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Megaregions among the large marine ecosystems of the Americas

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ABSTRACT

We organized environmental observations (Sea Surface Temperature, chlorophyll concentration, and primary productivity) and biological diversity indices based on reconstructed fisheries landings obtained from the *Sea Around Us* project to address two objectives: 1) to understand whether adjacent Large Marine Ecosystems (LMEs) of the Americas form megaregions for assemblages of commercially-valuable fish; and 2) to assess changes in the diversity of fisheries landings in LMEs of the Americas over time (1982 to 2010). To test for similarities between LMEs, we used the seascape approach of unsupervised clustering of annual mean environmental observations and fisheries-derived diversity indices. Beta-diversity estimates based on fisheries landings were used to evaluate the degree to which species spanned LMEs. Temporal trends were computed for each dataset by linear least-squares. Three megaregions emerged when considering similarities in species composition of fisheries landings, fisheries-derived diversity indices, and characteristic environmental conditions among LMEs. These include (A) the South Brazil Shelf, East Brazil Shelf, and North Brazil Shelf LMEs, (B) the Gulf of Mexico and Southeast U.S. Continental Shelf LMEs, and (C) the Northeast U.S. Continental Shelf, Scotian Shelf, and Newfoundland-Labrador Shelf LMEs. No megaregions emerged for the Pacific Ocean. While there were some shared species assemblages between the California Current and the Gulf of Alaska, the Gulf of California, and the Pacific Central-American Coastal LMEs, these showed different average environmental conditions and fishery-derived diversity indices, so they did not cluster as a megaregion. In the Pacific Ocean, the high dissimilarity in the fisheries is in part related to different top-down pressures and strong regional differences in oceanographic properties, including upwelling and impacts of El-Niño Southern Oscillation events. Overall, between 1982 and 2010, seven LMEs diversified their fisheries (Pacific Central-America Coastal, Patagonian Shelf, South Brazil Shelf, East Brazil Shelf, North Brazil Shelf, Southeast U.S. Continental Shelf, and Newfoundland-Labrador Shelf). This may be due to a number of reasons including decreasing fishing pressure but expansion of target stocks due to management quotas, changes in regional markets, competition, effort, or a decrease in particular target stocks. Three LMEs showed increasingly less diversified fisheries, namely the California Current, the Northeast U.S. Continental Shelf, and the Caribbean Sea LMEs. While in some cases this may be related to historical overfishing, such as in the Northeast U.S. Continental Shelf LME, the California Current LME has been subjected to strong and conservative management practices. The Caribbean Sea LME was likely subjected to heavy fishing at a time of rapid environmental change.

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1. Introduction

The health and economy of nearly 50% of humanity depends on uses of marine resources in the Exclusive Economic Zone (EEZ) of coastal nations. While in 2013 fisheries satisfied about 20% of the protein needs of the population in developing nations and 18% in "low-income food-deficit countries", these percentages have been growing (FAO, 2016). In industrialized countries this percentage is of the order of 11%, as consumption of other animal proteins continues to grow (FAO, 2016). These figures represent diverse fisheries efforts that contribute to the economies of coastal nations around the world.

Living marine resources located in the EEZ of coastal nations are at the core of several of the 17 Sustainable Development Goals (SDG) adopted by the United Nations in September 2015 (UNGA, 2015). Addressing the SDG's requires scientific information on the status and trends of the ecological condition of the world's large marine ecosystems (LMEs; Sherman et al., 2005; Sherman and Hamukuaya, 2016). Specifically, SDG 6 (availability and sustainable management of water), SDG 13 (combating climate change and its impacts), and SDG 14 (sustainable use of marine resources for sustainable development) are closely intertwined. They are relevant to SDG's that seek to end hunger and poverty, address education, and foster economic growth. The present study evaluates emergent patterns in the diversity in fisheries landings within LMEs of the Americas, in the context of marine dynamic seascapes that undergo continuous changes (Oliver and Irwin, 2008; Kavanaugh et al., 2014, 2016). We focused on LMEs because these are based on ecological criteria (bathymetry, hydrography, productivity, and trophic linkages). The LMEs have been used since 1984 as a practical framework to assess and manage coastal ocean goods and services based on indicators of changing states of LME productivity, fish and fisheries, pollution and ecosystem health, socioeconomics, and governance (Duda and Sherman, 2002; Sherman and Hempel, 2008; Sherman, 2014a, 2014b).

Marine biodiversity is at the core of productivity and resiliency of these ecosystems. The LMEs, which are largely contained in the EEZs of nations, show changes in their biogeographical seascapes due to impacts of climate change and the multiple uses of resources (Halpern et al., 2012; IPCC, 2013, 2014; Melillo et al., 2014). Understanding whether ecosystem processes are more sensitive to bottom-up controls, like those that would be due to temperature changes, or top-down controls (like fisheries) requires observations that can discriminate between decadal and longer variations from seasonal variability (Doney et al., 2009; Muller-Karger et al., 2010; Chavez et al., 2011; Taylor et al., 2012; Deutsch et al., 2015). Policy should be based on scientific knowledge collected through rigorous fishery independent and fisheries dependent observation programs, in order to facilitate assessments of

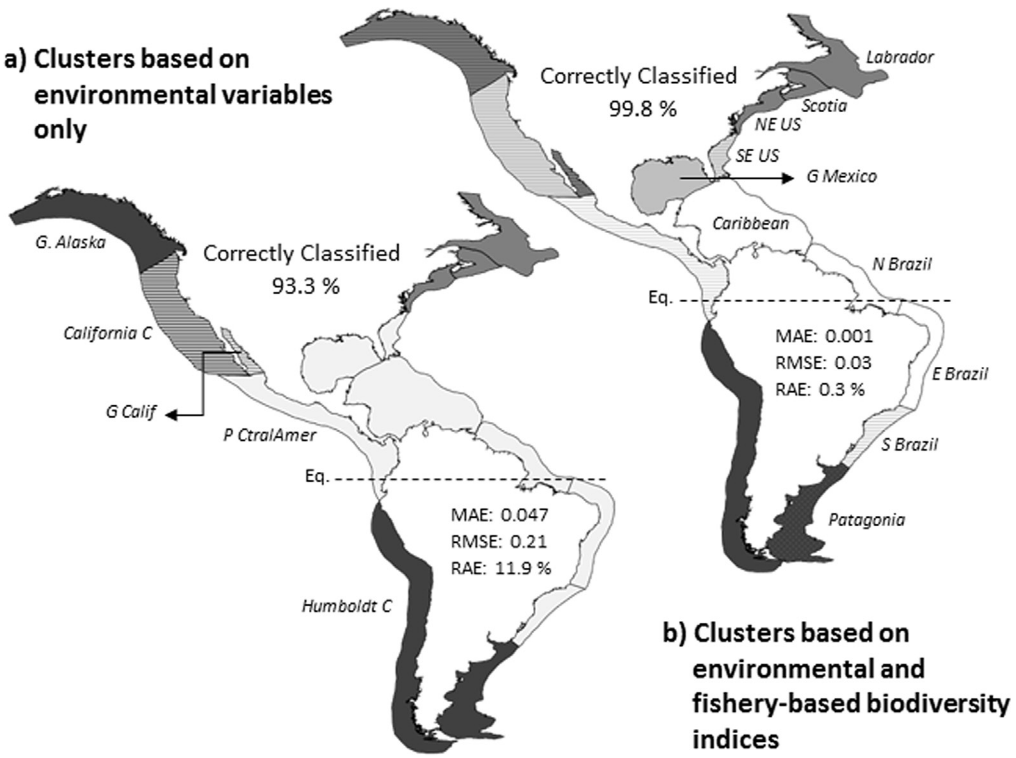

Fig. 1. Clustering of the Large Marine Ecosystems (LME) of the Americas. (a: left) Three LME clusters. were obtained based only on environmental variables (SST, chlorophyll-a concentration, primary productivity averages and corresponding standard deviations) (Clusters: high-latitude LMEs of the North Atlantic; high-latitude LMEs of the Pacific Ocean, both north and south, and the Patagonian Shelf in the Atlantic Ocean; and the tropical and mid-latitude LMEs of the Pacific and the Atlantic Ocean). (b) Four LME clusters were obtained based on environmental and fishery-based biodiversity variables (biodiversity indices including richness, dominance, evenness and diversity corrected for rarefaction). Shortened LME names are shown in italic (see Table 1). The percentage of Correctly Classified Instances is shown for each model, as well as the clustering error evaluation with Mean Absolute Error (MAE), Root Mean Square Error (RMSE), and Relative Absolute Error (RAE).

changes in living resources in Exclusive Economic Zones (EEZ). This can be addressed by an operational Marine Biodiversity Observation Network (MBON; Duffy et al., 2013; Muller-Karger et al., 2014). The MBON approach is to develop a global network of experts in biodiversity and of observing systems focused on life in the sea. It seeks to build capacity and engage scientists and operational agencies in integrated and collaborative data collection efforts. The goal is to understand the status and changing trends of living resources in coastal and marine areas.

In this study we organize a series of disparate environmental observations and evaluate the diversity of fisheries landings within the LMEs of the Americas to demonstrate the utility of an MBON. We combined observations from a range of technologies, from satellite remote sensing to fisheries landings statistics, to address two primary objectives. One objective was to understand whether adjacent LMEs of the Americas (Fig. 1) show similar patterns of environmental diversity and whether such variability allows broader ranges of fish distribution between LMEs. A second objective was to assess changes in the LMEs of the Americas over time.

At this stage, there are very few fisheries-independent studies of the scale of LMEs. Fishery landings data reflect ecological, economic, technological, and social factors. One way to compare LMEs is to evaluate differences in the type and amount of fisheries landings between LME. Also, if the diversity of landings from an LME changes over time, this may reflect a change in the physical and biological factors within the LME (bottom up pressures) or top-down pressures (changes in fisheries pressure), or both.

We used fisheries landings data compiled by the *Sea Around Us* project. Fishery catch data from the Food and Agriculture Organization of the United Nations (FAO) are based solely on 'reported catches' disclosed by national authorities. Often, these don't reflect the full extent of fishery exploitation. The FAO data may underestimate fishery catch from different countries by 30 to over 100% (Pauly and Zeller, 2016). The *Sea Around Us* project reconstructs catch data and amends some of the shortcomings of the FAO fisheries statistics including catch underestimation, unreported taxa, omission of subsistence, recreational and illegal fishing, omission of discarded bycatch, and other inaccurate reporting, in addition to taxonomic over-aggregation of catches reported to FAO (Tsikliras et al., 2007; Garibaldi, 2012; Zeller and Pauly, 2005, 2016). Fishery-derived diversity indices incorporate the uncertainties of fishery statistics, and they are subject to the influence of social, economic, and technological factors imposed on fisheries. Yet, since one of the goals of the LMEs is to help assess fisheries resources, aggregating data using ecological indices based on fisheries landings is simply a useful tool to compare LMEs of the Americas.

The study complements the fishery production potential of LMEs of Fogarty et al. (2016) and Bianchi et al. (2016). We examined the status and trends of the diversity and quantity of fish landed (i.e. the highest levels of the food web) in the context of phytoplankton concentration and productivity at the lowest levels of the food web. These variables were considered given the warming trend of the upper ocean over time (Huang et al., 2015; IPCC, 2013), including in LMEs around the world (Sherman et al., 2007; Gamito et al., 2015). The results of our study help understand how food webs in adjacent LMEs may be connected by environmental factors and how they share fisheries resources. We tested the possibility that adjacent LME may show similar environmental variability and diversity of fisheries, thus constituting 'megaregions'. LMEs in such megaregions may more easily serve as a source of diversity and resiliency to sustain the health of an adjacent LME over time. These concepts are part of an effort to help understand biodiversity patterns in the ocean and how these may be changing. This is also the core objective of the MBON.

2. Materials and methods

2.1. Study area

We analyzed fifteen contiguous Large Marine Ecosystems (LME) around the Americas, from the Gulf of Alaska LME in the Pacific Ocean to the Newfoundland-Labrador Shelf LME in the Atlantic Ocean (Table 1). We did not include the LME of the high Arctic in this study because the satellite data used to evaluate environmental conditions is sparse in that region. The spatial boundaries of the LMEs were obtained as GIS shape files from the NOAA LME website (http://www.lme.noaa.gov/; accessed in July 2016). We

Table 1
Large Marine Ecosystem number and names (as per http://www.lme.noaa.gov/), and the short name used in the figures.

Number	Official Name	Short Name
LME 2	Gulf of Alaska	G Alaska
LME 3	California Current	California C
LME 4	Gulf of California	G Calif
LME 5	Gulf of Mexico	G Mexico
LME 6	Southeast U.S. Continental Shelf	SE US
LME 7	Northeast U.S. Continental Shelf	NE US
LME 8	Scotian Shelf	Scotia
LME 9	Newfoundland-Labrador Shelf	Labrador
LME 11	Pacific Central-American Coastal	P CtralAmer
LME 12	Caribbean Sea	Caribbean
LME 13	Humboldt Current	Humboldt C
LME 14	Patagonian Shelf	Patagonia
LME 15	South Brazil Shelf	S Brazil
LME 16	East Brazil Shelf	E Brazil
LME 17	North Brazil Shelf	N Brazil

recognize that marine seascapes are dynamic, and that their boundaries shift on seasonal and interannual scales (e.g. Oliver and Irwin, 2008; Kavanaugh et al., 2014, 2016). However, an important first step is to validate and compare these patterns using the historical LME framework. The results are intended to guide subsequent studies on the benefits of using seascapes.

2.2. Fishery data and fisheries diversity indices

'Reconstructed' annual catch data from 1950 to 2010 within LME boundaries were obtained from the *Sea Around Us* project (Pauly, 2007; Pauly and Zeller, 2015; Zeller et al., 2016). Marine fisheries catch data from the *Sea Around Us* combine official reported catch data and reconstructed estimates of unreported catches including major discards for species by analyzing additional available sources of fisheries, socio-economic and population data (Zeller and Pauly, 2015). For each LME, we integrated the catch data from the *Sea Around Us* in each LME, i.e. adding catches from all countries, sectors, and catch type (i.e. 'fishing_entity'; 'fishing_sectors' whether industrial, artisanal, subsistence, or recreational); 'catch_type' whether landings or discards; and 'reporting_status' in terms of reported or unreported. We think that the reconstructed landings data provide more realistic values of the catch landing and, especially, of the species composition.

We calculated a suite of fisheries diversity indices based on the reconstructed fisheries landing levels, including measures such as richness, diversity, dominance, and evenness corrected for rarefaction based on fisheries species composition and abundance (Table 2). Total annual catch (tons) was used as the sample size (N). Annual catch in tons per species was used as the 'number of individual' per species (N_i). Rarefaction (Hurlbert, 1971) was computed to standardize unequal sampling size (i.e. catch size for each LME). This is useful to correct richness indices, which are sensitive to sampling effort. In order to correct for rarefaction, the proportional abundance of species (i.e. N_i or tons caught per species) was normalized by the sample size of the smallest annual total catch (all species combined) in the Americas time series of LMEs. The three richness indices behaved similarly for each LME after the rarefaction correction (Fig. 2). The smallest annual catch reported was that for the East Bering Sea in 1953 (47,682 t). Beta-diversity, or a measure of the difference in species composition of fisheries landings between regions, was calculated between pairs of LMEs following Wilson and Shmida (1984) and Koleff et al. (2003) (Table 2).

2.3. Environmental variables

Environmental conditions within LME boundaries were evaluated using time series of satellite-derived observations. Specifically, given that we worked with annual fisheries catch data, we derived annual means of Sea Surface Temperature (SST), chlorophyll-a concentration estimates, net primary productivity and their respective standard deviations for each LME, as described below. At present there are limited time series of water column hydrographic, biogeochemical, and biological observations, particularly at the scale of entire LMEs. Satellite observations reflect only conditions at the ocean surface, but they provide a first-order, synoptic measure of biogeographic changes in the ocean.

SST series were derived from daily satellite observations spanning 1982–2012, but the data were used only through 2010 (28 years) to match the most recent year available for the *Sea Around Us* fisheries records. SST was derived from the Advanced Very High Resolution Radiometer (AVHRR) Pathfinder Version 5.2 (PFV5.2) dataset. Data extracted for each LME were arithmetically averaged in space and over time to first monthly means, and then averaged in time to obtain annual means and standard deviations based on the monthly means. Data were obtained from the U.S. National Oceanographic Data Center (NODC, now National Centers for Environmental Information or NCEI) and the Group for High Resolution Sea Surface Temperature (GHRSST) (http://pathfinder.nodc.noaa.gov; Casey et al., 2010). The Pathfinder v5.2 dataset has a gap, from October 2, 1994 to January 17, 1995.

Table 2
Diversity indices computed based on fishery catch statistics from the *Sea Around Us* project.

Richness	(S) number of species caught per year
Total_tons	(N) total annual catch in tons per LME
	(N_i)= annual catch in tons per species per LME
sum_p_i^2	$p_i^2=\Sigma(N_i/N)^2$
Rich_Marg	(S−1)/ln(N), Margalef
Rich_Menh	S/sqrt(N), Menhinick
Div_Shann	- Σ (p_i * ln(p_i)), Shannon diversity
Div_Simp	1- Σ(p_i^2), Simpson diversity
Div_Simp_inv	1 / Σ(p_i^2), Simpson diversity inverse
Even_Shann	Div_Shann / log(S), Shannon evenness
Even_Simp	Div_Simp / S, Simpson evenness
Even_Simp_inv	Div_Simp_inv / S, Simpson inverse evenness
Dom_abs	max(N), Absolute dominance
DomRel	max(p_i), Relative dominance
Dom_mcNaught	(pi (1st)+pi (2nd))*100, McNaughton dominance: with the two most dominant species
Beta-Diversity	(b + c) / (2a + b + c), following Wilson & Schmida (1984) and re-expresed by Koleff et al. (2003)a = number of species shared between the pair of areas 1 and 2; b and c = number of species of areas 1 and 2 minus the shared species (a)

All the diversity indices were calculated from rarefied tons (Hurlbert, 1971) by the minimum number of N (tons) for the whole time series (47,682 t in the East Bering Sea, in 1953).

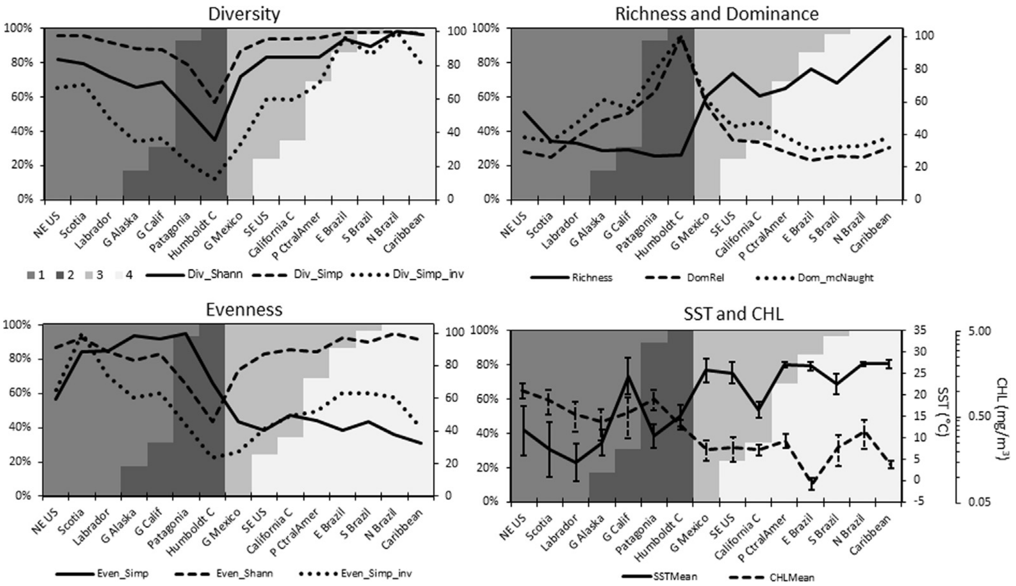

Fig. 2. Clustering of the Americas LMEs based on the environmental and fishery diversity variables (see groups in Fig. 1b). At the narrowest classification overlap (smallest percentage in all panels), four broad LME clusters were identified (1: Northwest Atlantic, 2: High latitudes, 3: Subtropical latitudes, 4: Tropical latitudes). LMEs were ordered by their relative proportion in the cluster composition results. Lines show long-term averages of fisheries diversity indices for the different LMEs (standardized by rarefaction and shown here as percentages), and characteristic long-term annual average SST and chlorophyll concentration. Rarefied Richness was similar for the three fisheries species richness indices calculated (see Table 2).

Chlorophyll-a concentrations (CHL, 1996–2014) were derived from merged data from five ocean color sensors (OCTS, SeaWiFS, TERRA MODIS, AQUA MODIS, and MERIS). Again, data were used only through 2010 to match the fisheries records. Monthly averages of all observations within an LME were computed as geometric means, i.e. based on the mean of log-transformed chlorophyll-a data. The annual means and standard deviations were also computed based on the log-transformed data. An inverse log (anti-log) was applied to obtain final chlorophyll concentration values. Euphotic zone integrated net primary productivity (PP, 1997–2014) was derived using an algorithm based on the “Ocean Production from the Absorption of Light” (OPAL) model of Marra et al. (2003); see also O’Reilly and Sherman (2016). The model comparisons conducted by Carr et al. (2008) show that the OPAL model gives results comparable to those from the Behrenfeld and Falkowski (1997) model using the Eppley temperature function for the Assimilation Number computation. The annual averages for NPP are arithmetic means of the monthly observations within the LME boundaries. The PP time series was processed in a consistent manner and is used to compare the characteristics of different LMEs. Only data through 2010 were used in the analyses to match the fisheries records. Both the merged chlorophyll and the primary productivity data sets were provided by John O’Reilly from the NOAA National Marine Fisheries Service (NMFS). These data were generated by the NMFS as part of an effort to provide reliable environmental information in usable formats for LME studies, in response to requirements of the United Nations Environment Programme (UNEP).

2.4. Statistical analysis: trends and clusters

To test for possible ecological similarities between LMEs, we used the seascape approach (Kavanaugh et al., 2016). Two major analyses were run including all LMEs using unsupervised clustering with the k-means algorithm and Euclidean distance. One analysis focused only on the environmental variables (i.e. SST, Chl-a, PP, and their respective standard deviations), and one in which the environmental variables and the fishery-derived diversity indices for each LME were considered together. We applied the clustering algorithms taking full advantage of the coincident SST and fisheries landings data (i.e. the period 1982–2010); for the period spanning 1982–1996, when satellite ocean color data were not available, we used the long-term annual mean and standard deviation of the chlorophyll concentration and primary production numbers calculated with data from 1997 to 2010. The classification analysis was conducted with the Weka open-source data mining software from the University of Waikato (Hall et al., 2009).

We computed temporal trends by linear least-squares analyses of each annual average environmental fisheries catch, fisheries diversity index, and SST against time (year). We report the correlation coefficient (r) to preserve the sign of the trend (positive is increasing in time, negative is decreasing in time), and as a measure of the strength of that trend.

3. Results and discussion

3.1. Environmental and ecological patterns in the LMEs

The similarity analysis based on environmental variables yielded three separate clusters of LMEs around the Americas (Fig. 1a). Cluster 1 encompassed the group of high-latitude LMEs of the North Atlantic. Cluster 2 grouped together the high-latitude LMEs from the Pacific Ocean (both north and south) and the Patagonian Shelf in the Atlantic Ocean. Cluster 3 comprised the tropical LMEs of the Pacific and the tropical and subtropical LMEs of the Atlantic Ocean, including the Caribbean Sea and the Gulf of Mexico. These groups were largely defined by latitudinal gradients of SST and CHL, and differences in SST and CHL variability. In comparison, PP had only a marginal contribution to the clustering and therefore was not used further in the analyses. We did not consider the similarities between regions in different oceans to have physical meaning in terms of ecological connectivity, since these similarities simply mean that there are similar patterns of temporal variability in some environmental variables.

The analysis run with both the environmental variables and fisheries diversity indices revealed four separate LME clusters (Figs. 1b and 2). The high-latitude LMEs of the North Atlantic were again grouped together (cluster 1: Northeast U.S. Continental Shelf, Scotian Shelf, and Newfoundland-Labrador Shelf LMEs). Those at higher latitudes in the South Atlantic and South Pacific were grouped together (cluster 2: Patagonian Shelf LME and Humboldt Current LME). The Gulf of Alaska and the Gulf of California LMEs showed characteristics of cluster 1 and, to a lesser degree, of cluster 2 (Fig. 2). Tropical and subtropical LMEs were separated into two clusters. The Gulf of Mexico and the Southeast U.S. Continental Shelf LMEs shared substantial environmental and fisheries diversity characteristics (cluster 3; Figs. 2 and 3). The Caribbean Sea, the North Brazil Shelf, the East Brazil Shelf, and the South Brazil Shelf LMEs were also grouped together (cluster 4).

The high-latitude LME clusters (i.e., clusters 1 and 2) showed the lowest average SST and the highest chlorophyll (Fig. 2). The high-latitude North Atlantic LMEs together showed high interannual SST variability and high species diversity and evenness compared to those of the high-latitude southern hemisphere (Fig. 2). The tropical and subtropical LMEs of the Atlantic Ocean, which formed one cluster based on environmental characteristics (Fig. 1a), were separated into two clusters when fisheries diversity was considered (clusters 3, 4, and mixed clusters; Figs. 1b and 2). These showed the highest SST, very low interannual SST variation, and very low chlorophyll concentrations. They both show high fisheries richness, but were separated ecologically by a higher diversity in cluster 4.

Clusters tended to show unique combinations of diversity indices. The North Atlantic high-latitude cluster showed higher mean fisheries diversity and evenness with low dominance of species compared to the southern hemisphere high-latitude cluster (Fig. 2). Fisheries diversity and species richness indices were high for the tropical and subtropical Atlantic Ocean clusters, but these showed low dominance (Fig. 2). Dominance was especially high, and diversity especially low, for the Patagonian Shelf and Humboldt Current LMEs relative to all other LMEs.

Different evenness indices behaved differently between LMEs. Both the Simpson and Simpson inverse evenness indices were higher for the high-latitude clusters and lower for the middle and lower latitude clusters (Fig. 2). Shannon evenness was high among most LMEs except for the Humboldt Current and Patagonian Shelf LMEs, where it was low. The Simpson indices are more heavily

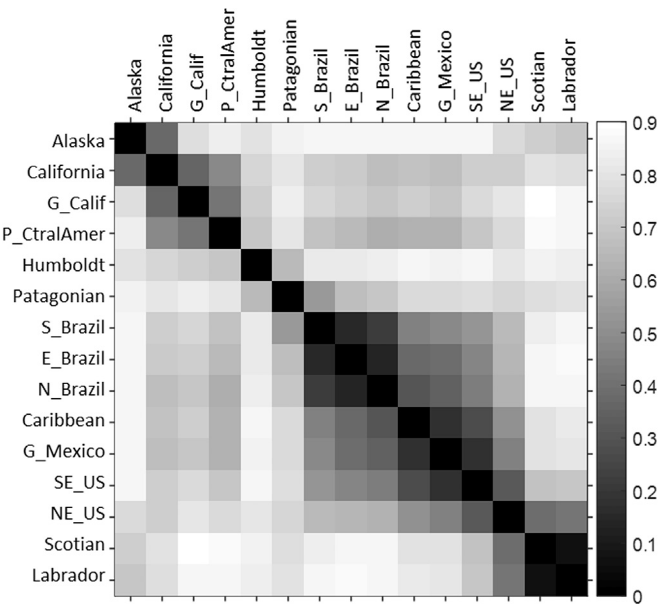

Fig. 3. Pair-wise LME comparison of beta diversity for the LMEs of the Americas based on fisheries landing statistics from the *Sea Around Us* project (1982–2010). Values close to zero mean a higher number of species is shared between a pair of LMEs. Higher Beta diversity means that fewer species are shared between regions. LMEs are ordered by geographic location, counterclockwise from the Gulf of Alaska LME around the Americas to the Newfoundland-Labrador Shelf LME.

weighted by dominant species, and therefore seem to be more sensitive and representative of changes in the distribution of species across LMEs.

The two major western boundary upwelling systems, namely the California Current and Humboldt Current LMEs, showed contrasts in fisheries diversity indices. The Humboldt Current LME had the lowest overall species richness and diversity, and the highest species dominance. This reflects the highly specialized fishery off Peru, which focuses on the small but highly profitable pelagic species of anchoveta in the Humboldt Current LME (Heileman et al., 2009). The California Current LME instead showed intermediate richness, diversity, evenness, and dominance. This may be a function of the diversity of fisheries and top-down pressures, strong regional differences, or dynamic seascape boundaries (Kavanaugh et al., 2016). Even though it has a relatively high average annual SST, the Gulf of California shares some characteristics with mid-and high-latitude LMEs, such as high interannual SST variability, and the fisheries show lower species richness, and relatively high evenness (i.e., an intermediate level of fisheries biodiversity).

The evaluation of beta-diversity between pairs of LMEs (Fig. 3) showed that LMEs located next to each other geographically within the same ocean basin shared a higher number of species (i.e. show lower beta-diversity) than LMEs farther separated from each other. In the Atlantic Ocean, a higher number of contiguous LMEs shared similar fishery species composition. For example, the six contiguous LMEs from the South Brazil Shelf to the Southeast U.S. Continental Shelf showed intermediate to low beta-diversity. Within these, the three Brazil Shelf LMEs showed very high similarity in species composition with the lowest beta-diversity (< 0.2) among the LMEs of the Americas. They also shared high species diversity, lower richness and evenness, warm SST, and low chlorophyll, characteristic of cluster 4 (Fig. 2). The three high-latitude LMEs in the North Atlantic showed intermediate beta-diversity (< 0.4) and similar ecological characteristics, with low and variable SST, high CHL, lower richness and dominance, and high diversity and evenness (cluster 1). The contiguous LMEs of the Caribbean Sea, Gulf of Mexico, and the Southeast U.S. Continental Shelf shared many species (beta-diversity < 0.3) but the Caribbean Sea was clustered apart based on its differences in environmental variables and fisheries diversity indices (Fig. 2).

Both the clustering and the beta-diversity analyses suggest that there are three megaregions among the Atlantic LMEs: One megaregion formed by the three Brazil LMEs (namely the North Brazil Shelf, the East Brazil Shelf, and the South Brazil Shelf), another one composed by the Gulf of Mexico and the Southeast U.S. Continental Shelf, and a third megaregion encompassing the three high-latitude Atlantic LMEs (namely the Northeast U.S. Continental Shelf, the Scotian Shelf, and the Newfoundland-Labrador Shelf LMEs). The results suggest that there are wide latitudinal corridors for fish assemblages across the Atlantic Ocean LMEs.

In the North Pacific Ocean, the LMEs comprised by the California Current, the Gulf of California, and the Pacific Central America Coastal LMEs, shared some assemblages of fish species (mid-range beta-diversity of fisheries landings, < 0.5). The California

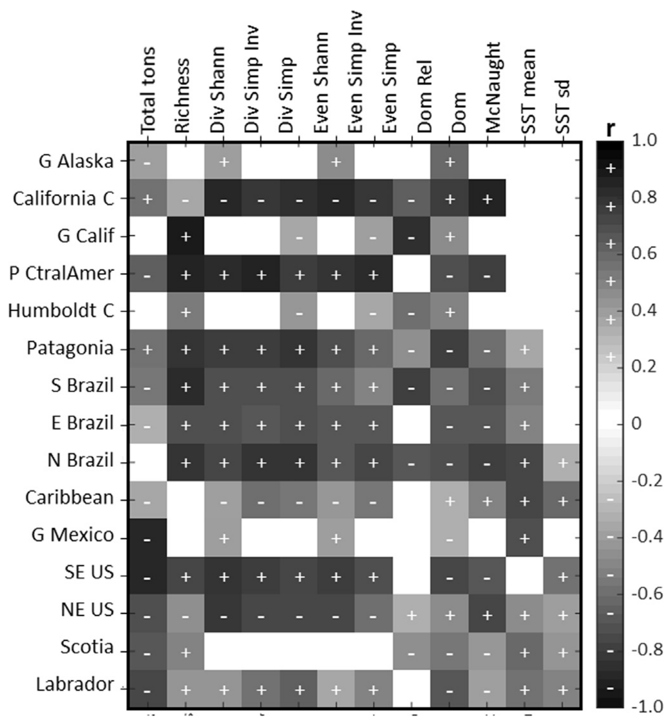

Fig. 4. Long term trends of various characteristics of the LMEs of the Americas illustrated as correlation coefficients (r), calculated by evaluating linear trends in fisheries-based ecological indices and SST (1982–2010) with time (years). Only significant values (p < 0.1) are shown; non-significant values were colored white. Cells are coded in grey level and with negative and positive sign, with higher values shown as increasingly darker shades of grey and extreme values in black. Fishery-dependent diversity indices were calculated using rarefied tons. LMEs are ordered by geographic location counterclockwise from the Gulf of Alaska LME around the Americas to the Newfoundland-Labrador Shelf LME.

Current LME also shared species with the Gulf of Alaska LME (beta-diversity < 0.4). However, these did not cluster together based on either environmental variables or fisheries diversity indices (Fig. 2). The California Current LME has been historically subjected to strong fisheries conservation measures, which may affect trends in fisheries landings and fisheries-derived diversity indices relative to other LMEs. The Pacific Central American Coastal LME, the Humboldt Current LME, and the Patagonian Shelf LME showed the lowest similarity in species composition among contiguous LMEs (Fig. 3).

The LMEs of the Pacific Ocean are indeed very different from those in the Atlantic. The narrow continental shelf of the Pacific Ocean seaboard shows strong ocean boundary upwelling, such as off California and Peru. The entire Pacific Ocean seaboard also shows important variability forced by El-Niño Southern Oscillation episodes. This variability imposed on quasi-persistent upwelling features defines boundaries between LMEs that limit the establishment of megaregions for extended periods of time. It is likely that few species are able to migrate between these LMEs in the Pacific Ocean. For example, even though there were some similarities between the Patagonian Shelf and the Humboldt Current LMEs that led to their clustering together based on environmental variability and fishery-based biodiversity indices, these two LMEs could not be considered a megaregion because the actual fisheries assemblages were very different (Fig. 3).

3.2. Trends in fisheries diversity indices

Trends in the diversity of fish landings in an area, such as within an LME, depend on a number of factors that are difficult to separate. These factors include fishing pressure, regulations, and other social and economically-driven changes in fishing practices, in addition to environmental pressures. In this section we examine the trends in the make-up of fisheries landings and suggest factors that may have led to changes in any one particular LME. An in-depth evaluation of socio-economic factors including changes in regulation is beyond the scope of this study but ultimately needs to be conducted.

Total fish catch decreased along the entire eastern seaboard of North America from 1982 to 2010, from the Gulf of Mexico to the Newfoundland-Labrador Shelf (Fig. 4). Historically, the LMEs of the eastern U.S. have been overfished, and there continues to be controversy over whether overfishing off the northeast U.S. ended or not during the first decade of the 2000's (Rothschild et al., 2013). In terms of fisheries diversity, different LMEs showed different ecological trends. For example, the Southeast U.S. and the Newfoundland-Labrador Shelf LMEs, showed increased diversity in their fisheries. The diversification evident in those LMEs is partly related to decreasing fishing pressure due to management quotas (Aquarone, 2009; Aquarone and Adams, 2009a).

Diversification of the fishery in an LME may be due to other reasons as well, including changes in regional markets, competition, effort, decrease in particular target stocks, or environmental change. For example, both the Southeast U.S. Continental Shelf and Pacific Central America Coastal LMEs showed decreasing trends in total catch but increasing fishery diversification. This focus away from typical targeted species is likely the result of different processes in the different LME. Strong fluctuations of species composition in the Pacific Central America Coastal LME seem to be related to decadal-scale regime shifts in fish populations. The fishery dominated by anchoveta changed after the 1970s to one targeting four different species of small pelagics (Heileman, 2009a). In the Southeast U.S. Continental Shelf LME, the trend toward higher diversity may be related to a higher degree of regulation (Aquarone, 2009). Over 80% of the fishery stocks in both the Pacific Central America Coastal LME and the Southeast U.S. Continental Shelf LME, however, have collapsed and are overexploited (Heileman, 2009a; Aquarone, 2009).

The Gulf of Mexico and Scotian Shelf LMEs showed no particular trend in fisheries diversity. Two areas showed increasing trends in total fish catch, namely the California Current and Patagonia Shelf LMEs. Both the California Current and the Northeast U.S. Continental Shelf LMEs showed a decreasingly diversified fishery, which shows an increasing specialization in the fish caught in these LMEs. In the California Current LME, this is likely due to an increased level of regulation and to economic constraints (Aquarone and Adams, 2009b). In the Northeast U.S. Continental Shelf LME, the fisheries seem to be affected by top-down pressure, i.e., overfishing (Aquarone and Adams, 2009c; Rothschild et al., 2013).

All the LMEs of the southern Atlantic Ocean, from the Patagonian Shelf to the North Brazil Shelf, showed a trend toward increasing species richness, diversity, and evenness, while showing decreased dominance (Fig. 4). However, the reasons of this increased diversity seem to be different for the various LMEs. In the Patagonian Shelf LME, the increase in fishery diversity seems to be related to an increasing total catch (Fig. 4; Heileman, 2009b), and to policies and regulations for the protection and management of the fishery resources. The three Brazil Shelf LMEs have characteristic multispecies, multigear fisheries, with excessive bycatch, discards, and other destructive practices (Heileman, 2009c, 2009d, 2009e). Total discards averaged over 50% of the industrial and artisanal landings (Freire et al., 2014). The three Brazil Shelf LMEs also showed strong declines in their primary fishery stock, i.e., *Sardinella brasiliensis* (Freire, 2004). This causes a redistribution of the effort to other species, and hence a higher fishery diversity (Fig. 4). The three Brazilian Shelf LMEs lack strong and concerted fishery regulations and policies, and there is a disconnect between fisheries management agencies and conservation efforts (Heileman, 2009c, 2009d, 2009e).

Overall, during the period 1982–2010, seven different LMEs showed diversification in their fisheries (Pacific Central America Coastal, Patagonian Shelf, South Brazil Shelf, East Brazil Shelf, North Brazil Shelf, the Southeast U.S. Continental Shelf, and Newfoundland-Labrador Shelf LMEs). Three LMEs showed tendencies toward less diversified fisheries, namely the California Current, the Northeast U.S. Continental Shelf, and the Caribbean Sea. A decrease in fisheries diversity may be due to a wide range of causes. While in some cases it is likely related to historical overfishing, such as in the Northeast U.S. Continental Shelf LME (e.g., Rothschild et al., 2013), the California Current LME fisheries have been subjected to strong and conservative management practices, such as those applied in the rockfish and groundfish fisheries. The Caribbean Sea LME fisheries may have been subjected to both heavy fishing at a time of rapid warming and other environmental changes in the 1980–2010 timeframe, with substantial ecological repercussions (e.g., Taylor et al., 2012; Pinckney et al., 2015; Irwin et al., 2015).

All LMEs of the Americas in the Atlantic Ocean showed a trend toward increasing SST and increasing SST interannual variability, while those in the Pacific Ocean showed no significant trends in SST (Fig. 4). In general, LMEs with warming trends also showed reduced fish landings (Fig. 4). This may be attributed to a poleward shift of fish species as a response to ocean warming or as new habitat becomes available (Gamito et al., 2015). The warming SST trends along all the Atlantic LMEs create a new set of challenges for future fisheries management (c.f., Muhling et al., 2016).

4. Conclusions

Among the Large Marine Ecosystems (LME) of the Americas, there are some that share substantial environmental and fisheries-derived ecological characteristics. Based on an analysis of the variability in sea surface temperature, chlorophyll concentration, primary productivity, and variability in fishery-derived ecological indices, three megaregions were evident in the Atlantic Ocean. Specifically, these include (A) the South Brazil Shelf, the East Brazil Shelf, and the North Brazil Shelf LMEs, (B) the Gulf of Mexico and Southeast U.S. Continental Shelf LMEs, and (C) the Northeast U.S. Continental Shelf, the Scotian Shelf, and the Newfoundland-Labrador Shelf LMEs. No apparent megaregions emerged for the Pacific Ocean. This is likely due to strong ecological differences between these LMEs, higher dissimilarity in species composition of fisheries landings, different top-down pressures, and strong regional differences in oceanographic properties related to variability along the Americas in upwelling processes and by the wide range of impacts caused by recurrent El-Niño Southern Oscillation events. While the Patagonian Shelf and the Humboldt Current LMEs clustered together statistically based on environmental variability and fishery-based biodiversity indices, these LMEs were not considered a megaregion because the actual fisheries assemblages were very different.

During the period 1982–2010, seven different LMEs diversified their fisheries (Pacific Central-America Coastal, Patagonian Shelf, South Brazil Shelf, East Brazil Shelf, North Brazil Shelf, Southeast U.S. Continental Shelf, and Newfoundland-Labrador Shelf). Three LMEs showed increasingly less diversified fisheries, namely the California Current, the Northeast U.S. Continental Shelf, and the Caribbean Sea LMEs.

In order to properly address the various U.N. Sustainable Development Goals (SDG), such as SDG 14, it will be important to better understand the changing physical and biological forces that facilitate the expansion of range of species to encompass more than one LME, and understand the ecological significance of access to such large ecosystems for particular species.

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