respond to this

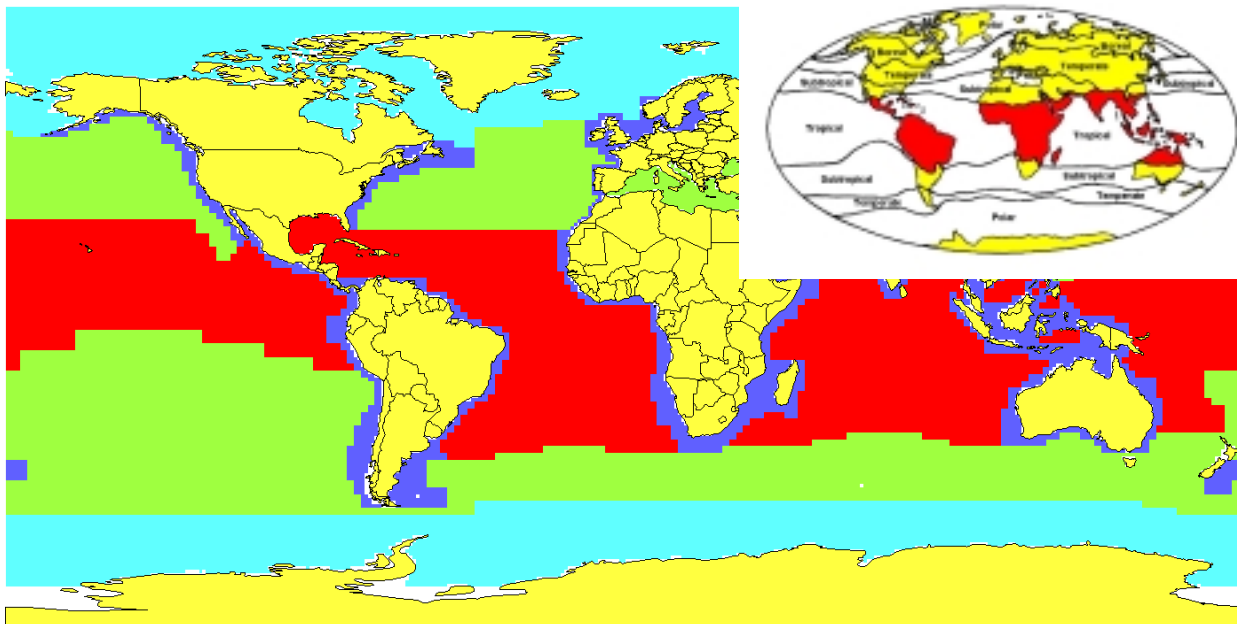


Figure 1. Map of the world ocean's biomes, the highest category in the proposed classification of the world oceans. Note its overall similarity to a conventional map of the atmospheric climate (inset, adapted from Anon. 1991). (Polar is lightest, Coastal is next darkest, followed by Westerlies and Trades)

variability are discussed for primary production and related studies by Platt and Sathyendranath, (1999). However, such dynamic schemes are neither practical nor necessarily useful for biodiversity and fisheries studies. For example, one of the tasks facing biodiversity studies are the creation of global maps documenting the distribution of hundred of thousands of marine species. Requiring that these distributions are assigned to habitats with variable boundaries would make even simple, first-order assignments of species extremely difficult and postpone the delivery of products whose need is already keenly felt by students of biodiversity.

Thus, in the case of fishes, of which about 15,000 species are marine, the assignment within FishBase (see www.fishbase.org) of species to climate type (as defined in the insert of Figure 1), required us to distinguish tropical from non-tropical species (see Pauly 1998), and this task alone required several person-months worth of work to complete.

Moreover, there are numerous types of floral or faunal assemblages whose location does not vary, though their habitat is part of, or affected by a surrounding or overlying pelagic ecosystem. Thus, the reef fishes of the Galapagos do not change their location when an El Niño event strikes the archipelago. Rather, it is their abundance which is affected (Grove 1985, Grove and Lavenberg 1997). A similar argument applies

to benthic communities, whose boundaries will tend to reflect the long term average location of the boundaries of the overlying pelagic systems, rather than tracking their changing location (Ekman 1967).

The ecosystem classification scheme proposed here is thus deliberately fixed in space. On the other hand, we anticipate that its use by various authors will quickly lead to the identification and quantification of changes in species compositions, thus reintroducing the dynamic element required at various spatial and temporal scales (Levin 1990).

Oceanographic conditions within the four biomes are obviously not uniform, and each can be subdivided further using the same set of principles as determined the biomes themselves. For example, in both the westerlies and trades biomes there are definable ocean regions where heavy tropical rainfall or excessive continental fresh water runoff lead to the existence of a quasi-permanent low salinity 'barrier-layer' occupying the upper portion of the thermally-stratified surface layer. This has important biological consequences and suggests that these regions should be recognized as individual partitions.

Using such methods, based on close examination of regional physical oceanography, the four primary biomes can be further partitioned into 57 provinces, the BGCs discussed above. Figure 2

illustrates these provinces as defined by Longhurst et al. (1995). This schema has been used to stratify the world ocean in two studies, pertaining to the global distribution of primary production (Longhurst et al. 1995) and tuna catches (Fonteneau 1998), with more forthcoming (Platt and Sathyendranath 1999, Pauly 1999).

Also, as part of the collaboration between the *Sea Around Us* project (details at www.fisheries.ubc.ca) and the FishBase project (Froese and Pauly, 2000), the world's marine fishes are presently being assigned to BGCPs, if somewhat tentatively in a few cases. We note that this work, which relies on a large number of local ichthyo-fauna lists, will require about 12 person-months to complete. However, it would require much longer were it necessary to compile first a global list of fish species, and to assign them directly to the BGCP, without prior assignment to FAO areas, countries, and oceanic islands, as is provided by FishBase.

This point is important with regards to invertebrate groups, whose global distribution will have to be mapped, in the long term, in a manner compatible to that used for fishes. This should, for example, be an important component of an Ocean Biogeographic Information System currently under consideration (Grassle and Stocks, 1999).

LARGE MARINE ECOSYSTEMS

In recent years, the formerly generic term 'Large Marine Ecosystem' (LME) has become specific, and is now mainly used for regions of ocean space encompassing coastal areas out to the seaward boundary of continental shelves and the outer margins of coastal current systems. As such, LMEs are regions of the order of 200,000 km² or greater, characterized by distinct bathymetry, hydrography and productivity patterns (Sherman 1994; Sherman and Duda 1999).

The 50 LMEs identified by Sherman and Duda (1999) are the source of about 95 % of the world's annual marine fisheries yields. Also, most of the global ocean pollution, overexploitation, and coastal habitat alteration occur within these 50 LMEs. They provide, therefore, a convenient framework for addressing issues of natural resources management. Moreover, given that most of them border developing countries, LMEs also provide a framework for addressing issues related to issues of economic development.

Various development agencies, notably the Global Environment Facility (GEF), the United Nations Development Programme, the UN Environment Programme, and the World Bank have endorsed the LME concept as framework for several of their

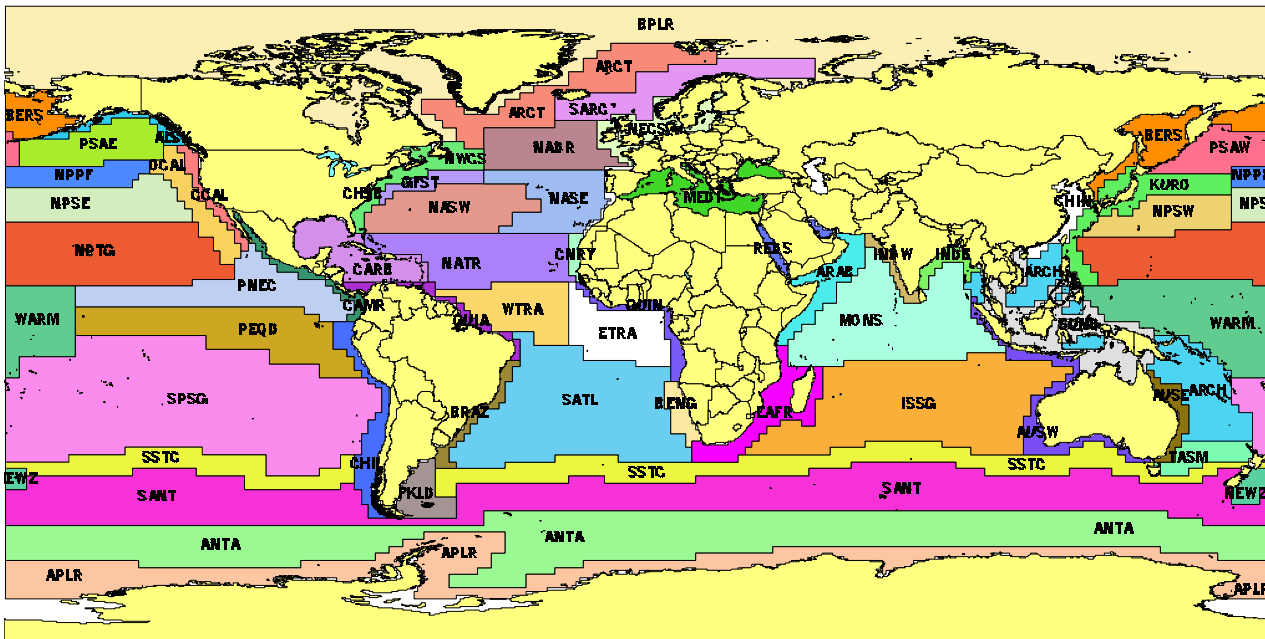


Figure 2. Map of the world ocean's 57 biogeochemical provinces, the second level in our proposed classification of the world oceans. (The borders of a few disjunct provinces, notably ARCH, will be simplified; detailed file available from www.fisheries.ubc.ca)

international development projects, for example in the Gulf of Guinea, with more such projects forthcoming (Sherman and Duda 1999). Given this considerable amount of interest, it is fortunate that a number of BCGP, i.e., those in the coastal domain, can easily be divided into 'sub-provinces' congruent with the 50 LMEs in the list of Sherman and Duda (1999). Thus, Figure 3 illustrates, for the North Atlantic, how the 15 LMEs occurring therein (including the Baltic Sea) can be mapped onto BCGPs of Figure 2, with some LMEs identified by two components (e.g. 'Southern' and 'Northern') when they straddle two provinces, and new subprovinces named where appropriate, i.e., for the parts of provinces not included in a defined LME. A similar map for the entire ocean, including all 50 LMEs in Sherman and Duda (1999) is currently in preparation (details on www.fisheries.ubc.ca).

This mapping provides, we believe, the elements that had been lacking within each of the systems thus rendered compatible. For BCGPs, we identify sub-provinces that are pragmatically defined to serve as framework for fisheries, coastal area and other applied research. As for the LMEs, they obtain, via their incorporation into the scheme of

biomes and BCGPs discussed above, explicit physical definitions, including borders (here implemented in steps of half-degree squares), that allow GIS-based computation of system properties, such as mean depth, temperature, primary production, etc.

Another consideration is that our scheme for embedding LME and other subprovinces into BCGPs can be used as an ecological complement to the coarse stratification scheme used by the Food and Agriculture of the United Nations (FAO) to present global marine fisheries data, and which relies on 18 FAO statistical areas (7 for the Atlantic ocean, 3 for the Indian Ocean and 8 for the Pacific Ocean).

To facilitate comparisons between catch data stratified by these two schemes, we split the five circumpolar BCGP into ocean-specific subprovinces. This procedure enables 'closure' of the Atlantic, Indian and Pacific oceans and thus allows direct comparisons, at least at ocean-level scale, between catch data stratified within the scheme proposed here, and that used by FAO for its global catch database. Note that our next task, in this context, is to assign the catches in the

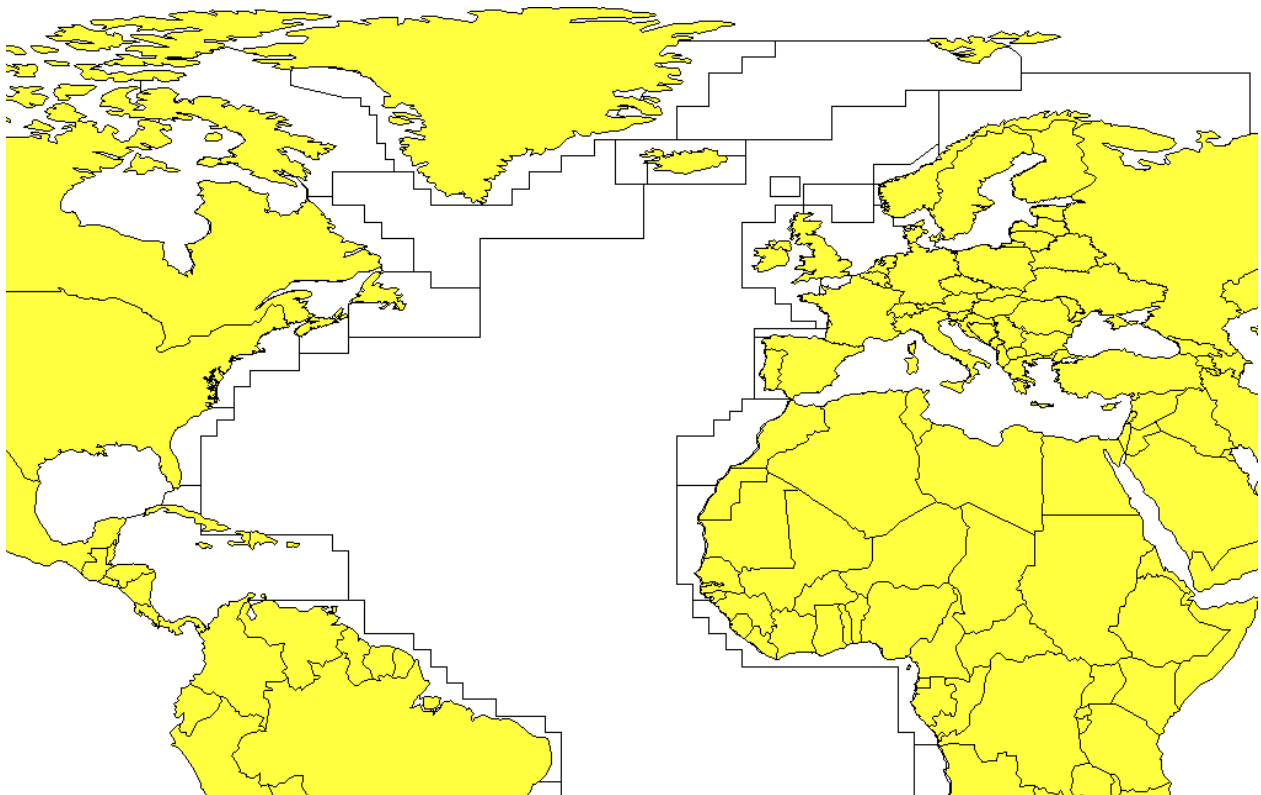


Figure 3. Map of the North Atlantic, illustrating how the LMEs identified for this basin (in Sherman and Duda 1999) can be identified with parts of biogeographical provinces (Figure 2). Note that some LMEs may be subdivided, and their subcomponents assigned to different provinces. Also note definition of various sub-provinces for areas not currently covered by LMEs).

global FAO data set to BGCP and sub-provinces (and/or LMEs), pending its gradual replacement, starting with the North Atlantic, by locally-derived data sets. Among other things, this will allow for rapidly arraying fisheries catches and related data for comparative analyses, i.e., data now usually assembled on an *ad hoc* basis (see e.g. Caddy et al. 1998, or Pauly et al. 1998a), at scales that are often inappropriate for the intended results.

EXCLUSIVE ECONOMIC ZONES

Allocating freshwater species and their catches to countries is straightforward, as the international borders of countries are usually well defined. This is more difficult in the marine realm, where the fishes and invertebrates caught off the coast of a given country may be caught outside its territorial waters. The International Law of the Sea provides, at least in principle, a solution to this, in form of Exclusive Economic Zones, usually reaching 200 miles into the open ocean, and linking countries with much of the productive areas, i.e., the shelves adjacent to their coasts.

However, not all countries have EEZ accepted by their neighbors, and in certain areas, such as the South China Sea, the same rocky outcrops are claimed by up to half a dozen countries (McManus 1992). It cannot be expected that this and similar situations in other parts of the world will be resolved soon, nor peacefully for that matter, and we cannot expect therefore, that official maps of the EEZ will appear that could be used for assigning fisheries catches to the countries of the world.

Nevertheless, various scholars, and institutions have published EEZ maps of various parts of the world (see e.g. Mahon 1987, for the Caribbean), based on the rules for definition of EEZ established by the Law of the Sea Convention (Charney and Alexander 1993). We propose that such maps can be used to derive a coherent single map for the EEZ of the world, especially if care is taken to incorporate into such map the delimitations so far agreed though bilateral or multilateral treaties (as compiled, e.g., in Charney and Alexander 1993).

The advantage of such map is that, unlike like the map of LME and provinces mentioned above, it will enable the assignment of fish and other species, and of fisheries catch statistics to *countries*. This will enable comparisons of various features of the use and productivity of various countries' EEZ, with enough degrees of freedom for multivariate analyses, as now routinely

performed for the land-based resources of various countries. It is clear, of course, that such a designation is unofficial and for scientific purposes only, and that it has no bearing, implicit or explicit, on the status of any disputes between sovereign nations about EEZ.

GLOBAL DISTRIBUTION OF CORAL REEF SYSTEMS

Coral reefs, though presently under threat throughout much of their range (Buddemeier and Smith 1999), support important fisheries wherever they occur (Munro 1996). However, quantifying these catches in reliable fashion has proven particularly difficult. One reason is that most countries with coral reefs are developing, with administrative infrastructures that preclude detailed monitoring of their fisheries.

As suggested by the pioneering work of Smith (1978), who performed the first analysis of this type, global assessment of present and potential fisheries yields from coral reefs would be much improved by comparative studies wherein the coral reef fish and invertebrate catches from various countries EEZ would be matched against the surface area of coral reefs within these same EEZ.

However, while it is possible to assign to coral reefs, at least roughly, a fraction of the catches of each country with reefs in the global FAO fisheries catch database, a matching set of coral reef area per country is not available, despite various global reviews of coral reefs (see e.g. Wells 1988; Polunin and Roberts 1996).

The model of Kleypas et al. (1999) can be used, however, to estimate expected coral reef area for any part of the world ocean with a well defined depth, temperature and light regime, and thus can be used to predict coral reef areas within each of the EEZ defined above. We anticipate, once this model becomes widely available, that plots of coral reef fish and/or invertebrate catches vs. reef area will allow us to identify countries with problematic catch data, and/or estimated reef areas, and thus to gradually improve the underlying databases and models.

SPATIAL EXPRESSION OF FISHERIES CATCH DATA

Fisheries catches are usually not reported on per-area basis (e.g. as $t \cdot km^{-2} \cdot year^{-1}$), though the areas from which they are derived are often specified. Maps of catch per area are rare, and indeed exist

only for local studies, often pertaining to single-species fisheries.

Thus, one additional reason for the hierarchical system proposed above is that would allow, and make worthwhile, consistent, basin-scale and ocean-wide mapping of catches onto the ecosystems from which they originate.

We anticipate the emergence of such maps, at the global level, from two successive steps:

- 1) Mapping the global FAO statistics onto their (presumed) ecosystem of origin, for each of the 18 FAO statistical areas, by half-degree square;
- 2) Improving the map in (1) through successive replacement, by LME, of the FAO data by local data sets.

As (1) is only to provide a 'default' map, i.e., the background for locally-enriched, presumably more accurate data sets, there seem no need to allocate massive resources to this step.

Our proposed approach therefore, is to proceed by successive 'subtractions', i.e., by first assigning fishes with clear affinities to certain LME, e.g. the anchoveta *Engraulis ringens* to the Humboldt Current LME, or the neritic fishes reported for Bangladesh to the Bay of Bengal LME, etc., each time subtracting the assigned fish groups from the database.

Several rounds of subtraction should quickly lead to small amounts of unallocated landings, pertaining mainly to fish landed in countries with distant water fleets (or providing flags of convenience to such fleets). Here, we assume that assigning the residual landings to the LME where these fleets are known to occur (see Bonfil et al. 1999 and references therein), in proportion to the catches per half-degree square previously allocated, would be sufficient for a first-pass allocation, especially since misallocations should generate visible patterns in the maps thus generated.

Note that this procedure, whose application to tunas would be very problematic, does not in fact need to be applied to this group, as Fontenau (1998), based on detailed catch data from ICCAT, IATTC, and IPTP, has already allocated global tuna catches to their BGCP of origin. Similarly, the fraction of fishes in the FAO database previously assigned to the coral reefs of different countries (see above) would not require this procedure, as they would have been previously subtracted, along with Fontenau's tunas.

Once (1) is completed, i.e., it will be straightforward to implement (2), i.e., to improve the maps for certain areas with better coverage than provided by the FAO catch statistics, e.g. the North Atlantic, where international data sets, from ICES and NAFO, and national data sets, from institutions such as DFO in Canada, NMFS in the USA, or IFREMER in France, are available.

ECOSYSTEM DESCRIPTION USING ECOPATH

The ECOPATH with ECOSIM (& ECOSPACE) modeling approach has been recently reviewed in several contributions (Christensen and Pauly 1992, Walters et al. 1997, 1999, Pauly et al. 2000, Christensen and Walters, 2000), and there is no need here to present its working or outputs.

ECOPATH models exist for numerous parts of the world (details in www.ecopath.org), including the North Atlantic. Currently, well over 100 models have been published, and more than 1800 colleagues in nearly 100 countries have registered as users of the ECOPATH software system.

However, the ecosystem model coverage of various ocean basins is still spotty at best, hence precluding simple raising of flows and rates from ecosystem to basin scales. Thus, a stratification scheme is required, based on the geographic structure outlined above, and which can be used to scale models from the sampling area of the field data used to parameterize the models to the wider area that is assumed represented by these same models. The strata for the North Atlantic are presented in Figure 4.

LMEs (and other subprovinces) are seen here as providing the key level for ecosystem model construction. For each LME, an Ecopath model must be constructed to describe the ecosystem resources and their utilization, and to ensure that the total fisheries catch of each LME is used as output constraint (just as their primary production will be used as input constraint). In addition, our stratification scheme must be such that it can straightforwardly accommodate any number of additional ECOPATH models for each LME. This can be done so as to simultaneously address the issue of parameter uncertainty, as briefly described below.

The LME ECOPATH models require information on abundance, production and consumption rates and diets for all ecosystem groupings. Such information can be obtained from the following sources:

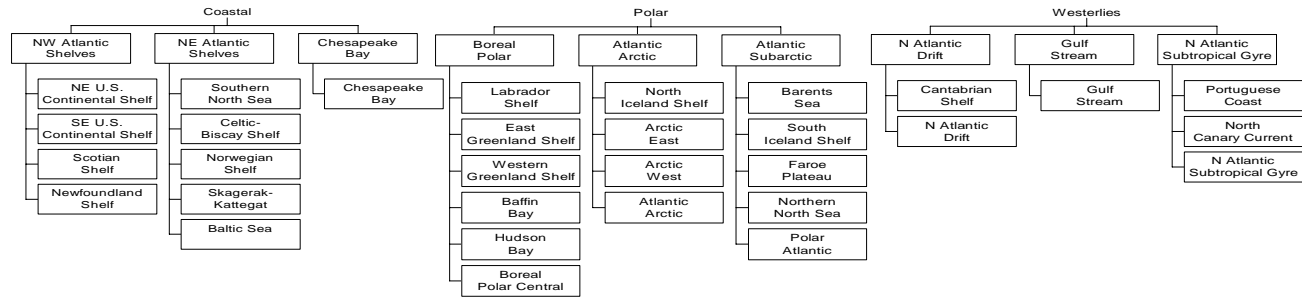


Figure 4. Proposed hierarchy of biomes, biogeochemical provinces and LME/subprovinces in the North Atlantic. Note implicit stratification, for use when, e.g., scaling up, from part of an LME, to basin or ocean-wide estimates; see also Figure 3).

- Abundance, production and consumption rates, and diets of marine mammals are available from the Sea Around Us database for all (117) species of marine mammals (see also Pauly et al 1998b, Trites and Pauly 1998);
- Fishery catches: available from the spatially structured catch database generated as described above, and covering all species groups;
- Occurrence, biology and ecology of marine fishes: soon to be available from FishBase (www.fishbase.org), presently available both at the BGCP level, and the LME/subprovince level as well. The relevant FishBase search routine option in question was designed for optimizing extraction of ECOPATH-relevant information, and is a result of the ongoing cooperation between FishBase and *Sea Around Us projects*;
- For marine invertebrates: only limited information (beyond the catches in the FAO database) is available from electronic databases, but a variety of publications provide extensive information. Production rates can be estimated from the well-founded empirical relationships of Brey (1999), now included in ECOPATH;
- Primary production estimates: establishment of a global database aimed at supplying fine grid level satellite based estimates of primary production is presently underway through a cooperation between the Space Applications Institute, EC Joint Research Centre, Ispra, Italy, and several authors of the present contribution.

The origin of each set of data (5 rate or state variable for each of the often 20-40 functional group in a model, plus a diet matrix) can be

described and a related confidence interval assigned to each of the input parameters. Confidence intervals can also be estimated, as 'posterior distributions' for the output parameters of models. In addition a module of ECOPATH is designed to describe the 'pedigree' of ECOPATH models, i.e., the degree to which the models are rooted in locally sample and reliable data, (described in more details by Christensen and Walters, 2000). This module estimates, based on the pedigree of its input data, an overall quality index for each model, which in turn can serve as weighting factor, as required when dealing with discrepancies (e.g. between local vs. LME-wide catches), i.e., when raising one or several model(s) to the LME/subprovince level.

The LME/subprovince-level ECOPATH models will thus make up the backbone of our approach for addressing province, basin and global issues related to abundance, productivity, interaction and impact for ecosystem resources e.g., by trophic levels. Being based on the best available estimates of productivity and utilization of the upper trophic levels, and on productivity for the primary producers, the models are constrained from the top as well as from below.

Where possible the LME-level models will be supplemented with additional models. The procedure for this is:

- New models are assigned to strata, based on the proportion of area covered that falls within each of the depth strata < 10 m, 10-50 m, 50-200 m, 200-1000 m, and > 1000 m;
- For each new model, the confidence intervals of input and output parameters are estimated along with the pedigree index of the model;
- The LME/subprovince-level model is assigned to depth strata based using weights based on the relative primary productivity in each of the depth strata;

- Within each of the depth strata productivity, abundance, etc., are raised to the LME/subprovince level using the quality index of the models as weighting factors for the associated confidence intervals.

With this structure in place, it will be easy to add new models as they become available, and it is feasible to assign confidence intervals to all estimates derived from the analysis.

CONCLUSIONS

The ecosystem classification proposed here is not meant as a panacea that will solve all our biogeographical problems, or all spatial problems of fisheries. It should not be necessary to stress this; however, it is likely that some readers will think we believe it. We don't. However, we know that no telephone registry would ever emerge, if regular debates were held as to the optimal way to arrange the letters in the alphabet.

The ecosystem classification proposed here will soon be implemented globally by FishBase, which will thus assign all marine fish species so far described to their LME(s) or subprovince(s). It will also be used to give a geographic structure to an unofficial, spatialized, version of the FAO database of global fisheries catches (see above), thus complementing the atlas of tuna catches compiled by Fonteneau (1998), and allowing both to be related to estimates of primary production for example, mapped in similar fashion by Longhurst et al. (1995).

Moreover, this classification is fully compatible with the LME approach of Sherman and co-workers, which has led to an extensive documentation of management issues at LME scale (see references in Sherman and Duda 1999), and a number of field projects designed to address these issues, funded by various international granting agencies.

Thus, we invite colleagues to join us in expressing their results using the classification and definitions proposed here. To support this collaboration, we will supply, via the Internet, tables presenting the details of the classification by half-degree squares.

ACKNOWLEDGMENTS

The members of the *Sea Around Us* Project thank the Pew Charitable Trusts for their support of the work leading to this contribution. Also, the first author acknowledges support of a grant from the

Canadian National Science and Engineering Research Council.

REFERENCES

- Anon. (1991) *Bartolomew Illustrated World Atlas*. Harper Collin, Edinburgh.
- Bonfil, R., Munro, G., Sumaila, U.R., Valtysson, H., Wright, M., Pitcher, T., Preikshot, D., Haggan, N. and Pauly, D. (1998) *Impacts of distant water fleets: an ecological, economic and social assessment*. pp. 11-111 In: *The footprint of distant water fleet on world fisheries*. Endangered Seas Campaign, WWF International, Godalming, Surrey, 111 pp.
- Brey, T. (1999) A collection of empirical relations for use in ecological modelling. *Naga*, the ICLARM Quarterly, 23(3), 24-28.
- Buddemeier, R.W. and Smith, S.V. (1999) Coral adaptation and acclimatization: a most ingenious paradox. *Amer. Zool.* 39:1-9.
- Caddy, J.F., Carocci, F. and Coppola, S. (1998) Have peak fishery production levels been passed in continental shelf areas? Some perspectives arising for historical trends in production per shelf area. *J. North Atl. Fish. Sci.* 23, 191-219.
- Charney, J.I. and Alexander, L.M.A. (eds) (1993) *International Maritime Boundaries*. The American Society of International Law. Kluwer, Dordrecht.
- Christensen, V. and Pauly, D. (1992) The ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61, 169-185.
- Christensen, V. and Walters, C.J. (2000) Ecopath with Ecosim: Methods, capabilities and limitations In: Pauly, D. and Pitcher, T.J. (eds) *Methods for evaluating the impacts of fisheries on North Atlantic ecosystems*. *Fisheries Centre Research Reports* 8(2), 79-105.
- Ekman, S. (1967) *Zoogeography of the Sea*. Sidgwick and Jackson, London, 417 pp.
- Fonteneau, A. (1998) *Atlas of tropical tuna fisheries*. Edition ORSTOM, Paris.
- Froese, R. and Pauly, D. (eds) *FishBase 2000: Concepts, Design and Data Sources*. *ICLARM*. [see www.fishbase.org]
- Golley, F.B. (1993) *A history of the ecosystem concept in ecology: more than the sum of its parts*. Yale University Press, New Haven and London, 254 pp.
- Grassle, J.F. and Stocks, K.I. (1999) A global ocean biogeographic information system (OSIS) for the Census of marine life. *Oceanography* 12(3), 12-16.
- Grove, J.S. (1985) Influence of the 1982-1983 El Niño event upon the ichthyofauna of the Galápagos archipelago. In: G. Robinson and del Pino, E.M. (eds.) *El Niño in the Galápagos Islands: the 1982-1983 event*. Publication of the Charles Darwin Foundation for the Galápagos Islands, Quito, 191-198.
- Grove, J.S. and Lavenberg, R.J. (1997) *The Fishes of the Galápagos Islands*. Stanford University Press, Stanford, 863 pp.
- Kleypas, J.A., McManus, J.W. and Meñez, L.A.B. (1999) Environmental limits to coral reef development: where do we draw the line? *Amer. Zool.* 39, 146-159.
- Levin, S.A. (1990) Physical and biological scales and the modelling of predator-prey interactions in Large Marine Ecosystems. In: K. Sherman, K., Alexander, L.M. and Gold, B.D. (eds) *Large Marine Ecosystems: patterns, processes and yields*. *Amer. Ass. Adv. Sci.* Washington, D.C., 179-187.
- Longhurst, A.R. (1995) Seasonal cycles of pelagic production and consumption. *Progress in Oceanography* 36, 77-167.

- Longhurst, A.R. (1998) *Ecological Geography of the Sea*. Academic Press, San Diego. 398 pp.
- Longhurst, A.R., Sathyendranath, S., Platt, T. and Caverhill, C.M. (1995) An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research* 17, 1245-1271.
- Mahon, R. (ed). (1987) Report and Proceedings of the Expert Consultation on Shared Fishery Resources in the Lesser Antilles. *FAO Fish. Tech. Pap.* 383, 278 pp.
- McManus, J. (1992) The Spratley Islands: a marine park alternative. *NAGA, the ICLARM Quarterly* 15(3), 4-8.
- Munro, J.L. (1996) The scope of coral reef fisheries and their management. In: Polunin, N.V.C. and Roberts, C.M. (eds) Reef Fisheries. Chapman & Hall, London, 1-14.
- NRC (1999) *Sustaining Marine Fisheries. National Research Council*. National Academy Press, Washington, D.C. 164 pp.
- Pauly, D. (1998) Tropical fishes: patterns and propensities. In: Langford, T.E., Langford, J. and Thorpe, J.E. (eds) Tropical Fish Biology. *J. Fish Biol.* 53 (Suppl. A), 1-17.
- Pauly, D. (1999) Review of A. Longhurst's "Ecological Geography of the Sea." *Trends in Ecology and Evolution* 14(3), 118.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Torres, F.C. Jr. (1998a) Fishing down marine food webs. *Science* 279, 860-863.
- Pauly, D., Trites, A., Capuli, E. and Christensen, V. (1998b) Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science*. 55, 467-481.
- Pauly, D., Christensen, V. and Walters, C.J. (2000) Ecopath, Ecosim and Ecospace as tools for evaluating the ecosystem impact of fisheries. *ICES J. Mar. Sci.* 57, 697-706.
- Polunin, N.V.C. and Roberts, C.M. (eds). *Reef Fisheries*. Chapman & Hall, London, 477 pp.
- Platt, T., Caverhill, C.M. and Sathyendranath, S. (1991) Basin-scale estimates of oceanic primary production by remote sensing: the North Atlantic. *Journal of Geophysical Research* 96, 15147-15159.
- Platt, T. and Sathyendranath, S. (1988) Oceanic primary production: estimation by remote sensing at local and regional scales. *Science* 241, 1613-1620.
- Platt, T. and Sathyendranath, S. (1999) Spatial structure of pelagic ecosystem processes in the global ocean. *Ecosystems* 2, 384-394.
- Platt, T., Sathyendranath, S., Ulloa, O., Harrison, W.G., Hoepffner, N. and Goes, J. (1992) Nutrient control of phytoplankton photosynthesis in the Western North Atlantic. *Nature* 356, 229-231.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. and Wall, D.H. (2000) Global Biodiversity Scenarios for the Year 2100. *Science* 287, 1770-1774.
- Sathyendranath, S. and Platt, T. (1993) Remote sensing of water-column primary production. *ICES Mar. Sci. Symp.* 197, 236-243.
- Sathyendranath, S., Platt, T., Caverhill, C.M., Warnock, R.E. and Lewis, M.R. (1989) Remote sensing of primary production: computations using a spectral model. *Deep-Sea Research* 36, 431-453.
- Sherman, K., Alexander, L.M. and Gold, B.D. (eds). (1990) *Large marine ecosystems: patterns, processes and yields*. Amer. Assoc. Adv. Sci. Washington D.C. 242 pp.
- Sherman, K., Alexander, L.M. and Gold, B.D. (eds). (1993). *Stress, mitigation and sustainability of large marine ecosystems*. Amer. Assoc. Advan. Sci., Washington D.C., 376 pp.
- Sherman, K. and Duda, A.M. (1999) An ecosystem approach to global assessment and management of coastal waters. *Marine Ecology Progress Series*. 190, 271-287.
- Smith, S.V. (1978). Coral reef area and the contribution of coral reefs to processes and resources of the world's ocean. *Nature* 273, 225-226.
- Sverdrup, H.U. (1953) On the conditions for vernal blooming of the phytoplankton. *J. Cons. Perm. Int. Explor. Mer.* 18, 287-295.
- Trites, A. and Pauly, D. (1998) Estimates of mean body weight of marine mammals from measurements of maximum body length. *Can. J. Zool.* 76, 886-896.
- Walters, C., Christensen, V. and Pauly, D. (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fish.* 7(2), 139-172.
- Walters, C., Pauly, D. and Christensen, V. (1999) Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2, 539-554.
- Wells, S.M. (ed) (1988) *Coral Reefs of the World*. International Union for the Conservation of Nature, Gland, and United Nations Environment Programme, Nairobi. 3 Volumes.