Vol. 24: 181–190, 2014
doi: 10.3354/esr00591

ENDANGERED SPECIES RESEARCH
Endang Species Res

Contribution to the Theme Section
'Geospatial approaches to support pelagic conservation planning and adaptive management'

Spatio-temporal assessments of biodiversity in the high seas

Ei Fujioka*, Patrick N. Halpin

Marine Geospatial Ecology Lab, Nicholas School of the Environment, Duke University, PO Box 90328 Durham, North Carolina 27708, USA

ABSTRACT: Biological diversity is one of the most important measures for marine conservation in the high seas. However, data and tools to assess and quantify biodiversity in the high seas are still not well developed. This hinders the development of the open-access tools necessary to assess biodiversity across space and time. Here, we examine prototype online mapping and visualization tools we developed within the OBIS-SEAMAP data center, a thematic node of the Ocean Biogeographic Information System (OBIS) specializing in marine mammal, seabird and sea turtle observations, to facilitate spatiotemporal assessments of biodiversity in the high seas. Our aims are to (1) summarize basic data needs for assessing biodiversity issues in the high seas; (2) discuss technical challenges to address such needs and establish a publicly accessible framework for biodiversity assessments; and (3) demonstrate how our prototype framework facilitates these assessments using a preliminary case study. We anticipate that this will serve as a model for marine researchers and managers to develop similar frameworks or improve the existing ones for ecological assessments. Of special importance is the application of these assessment tools to emerging high seas biodiversity identification processes such as the UN Convention on Biological Diversity, Ecologically or Biologically Significant Marine Areas.

KEY WORDS: Biogeographic database · Spatio-temporal ecological assessments · High seas · Marine conservation

HOW TO QUANTIFY BIODIVERSITY?

Conservation of biological diversity is one of the fundamental goals of establishing marine protected areas or planning for ecosystem-based management (Hooker & Gerber 2004). Biodiversity is also used to illustrate global patterns of taxonomic distributions or identification of hotspots (Roberts et al. 2002, Worm et al. 2005, Morato et al. 2010). At a practical level, marine spatial planning is regarded as a framework for assessing biodiversity and ecosystem services (Douvere 2008). However, as biodiversity is a complex concept and is multidimensional, it can be measured in different ways (Sala & Knowlton 2006) and there are no standardized methodologies on how to quantify it (Hamilton 2005). Many global-scale marine biodiversity studies use species richness as an indicator of biodiversity (e.g. Costello et al. 2010, Pompa et al. 2011, Tittensor et al. 2010), while ecosystem-based management tends to refer to habitat types as a proxy for biodiversity. At the scale of the local species assemblage, a variety of biodiversity indices have been proposed, assessed and criticized (Lande 1996, Rice 2003). One of the essential issues surrounding these biodiversity indices is biased sampling efforts and sample sizes, both spatially and temporally (Fautin et al. 2010, Webb et al. 2010, also see Stockwell & Peterson 2002 for effects of sample size of species distribution models).

There is growing awareness that biodiversity in the high seas, defined as all parts of the oceans that are not included in the exclusive economic zones (EEZs) (WWF/IUCN/WCPA 2001) and is used interchangeably with 'open oceans' in the present article, needs

---

*Corresponding author: efujioka@duke.edu

greater protection (Ardron at al. 2008). The Convention on Biological Diversity (CBD) has defined 7 criteria for the identification of Ecologically or Biologically Significant Marine Areas (EBSAs) in the open ocean and deep seas, one of which is high biodiversity; other criteria include uniqueness or rarity, special importance for life history of species, importance for threatened species and/or habitats, fragile or slow recovery, biological productivity and naturalness (CBD 2009). However, the conservation of the high seas poses additional complications. Addressing sampling bias is particularly challenging as traditional vessel or aerial surveys are more costly in the high seas than in coastal oceans (Evans & Hammond 2004, Marques et al. 2009). Biased sample sizes also increase the difficulty of assessing temporal changes in biodiversity in the high seas. Our ability to monitor temporal changes in biodiversity as an ecosystem indicator is one of the most fundamental measures for the performance evaluation of conservation efforts (Levin et al. 2009). Large vertebrates in the high seas tend to be highly mobile and exhibit annual migration patterns, moving between various types of habitats (e.g. feeding or breeding grounds) with different importance through different life history stages (Game et al. 2009). To be effective for conservation, marine protected areas for these mobile species may require dynamic or flexible boundaries in both space and time (Hyrenbach et al. 2000). Moreover, our knowledge of the biological features in the high seas is incomplete though it is advancing with the advent of novel sampling and analysis tools (Corrigan & Kershaw 2008). Thus, a static map of biodiversity aggregating occurrence data for all species and representing a single indicator is not sufficient to examine spatial and temporal variability in biodiversity and hence may not be an optimal tool for the delineation of EBSAs or protected areas in the high seas.

WHAT IS NEEDED TO ASSESS BIODIVERSITY IN THE HIGH SEAS?

There have been numerous research studies and recommendations on the planning and establishment of ecosystem-based management strategies and pelagic marine protected areas (Hemphill & Shillinger 2006, Sumaila et al. 2007). Establishment of a framework for systematic conservation planning has been proposed (Margules & Pressey 2000, Ban et al. 2013). Further, participation of stakeholders and the general public is a crucial consideration when assessing the success of conservation efforts (Jones-Walters & Çil 2011). Thus, a publicly accessible online framework that provides interactive tools to assess marine biodiversity from a variety of ecological perspectives would be an optimal tool for marine conservation planning. To our knowledge, however, there is no framework to facilitate such dynamic assessments of biodiversity in the high seas and incorporate the outcomes from the assessments into marine spatial planning, although there are several online biogeographic databases providing static maps of biodiversity (e.g. OBIS; Fujioka et al. 2012).

From a technical standpoint, we need to address 3 issues to establish this type of framework for biodiversity assessments. First, a framework needs to be established to share biogeographic data beyond national jurisdictions to fill taxonomic, spatial and temporal gaps. The framework also has to be flexible enough to accommodate a wide variety of data types.

Second, marine biodiversity must be assessed by taxonomically, spatially or temporally scale-dependent components (Lourie & Vincent 2004). In addition, ecosystem-based management requires spatial and temporal components to be included in the operational tools for this approach (Crowder & Norse 2008, Douvere 2008). Thus, a framework is required to provide an interactive tool set to assess different components of biodiversity at different scales.

Third, since criteria and appropriate quantitative measures of biodiversity vary depending on the project objectives and goals, no single biodiversity measurement is sufficient to cover all demands and needs. A tool set to represent and compare alternative indicators of biodiversity will greatly increase the usability of a framework for biodiversity assessments.

PROTOTYPE APPROACHES TO ASSESSMENTS OF BIODIVERSITY IN THE HIGH SEAS

Assessments of biogeographic data beyond national jurisdiction

The Ocean Biogeographic Information System Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP; http://seamap.env.duke.edu) has been accumulating data on marine mammals, seabirds and sea turtles from around the world and providing tools to interactively explore data in a spatially and temporally flexible platform (Halpin et al. 2006, 2009). All data in the OBIS-SEAMAP thematic node of the OBIS network are shared using the international OBIS portal operated under the International Oceanographic Data and Information Exchange

(IODE) of UNESCO-IOC. To broaden spatial, temporal and taxonomic coverage at a global scale, OBIS-SEAMAP incorporates different types of data including traditional visual line-transect sightings, telemetry of tagged animals, detections from passive acoustic monitoring (PAM) and sighting histories from photo-identification catalogs (Fujioka et al. 2014b). Whereas most of the vessel or aerial line-transect surveys focus on regions within jurisdictional boundaries, telemetry data trace animal movements across multiple jurisdictions and hence serve as an essential data source for ecological assessments in the high seas (e.g. Block et al. 2005, Hooker et al. 2007).

OBIS-SEAMAP provides spatial query features that allow researchers to extract data from one or more regions within a jurisdictional or biogeographic classification (e.g. EEZs or large marine ecosystems; Sherman & Hempel 2008) and to assess the extracted data from various ecological perspectives using spatially and temporally interactive tools. The ability to assess marine biodiversity data records within national EEZ boundaries can assist countries in meeting reporting requirements for the CBD Aichi 2020 biodiversity targets (CBD 2010). For biodiversity assessments in the high seas, we further refined these tools so that they are capable of extracting all data beyond the boundaries of the jurisdictional or biogeographic classification. Appling this to the EEZ layer allows the user to find all species occurrences beyond national jurisdictions. For the delineation of marine protected areas or assessments of criteria for marine spatial planning to be practical, biological data beyond national jurisdiction need to be further filtered based on target taxa in a region of interest during the period of time in question. These interactive tools are implemented on the OBIS-SEAMAP website (Halpin et al. 2009).

Alternative indicators of biodiversity

In addition to species richness (the number of distinct taxa in a sample), which is already provided in the OBIS-SEAMAP online mapping tools, we have now implemented the dynamic calculation of 3 biodiversity indices: the Shannon, Simpson and Hurlbert indices. Table 1 summarizes the formulas used to calculate these additional indices. Although the formulas are different, the common inputs are the numbers of animals per species for all species in a given sample (e.g. a study area). The integration of multiple data types in the OBIS-SEAMAP database helps fill taxonomic, spatial and temporal gaps (Fujioka et al. 2014b), which in turn improves the reliability of biodiversity indices. Careful consideration, however, must be paid to normalizing the quantities of each data type when conducting these statistical calculations. For example, with visual line-transect surveys, each record is assumed to represent an independent sighting and provides a quantification of the number of animals present (Buckland et al. 1993, Thomas et al. 2010). However, while a series of locations of a telemetry-tagged or photoidentified animal contribute a number of individual spatial location records, these records represent only one animal. Detections using PAM sensors also produce a number of individual records that may be associated with a single animal or a group of animals. However, the quantity of observations estimated from PAM records may have different meanings (Fujioka et al. 2014a), and the estimation of species abundance from detections is still at an early stage of development (Marques et al. 2009, Martin et al. 2013).

OBIS-SEAMAP uses unique classification codes to distinguish data types (Fujioka et al. 2014b) and the normalization of the species observations data for biodiversity index calculations is performed per data type before the results are aggregated. For example, after records are extracted based on taxonomic, spatial and temporal criteria, unique animal or device identifiers from records of photo-identified or telemetry-tagged animals, respectively, are counted and regarded as the number of individuals. For visual line-transect surveys, the group size is summed in calculations to represent the number of individuals sighted. Many of the PAM records in the OBIS-SEAMAP database represent the number of detections per binned time period and do not include an estimated group size (Fujioka et al. 2014a). The locations recorded are usually those of the sensors, unless the localized positions of the animals detected are deter-

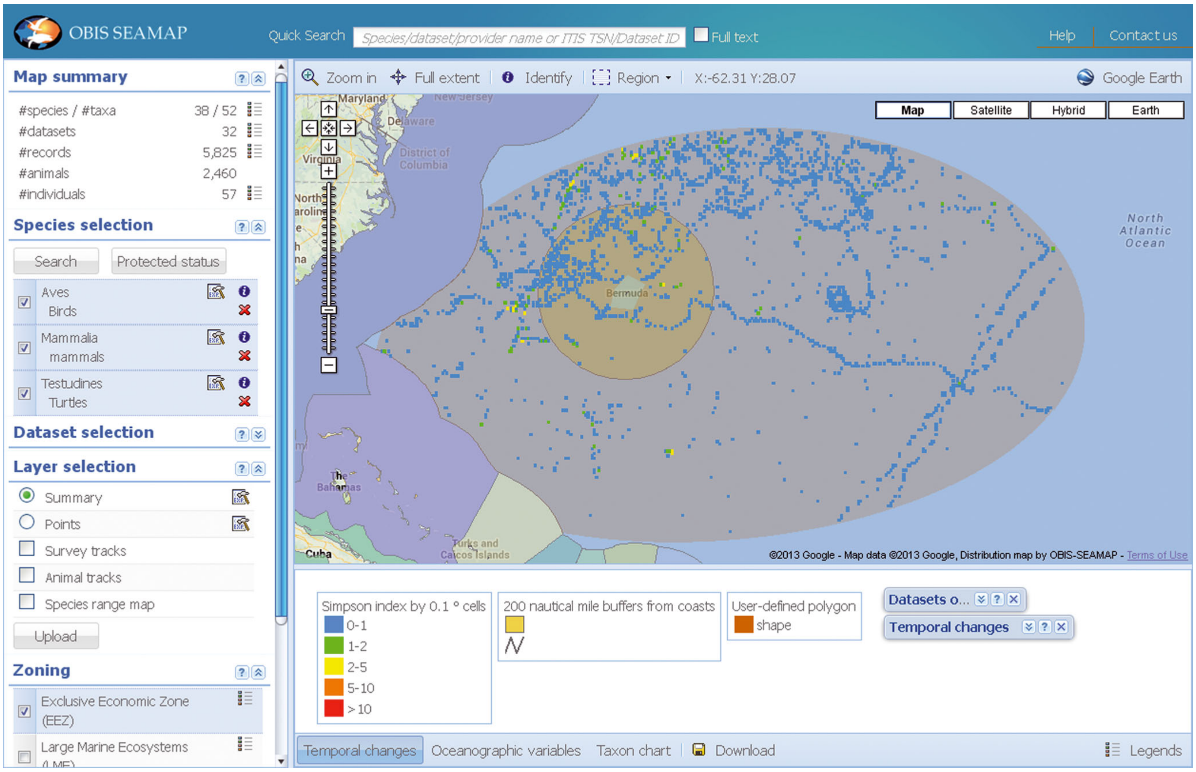
Table 1. Formulas for the species diversity indices implemented in OBIS-SEAMAP, where S is the number of species, N is the total number of individual animals, N_i is the number of individuals of the ith species, and p_i is the proportion of the ith species (N_i/N). In the Hurlbert index, n is a common sample size, which was arbitrarily chosen as 20 in the calculations

Index	Formula	Max. value	Reference
Shannon	$-\sum_{i=1}^{S} p_i \ln p_i$	$\ln S$	Shannon & Weaver (1962)
Simpson	$\frac{1}{\sum_{i=1}^{S} {p_i}^2}$	S	Simpson (1949)
Hurlbert	$\sum_{i=1}^{S}\left(1-\frac{(N-N_i)!(N-n)!}{(N-N_i-n)!N!}\right)$	S	Hurlbert (1971)

Table 2. Summary of how and where the species diversity calculations implemented in a prototype of the OBIS-SEAMAP database obtain the number of individuals from different data types

Data type	Number of individuals
Visual sighting	Group size in a record
Passive acoustic	
Number of detections	Unquantified and excluded from calculations
Presence or absence	Unquantified and excluded from calculations
Estimated group size with sensor locations	Estimated group size in a record but excluded from calculations due to location uncertainty
Estimated group size with animal locations	Estimated group size in a record
Telemetry	Number of unique device identifiers
Photo-identification	Number of unique animal identifiers

mined through intensive detection analyses and spatial triangulation. Due to these complexities, only PAM records having an estimated group size and localized animal position are included in the diversity calculations. Table 2 summarizes the treatments per data type. These data extraction and normalization processes are implemented in a single query to the OBIS-SEAMAP database in response to the user's inputs, allowing for dynamic calculations of multiple biodiversity indices simultaneously. For spatial representation, the diversity calculations are aggregated for a unit cell at a scale of 1.0, 0.1 or 0.01°. Users can choose one of the 4 species biodiversity indices to calculate and map the results (Fig. 1). The aggregation scale is automatically adjusted according to the current zoom-in level of the base map or users can select one of the 3 aggregation scales (Fig. 1). For temporal representation, the calculations are aggregated by a temporal scale of the user's choice from century to decade to year, and the results are visualized on interactive graphs (Fig. 2A). Scales of month and day are available as well, though these time scales may not be appropriate for biodiversity assessments. Estimation of seasonal changes over 4 seasons or 12 mo are also supported by these tools. To mitigate the possibility of misrepresentation of the species diversity indices due to biased sampling effort, the number of records these indices are calculated from or the effort hours of the surveys the records came from can be added to the graph so that changes in diversity indices are understood in the context of sample size and effort (Fig. 2).



#species / #taxa	38 / 52
#datasets	32
#records	5,825
#animals	2,460
#individuals	57

Simpson index by 0.1 ° cells
- 🟦 0-1
- 🟩 1-2
- 🟨 2-5
- 🟧 5-10
- 🟥 > 10

200 nautical mile buffers from coasts
- 🟨

User-defined polygon
- 🟧 shape

Fig. 1. Prototype map from the OBIS-SEAMAP data center showing the Simpson index calculated from biological data of marine megavertebrates within the Sargasso Sea study area, based on Laffoley et al. (2011). A spatial scale of 0.1° was chosen

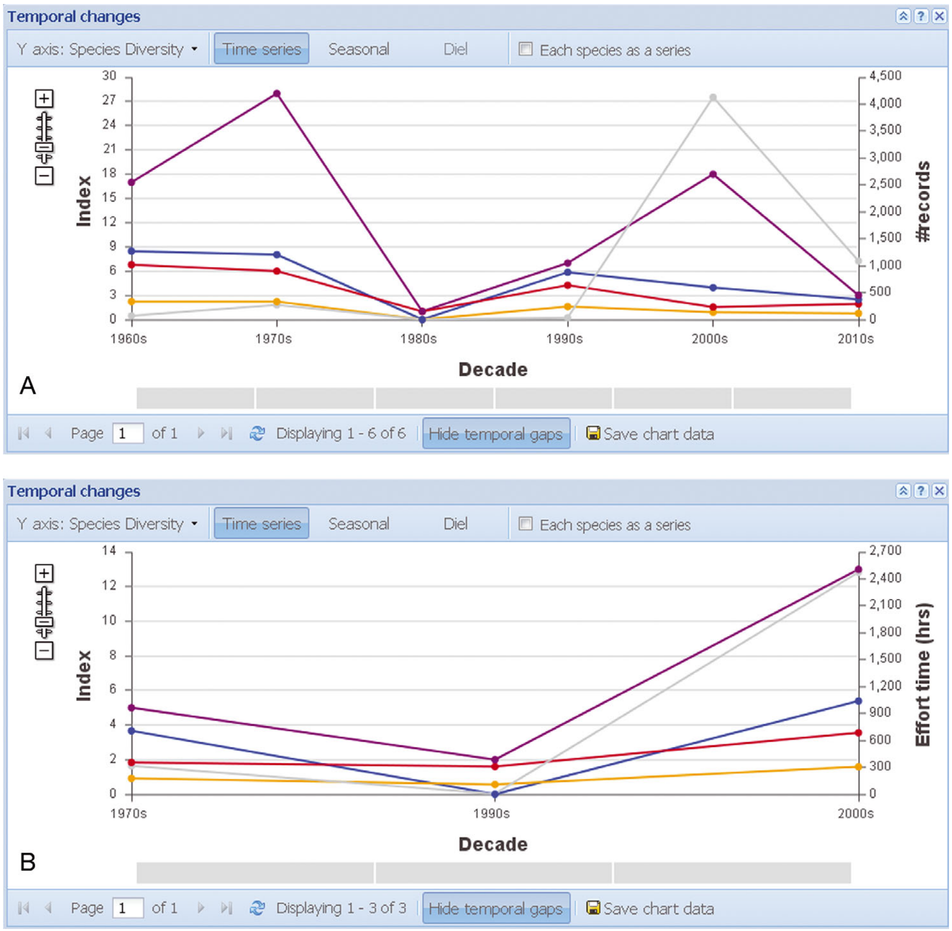


Fig. 2. Decadal changes in the 4 species biodiversity indices (purple: richness; blue: Hurlbert; red: Simpson; orange: Shannon) in the Sargasso Sea study area along with the number of records (A) and effort hours (B). The charts were captured from the OBIS-SEAMAP site. Gray lines represent the number of records (A) or effort hours (B) on the right-hand y-axis. Users can show or hide species richness for a better display, as it tends to be higher than the other 3. Users can also show or hide temporal gaps. The gap in the 1980s is hidden in (B)

CASE STUDY: BIODIVERSITY IN THE SARGASSO SEA

To demonstrate a potential use of the prototype tools for biodiversity assessments in the high seas, we examined the 4 species diversity indices in the greater Sargasso Sea ecosystem. The Sargasso Sea is a unique high sea ecosystem within the North Atlantic Subtropical Gyre characterized by floating *Sargassum* mats (Laffoley et al. 2011). The Sargasso Sea is believed to serve as an important migration pathway and feeding ground for many taxa (e.g. Martin et al. 1984, Laffoley et al. 2011), including sea turtles (Schwartz 1988, Manzella & Williams 1991, Hays et al. 2004), cetaceans (Stone & Katona 1987, Gero et al. 2009) and seabirds (Haney 1986). The Sargasso Sea was described as a site meeting the EBSA criteria through the CBD regional workshop process in 2012. The Sargasso Sea was ranked 'high' in all the 7 EBSA criteria except naturalness (CBD 2012).

Methods

We used the expected boundary of the Sargasso Sea compiled by the Sargasso Sea Alliance (Ardron et al. 2011, Laffoley et al. 2011). An ESRI shapefile of the boundary was uploaded as a study area using the region delineation feature of the OBIS-SEAMAP site and the extracted occurrence records of marine megavertebrates (marine mammals, seabirds and sea turtles) were mapped (Fig. 1). We qualitatively examined decadal changes of the 4 species biodiversity indices using the temporal chart features (Fig. 2).

To address the effect of sample size on the biodiversity indices, we investigated the relationship between the indices and the number of records or effort hours through simple linear regressions. The values of these measures were downloaded from the OBIS-SEAMAP site.

Results

Within the Sargasso Sea study area, 38 marine mammal, sea turtle and seabird species were observed in 5825 observation records from 32 data sets with a temporal coverage of 1966 through 2013. The records included telemetry data from 57 tagged animals of 4 sea turtles (*Caretta caretta*, *Chelonia mydas*, *Dermochelys coriacea* and *Eretmochelys imbricata*), 2 seabirds (*Puffinus gravis* and *Sterna paradisaea*) and 1 whale (*Physeter macrocephalus*).

Qualitatively, the species diversity indices except richness show a similar decadal trend with a continued decline since the 1960s, excluding the 1980s, when only 1 record was found (Fig. 2A, Table 3). Species richness increased from the 1990s to the 2000s but did not reach the same level as in the 1970s (Fig. 2A, Table 3). Effort data were associated with 7 data sets, and 25 data sets without effort data were excluded from the diversity calculation, resulting in a reduced temporal coverage from the 1970s to the 2000s with a gap in the 1980s (Fig. 2B, Table 3). With data sets limited to those having effort, the 3 indices also increased in the 2000s compared with the 1970s, similar to species richness. There were only 4 records in the 1990s, and Hurlbert's index was not calculated.

The number of records exhibits a positive but not significant effect on each of the 4 indices ($R^2 = 0.14$, $p = 0.46$; $R^2 = 0.11$, $p = 0.46$; $R^2 = 0.05$, $p = 0.60$; $R^2 = 0.28$, $p = 0.22$ for the Hurlbert, Shannon and Simpson indices, and species richness, respectively). Similarly, there is also a positive but not significant relationship found between the species diversity indices (except richness) and effort hours ($R^2 = 0.79$, $p = 0.30$; $R^2 = 0.78$, $p = 0.12$; $R^2 = 0.76$, $p = 0.13$ for Hurlbert, Shannon and Simpson, respectively). However, species richness is significantly affected by effort hours ($R^2 = 0.92$, $p = 0.04$).

DISCUSSION AND FUTURE DIRECTIONS

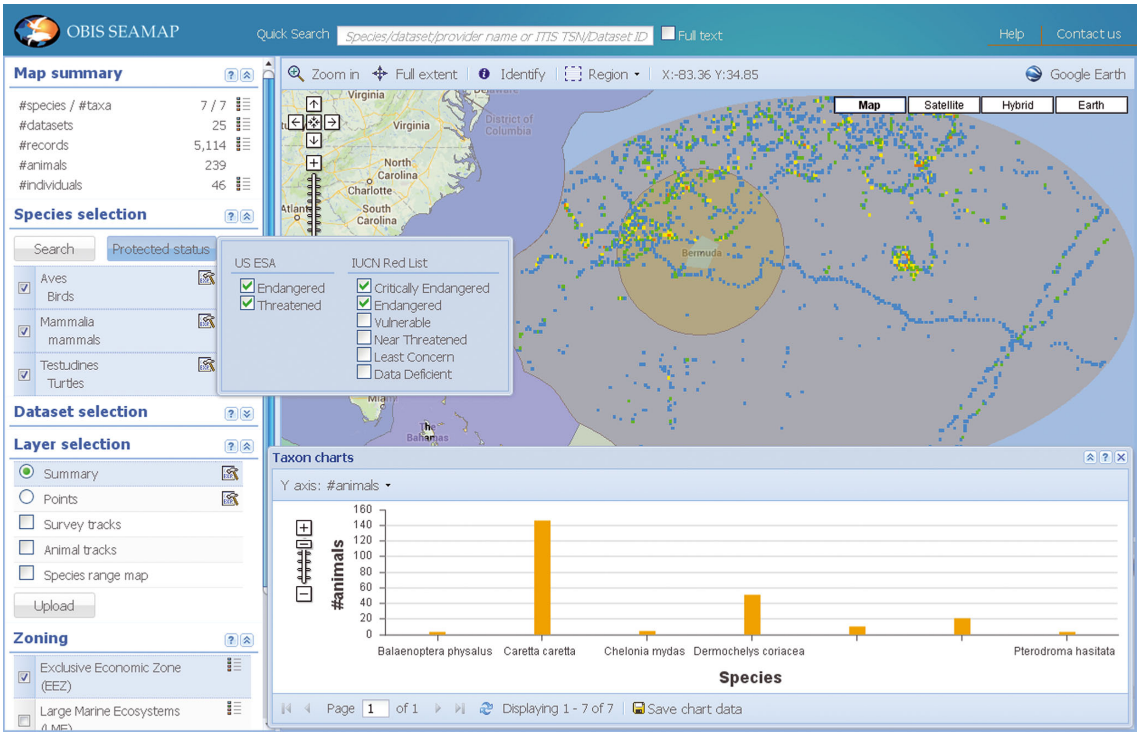
Data deficiency is a significant challenge in assessing marine biodiversity (Fautin et al. 2010, Webb et al. 2010), even for relatively well-studied marine mammals (Schipper et al. 2008). There has been little work to develop fully synthetic approaches to the design and management of marine protected areas (Halpern 2003, Halpern et al. 2007). The situation is even more challenging for conservation management in the high seas because the data coverage and knowledge is less complete and consistent than in coastal waters (Weaver & Johnson 2012). By definition, the high seas are beyond national jurisdictions and, thus, it is more difficult to accumulate biological data in the high seas than coastal waters as such data are usually archived in disparate institutions or national data centers. Our approaches to addressing these issues through the continued development of the global OBIS biogeographic data center are 3-fold: (1) to collect data from individual providers worldwide while establishing strong collaborative relationships with national agencies; (2) to integrate multiple data types to extend coverage of taxonomic, spatial and temporal gaps; and (3) to develop a publicly accessible research and development framework to provide complementary, multi-perspective approaches to ecological assessments through an integrated biological database that facilitates marine conservation activities. For example, identifying which protected species occur in a particular area and how and when they use different habitats is a critical step to designing conservation strategies for those species (Hooker et al. 1999, Louzao et al. 2006). In the Sargasso Sea study area, 7 species listed as endangered or threatened by the US Endangered Species Act and the IUCN Red List (2 cetaceans, 1 seabird and 4 sea turtles) were recorded in 25 data sets (Fig. 3). In addition to species status, better understanding of the seasonal distributions or move-

Table 3. Decadal change in number of records, effort hours, and species diversity indices in the Sargasso Sea study area. Values to the left and right of a slash (/) were calculated from all 32 datasets and 7 datasets for which effort data were available, respectively. NA: not available

Decade	No. of records	Effort hours	Richness	Shannon	Simpson	Hurlbert
1960s	69/NA	NA	17/NA	2.23/NA	6.79/NA	8.47/NA
1970s	271/9	316.35	28/5	2.22/0.92	6.00/1.84	8.04/3.67
1980s	1/NA	NA	1/NA	0/NA	1/NA	NA/NA
1990s	34/4	4.50	7/2	1.60/0.56	4.25/1.60	5.85/NA
2000s	4130/104	2474.68	18/13	0.90/1.59	1.55/3.56	3.95/5.39
2010s	1088/NA	NA	3/NA	0.76/NA	1.93/NA	2.49/NA

ments of target species is essential for delineating dynamic marine management areas. Our prototype framework is capable of visualizing seasonal changes in the number of individuals sighted in a particular region (e.g. the Sargasso Sea; Fig. 4).

For a better understanding of biological data and derived species diversity indices with limited data, it is crucial to examine where and when the data collection effort was conducted. Our prototype framework maintains effort data for both visual line-transect



#species / #taxa	7 / 7
#datasets	25
#records	5,114
#animals	239
#individuals	46

X:-83.36 Y:34.85

☑ Aves Birds
☑ Mammalia mammals
☑ Testudines Turtles

US ESA
☑ Endangered
☑ Threatened

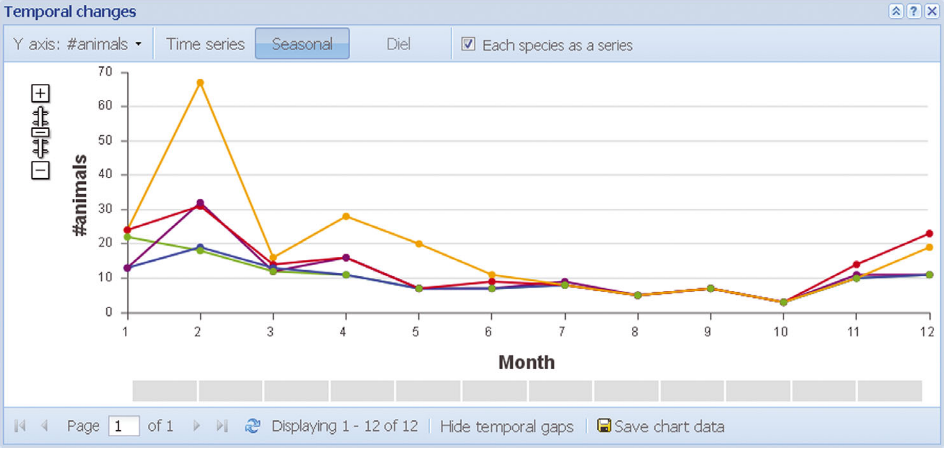
IUCN Red List
☑ Critically Endangered
☑ Endangered
☐ Vulnerable
☐ Near Threatened
☐ Least Concern
☐ Data Deficient

● Summary
○ Points
☐ Survey tracks
☐ Animal tracks
☐ Species range map

☑ Exclusive Economic Zone (EEZ)
☐ Large Marine Ecosystems (LME)

Y axis: #animals

Fig. 3. Prototype map from the OBIS-SEAMAP website showing occurrences of species listed as endangered or threatened in the US Endangered Species Act (ESA) and IUCN Red List in the Sargasso Sea study area along with a taxon chart displaying the number of individuals observed per species. Bars from left to right are *Balaenoptera physalus*, *Caretta caretta*, *Chelonia mydas*, *Dermochelys coriacea*, *Eretmochelys imbricata*, *Megaptera novaeangliae* and *Pterodroma hasitata*. Two of the *x*-axis labels are not shown due to space constraints



Y axis: #animals

☑ Each species as a series

Fig. 4. Monthly changes in the 5 protected species observed in the Sargasso Sea study area (orange: *Caretta caretta*; red: *Dermochelys coriacea*; blue: *Chelonia mydas*; purple: *Megaptera novaeangliae*; green: *Eretmochelys imbricata*). The graphing feature of the OBIS-SEAMAP website allows users to display the top 5 species in terms of the *y*-axis measure (e.g. the number of individuals observed, in this case) when the 'Each species as a series' checkbox is checked

surveys and PAM. By adding a time series of the effort hours to the decadal change in the species diversity indices in the Sargasso Sea case study, the chart qualitatively indicated that species richness followed a trend related to effort hours, which was also supported by a simple linear regression. The peak of the species richness in the 2000s in the Sargasso Sea study area can be attributed to the fact that more surveys were conducted and a wider variety of taxa was observed in this period. The other 3 diversity indices did not present a strong relationship with either the number of records or the effort hours. However, the decadal trend was different when the observation data were limited to those associated with effort. More intensive statistical analyses will be required to further investigate the relationship between additional covariates, but this case study indicates that the incorporation of survey effort data is a necessary component for the appropriate interpretation of biodiversity assessments. It is also worth reiterating the challenge of data deficiency. In the Sargasso Sea case study, the number of records was significantly reduced when data sets were limited to those associated with effort data in the 1970s, 1990s and 2000s, and the diversity indices were not calculated in the 1960s, 1980s and 2010s due to the lack of records from data sets with effort (Table 3). More high-quality data need to be gathered to produce more reliable statistical results.

We posit that the development of spatio-temporal exploratory tools to allow for the comparison of alternative biodiversity indices and to assess biogeographic data in a global biogeographic database is essential to support ongoing biodiversity assessment and conservation efforts in the high seas, such as the CBD EBSA identification process. We also believe this framework will prove to be useful for the implementation of ecosystem-based management and the potential delineation of marine protected areas. This article is not intended to promote the exclusive use of the 3 biodiversity indices examined here for all biodiversity assessments in the high seas but to illustrate the application of prototype tools in combining multiple data types and assessing different components and scales of biodiversity. We encourage researchers to devise and suggest additional approaches to estimate biodiversity for different objectives, approaches and goals of marine conservation and management (e.g. Halpern et al. 2012, Stuart-Smith et al. 2013). Since the OBIS prototype framework is flexible, new approaches or indices can be readily incorporated into future efforts.

Acknowledgements. The OBIS-SEAMAP project, launched in 2002 through support from the Alfred P. Sloan Foundation, has been supported by funding from NOPP/NSF (NSF-OCE-07-39199 & NSF-OCE-11-38046). The development of this manuscript was specifically supported through the UNESCO-IOC project: OBIS Biodiversity Analysis Support for The UN-CBD EBSA Process. The implementation of dynamic biodiversity indices in OBIS-SEAMAP would not have been possible without the initial efforts of Edward Vanden Berghe in the development of the OBIS database and index calculation methods. We also thank the past and present OBIS-SEAMAP project members, including Ben Best, Ben Donnelly, Jesse Cleary and Connie Kot at the Marine Geospatial Ecology Lab, Duke University. Finally, we express the deepest appreciation to OBIS-SEAMAP data providers worldwide.

LITERATURE CITED

Ardron J, Gjerde K, Pullen S, Tilot V (2008) Marine spatial planning in the high seas. Mar Policy 32:832–839

Ardron J, Halpin P, Roberts J, Cleary J, Moffitt M, Donnelly J (2011) Where is the Sargasso Sea? A report submitted to the Sargasso Sea Alliance. Duke University Marine Geospatial Ecology Lab & Marine Conservation Institute. Sargasso Sea Alliance Science Rep Ser, No. 2. www.sargassoalliance.org/storage/documents/No2_WhereistheSS_HI.pdf

Ban NC, Mills M, Tam J, Hicks CC and others (2013) A social–ecological approach to conservation planning: embedding social considerations. Front Ecol Environ 11:194–202

Block BA, Teo SLH, Walli A, Boustany A and others (2005) Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434:1121–1127

Buckland ST, Anderson DR, Burnham KP, Laake JL (1993) Distance sampling: estimating abundance of biological populations. Chapman & Hall, London

CBD (Convention on Biological Diversity) (2009) Expert Workshop on Scientific and Technical Guidance on the Use of Biogeographic Classification Systems and Identification of Marine Areas Beyond National Jurisdiction in Need of Protection. Secretariat of the Convention on Biological Diversity, Ottawa, Canada

CBD (2010) Strategic Plan for Biodiversity 2011-2020 and the Aichi Targets. Secretariat of the Convention on Biological Diversity, Montreal, Canada. www.cbd.int/sp/targets/

CBD (2012) Decisions adopted by the Conference of the Parties to the Convention on Biological Diversity at its Eleventh Meeting. Secretariat of the Convention on Biological Diversity, Montreal. www.cbd.int/doc/decisions/cop-11/full/cop-11-dec-en.pdf

Corrigan C, Kershaw F (2008) Working toward high seas marine protected areas: an assessment of progress made and recommendation for collaboration. UNEP, WCMC, Cambridge, UK

Costello MJ, Coll M, Danovaro R, Halpin P, Ojaveer H and others (2010) A census of marine biodiversity knowledge, resources, and future challenges. PLoS ONE 5(8): e12110

Crowder L, Norse E (2008) Essential ecological insights for marine ecosystem-based management and marine spatial planning. Mar Policy 32:772–778

Douvere F (2008) The importance of marine spatial planning in advancing ecosystembased sea use management. Mar Policy 32:762–771

Evans PGH, Hammond PS (2004) Monitoring cetaceans in European waters. Mammal Rev 34:131–156

Fautin D, Dalton P, Incze LS, Leong JAC and others (2010) An overview of marine biodiversity in United States waters. PLoS ONE 5:e11914

Fujioka E, Vanden Berghe E, Donnelly B, Castillo J and others (2012) Advancing global marine biogeography research with open source GIS software and cloud computing. Trans GIS 16:143–160

Fujioka E, Soldevilla MS, Read AJ, Halpin PN (2014a) Integration of passive acoustic monitoring data into OBIS-SEAMAP, a global biogeographic database, to advance spatially-explicit ecological assessments. Ecol Inform 21:59–73

Fujioka E, Kot CY, Wallace BP, Best BD and others (2014b) Data integration for conservation: leveraging multiple data types to advance ecological assessments and habitat modeling for marine megavertebrates using OBIS-SEAMAP. Ecol Inform 20:13–26

Game ET, Grantham HS, Hobday AJ, Pressey RL and others (2009) Pelagic protected areas: the missing dimension in ocean conservation. Trends Ecol Evol 24:360–369

Gero S, Engelhaupt D, Rendell L, Whitehead H (2009) Who cares? Between-group variation in alloparental caregiving in sperm whales. Behav Ecol 20:838–843

Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecol Appl 13:117–137

Halpern BS, Selkoe KA, Micheli F, Kappel CV (2007) Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. Conserv Biol 21: 1301–1315

Halpern BS, Longo C, Hardy D, McLeod KL and others (2012) An index to assess the health and benefits of the global ocean. Nature 488:615–620

Halpin PN, Read AJ, Best BD, Hyrenbach KD and others (2006) OBIS-SEAMAP: Developing a biogeographic research data commons for the ecological studies of marine mammals, seabirds, and sea turtles. Mar Ecol Prog Ser 316:239–246

Halpin PN, Read AJ, Fujioka E, Best BD and others (2009) OBIS-SEAMAP: the world data center for marine mammal, sea bird, and sea turtle distributions. Oceanography 22:104–115

Hamilton AJ (2005) Species diversity or biodiversity? J Environ Manage 75:89–92

Haney JC (1986) Seabird patchiness in tropical ocean waters: the influence of *Sargassum* 'reefs'. Auk 103:141–151

Hays GC, Houghton JDR, Myers AE (2004) Endangered species: Pan-Atlantic leatherback turtle movements. Nature 429:522

Hemphill AH, Shillinger G (2006) Casting the net broadly: ecosystem-based management beyond national jurisdiction. Sustain Dev Law Policy 7:56–59

Hooker SK, Gerber LR (2004) Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. Bioscience 54:27–39

Hooker SK, Whitehead H, Gowans S (1999) Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. Conserv Biol 13:592–602

Hooker SK, Biuw M, McConnell BJ, Miller PJO, Sparling CE (2007) Bio-logging science: logging and relaying physical and biological data using animal-attached tags. Deep-Sea Res II 54:177–182

Hurlbert SH (1971) The non-concept of species diversity: a critique and alternative parameters. Ecology 52:577–586

Hyrenbach KD, Forney KA, Dayton PK (2000) Marine protected areas and ocean basin management. Aquatic Conserv: Mar Freshw Ecosyst 10:437–458

Jones-Walters L, Çil A (2011) Biodiversity and stakeholder participation. J Nat Conserv 19:327–329

Laffoley Dd'A, Roe HSJ, Angel MV, Ardron J and others (2011) The protection and management of the Sargasso Sea: the golden floating rainforest of the Atlantic Ocean. Summary science and supporting evidence case. Sargasso Sea Alliance. www.sargassoalliance.org/storage/documents/Sargasso.Report.9.12.pdf

Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76:5–13

Levin PS, Fogarty MJ, Murawski SA, Fluharty D (2009) Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. PLoS Biol 7:e14

Lourie SA, Vincent AC (2004) Using biogeography to help set priorities in marine conservation. Conserv Biol 18: 1004–1020

Louzao M, Hyrenbach KD, Arcos JM, Abelló P, Sola LGD, Oro D (2006) Oceanographic habitat of an endangered Mediterranean procellariiform: implications for marine protected areas. Ecol Appl 16:1683–1695

Manzella S, Williams J (1991) Juvenile head-started Kemp's ridleys found in floating grass mats. Mar Turtle Newsl 52: 5–6

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253

Marques TA, Thomas L, Ward J, DiMarzio N, Tyack PL (2009) Estimating cetacean population density using fixed passive acoustic sensors: an example with Blainville's beaked whales. J Acoust Soc Am 125:1982–1994

Martin AR, Katona SK, Mattila D, Hembree D, Waters TD (1984) Migration of humpback whales between the Caribbean and Iceland. J Mammal 65:330–333

Martin SW, Marques TA, Thomas L, Morrissey RP and others (2013) Estimating minke whale (*Balaenoptera acutorostrata*) boing sound density using passive acoustic sensors. Mar Mamm Sci 29:142–158

Morato T, Hoyle SD, Allain V, Nicol SJ (2010) Seamounts are hotspots of pelagic biodiversity in the open ocean. Proc Natl Acad Sci USA 107:9707–9711

Pompa S, Ehrlich PR, Ceballos G (2011) Global distribution and conservation of marine mammals. Proc Nat Acad Sci 108:13600–13605

Rice J (2003) Environmental health indicators. Ocean Coast Manage 46:235–259

Roberts CM, McClean CJ, Veron JE, Hawkins JP and others (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1280–1284

Sala E, Knowlton N (2006) Global marine biodiversity trends. Annu Rev Environ Resour 31:93–122

Schipper J, Chanson JS, Chiozza F, Cox NA and others (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322: 225–230

Schwartz FJ (1988) Aggregations of young hatchling loggerhead sea turtles in the *Sargassum* off North Carolina. Mar Turtle Newsl 42:9–10

Shannon CE, Weaver W (1962) The mathematical theory of communication. University of Illinois Press, Urbana, IL

Sherman K, Hempel G (eds) (2008) The UNEP Large Marine Ecosystem Report: a perspective on changing conditions in LMEs of the world's regional seas. UNEP Regional Seas Report and Studies No. 182. United Nations Environment Programme, Nairobi

➤ Simpson EH (1949) Measurement of diversity. Nature 163: 688

➤ Stockwell DR, Peterson AT (2002) Effects of sample size on accuracy of species distribution models. Ecol Model 148: 1–13

➤ Stone GS, Katona SK (1987) History, migration and present status of humpback whales *Megaptera novaeangliae* at Bermuda. Biol Conserv 42:133–145

➤ Stuart-Smith RD, Bates AE, Lefcheck JS, Duffy JE and others (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature 501: 539–542

➤ Sumaila UR, Zeller D, Watson R, Alder J, Pauly D (2007) Potential costs and benefits of marine reserves in the high seas. Mar Ecol Prog Ser 345:305–310

➤ Thomas L, Buckland ST, Rexstad EA, Laake JL, and others (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. J Appl Ecol 47:5–14

➤ Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Vanden Berghe E, Worm B (2010) Global patterns and predictors of marine biodiversity across taxa. Nature 466:1098–1101

➤ Weaver P, Johnson D (2012) Biodiversity: think big for marine conservation. Nature 483:399–399

➤ Webb TJ, Vanden Berghe E, O'Dor R (2010) Biodiversity's big wet secret: the global distribution of marine biological records reveals chronic under-exploration of the deep pelagic ocean. PLoS ONE 5:e10223

➤ Worm B, Sandow M, Oschlies A, Lotze HK, Myers RA (2005) Global patterns of predator diversity in the open oceans. Science 309:1365–1369

WWF/IUCN/WCPA (World Wildlife Fund/International Union for Conservation of Nature/World Commission on Protected Areas) (2001) The status of natural resources on the high-seas. WWF/IUCN, Gland

Editorial responsibility: Lisa Wedding,
Santa Cruz, California, USA

Submitted: June 3, 2013; Accepted: February 15, 2014
Proofs received from author(s): May 6, 2014