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Short communication

Mapping species richness and human impact drivers to inform global pelagic conservation prioritisation

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ABSTRACT

Given the widely recognized need to better protect the oceans but limited resources to do so, methods for prioritizing potential protected area sites are important. This is particularly true for the open oceans, where few protected areas currently exist and data availability is limited. Here, we examine the relationship between the distributions of tuna and billfish species richness (an indicator of pelagic biodiversity), the human impact drivers of fishing pressure (quantified as cumulative removals) and sea surface temperature increase (quantified as the increase in large positive anomalies) in tropical to temperate oceans at the scale of a 5° × 5° grid. We investigate relationships using Generalised Additive Models and Regression Tree analysis, and identify the top 50 "hotspot" cells for species richness and each of the two impact drivers. We find that both impact drivers significantly overlap with high species richness, but relationships are complex, non-linear and ocean-basin specific. Higher fishing pressure is associated with higher species richness in the Indian and Pacific Oceans, and this overlap is particularly prominent in the central Pacific, and in the Indian Ocean around Sri Lanka. In the Pacific and Atlantic Oceans, species richness is generally higher in areas that have seen lower levels of change in sea surface temperature and only one cell, near Easter Island, is a hotspot for species richness and sea surface temperature increase. While species richness and impact drivers overlap in some areas, there are many areas with high species richness and limited apparent impact. This suggests that area-based conservation strategies that aim to protect areas of high pelagic biodiversity may be achievable with limited displacement of fishing effort.

1. Introduction

Many marine ecosystems have come under severe stress from increasing human impacts (Halpern et al., 2008; Myers and Worm, 2003; Nellman et al., 2008; Roberts, 2003; Sala and Knowlton, 2006; Worm et al., 2006) and the last decade has seen considerable progress in the development of conservation and restoration strategies to mitigate these impacts. Such strategies typically involve some system of restriction on fisheries (Worm et al., 2009), and improved spatial management with Marine Protected Areas (MPAs) as an important component (Hughes et al., 2007; Norse et al., 2003). Establishing the relative priority of areas for protection has been a key part of this process, particularly in coastal ecosystems such as coral reefs (Roberts et al., 2002). However, there has been less progress in developing conservation strategies for the open ocean, particularly those waters beyond national jurisdictions that make up 65% of global oceans by area. These open ocean waters are presently very poorly represented with respect to protected area coverage; depending on what is considered a protected area, between 0.08% and 0.65% of the open ocean currently falls within MPAs (Wood et al., 2008). The critical importance of improving management of the open oceans is increasingly recognized (Game et al., 2009; Wood et al., 2008) and although there has been some controversy around the issue, future efforts will likely involve the establishment of large-scale MPAs, among other measures (Alpine and Hobday, 2007; Game et al., 2009; Mills and Carlton, 1998; Norse et al., 2003; Sumaila et al., 2007).

Conservation resources are limited (Halpern et al., 2006), and in order to ensure that these limited resources are directed effectively it is important to identify clear conservation objectives and to

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pinpoint priority areas that can meet these objectives most effectively (Margules and Pressey, 2000). A common (but by no means the only) objective for conservation is to protect biodiversity. Like terrestrial and coastal ecosystems, the open ocean is not homogenous and distinct areas exist where many species aggregate (Sydeman et al., 2006; Trebilco et al., 2009; Worm et al., 2003, 2005). Similarly, the distribution of human activities likely to impact upon biodiversity is not uniform (Halpern et al., 2008). Relative conservation priorities will depend on area-specific combinations of these and other factors. Describing the spatial distribution of factors that contribute to conservation priorities in the open ocean will be necessary to inform management strategies aiming to protect biodiversity values.

Among open ocean species, there is particular concern for large predators including tunas, billfish, sharks and sea turtles, and a growing number of these have been listed as threatened or endangered by the International Union for Conservation of Nature (IUCN). In contrast to most taxa found on land, species richness of tunas and billfish consistently peaks at intermediate latitudes, around 20–30° N or S (Worm et al., 2003, 2005). This latitudinal pattern has been relatively stable over the last 50 years (Worm et al., 2005) and is also found in foraminiferan zooplankton (Rutherford et al., 1999), marine mammals (Schipper et al., 2008; Whitehead et al., 2008), oceanic sharks, squids, and Euphausiids (Tittensor et al., 2010). This illustrates that broad diversity patterns are consistent across taxonomically distant pelagic taxa at regional scales (Tittensor et al., 2010), and suggests that large predators may have the potential to act as umbrella species in developing spatial conservation strategies that aim to protect pelagic biodiversity values.

Consideration of pelagic diversity patterns will be useful in assessing global conservation priorities in the open ocean (Tittensor et al., 2010; Worm et al., 2005). However, experiences in terrestrial and coastal environments have shown that prioritisation is far more informative when planning is informed by additional information on the distribution of human impacts or other socio-economic drivers (Brooks et al., 2006; Myers, 2003; Myers et al., 2000; Possingham and Wilson, 2005; Sala et al., 2002; Wilson et al., 2006).

Available global datasets for human impact drivers in the oceans were recently mapped and overlaid for the first time (Halpern et al., 2008). In this paper, we examine the distribution of tuna and billfish species richness, an indicator of pelagic biodiversity, in relation to relevant impact drivers including fishing pressure and sea surface temperature (SST) increase. Both fishing and SST have well-known impacts on pelagic biodiversity, and are considered the two major drivers (Boyce et al., 2008; Lehodey et al., 2003; Sund et al., 1981). While there are other factors that will need to be considered in developing conservation priorities for pelagic ecosystems (such as the cost of protection) here we focus on biodiversity and human impact. We present the relationship between these factors as one of several sources of information that may be used in developing conservation priorities for pelagic waters. We anticipate that observed relationships will inform efforts to develop a conservation priority landscape for the open oceans.

If the primary goal of conservation is to protect biodiversity values, it is useful to group the relationship between biodiversity and these two major impact drivers into four categories:

(1) Areas with high levels of both human impact and biodiversity will be "hotspots" of threat to biodiversity, and are likely to experience large biodiversity losses. Therefore they typically rank as high conservation priorities. This hotspots approach has long been promoted for setting conservation priorities on land (Mittermeier et al., 2004; Myers, 2003; Myers et al., 2000).
(2) Areas with high biodiversity and low impact may also be considered conservation priorities, to be protected from future impacts, although the urgency for immediate protection may be lower (Game et al., 2008; Wilson et al., 2007). For impacts associated with fishing, these areas would involve minimal displacement of fishing effort, which limits negative impacts on other areas (Worm et al., 2003).
(3) Areas with low biodiversity and high impact may often be of lower conservation priority. However, it will be important to determine whether historical impacts have reduced biodiversity in such areas, and if so, whether recovery is possible. In addition, some low-biodiversity areas may be considered to be of high conservation value for other reasons (e.g. provision of ecosystem goods and services), and may also be less resilient to additional impacts (such as climate change) than higher diversity systems (Kareiva and Marvier, 2003).
(4) Finally, those areas of low biodiversity and low impact may be of lowest immediate conservation concern, although they may have other intrinsic values worthy of conservation.

Choosing which of these four categories to focus on depends on conservation objectives and available resources. This paper focuses on categories 1 and 2, but the richness and impact overlay it presents could inform open ocean research and area protection prioritisation more generally. We recognise that species richness may not be the most appropriate indicator of biodiversity in all contexts; for instance, 'representative' rather than absolute biodiversity may be more important in some situations. We also recognise that the hotspots approach may overemphasise areas that include environmental transition zones and wide-ranging species (Eken et al., 2004; Williams et al., 1997). This is likely to be disadvantageous in terrestrial environments, as such areas may not capture sites with maximum ecological significance. However, in the open ocean, a measure that emphasizes zones of transition and wide-ranging species may be advantageous, as transitional areas with steep environmental gradients such as persistent fronts, eddies and zones of upwelling are well recognized as being highly productive and ecologically significant. In addition, the majority of pelagic species are wide-ranging, so approaches that emphasise this characteristic may be expected to be less problematic than on land.

2. Methods

2.1. Data layers

Biodiversity data represent tuna and billfish species richness. Species richness was derived by rarefaction estimation of the expected number of species per 50 individuals from Japanese longline logbook data (1990–1999) as reported in Worm et al. (2005). Data were available at a $5^\circ \times 5^\circ$ grid scale. This dataset was selected because of the global coverage and because the congruence of tuna and billfish diversity patterns with those for other pelagic taxa across a range of trophic levels suggests that species richness of tuna and billfish is a useful indicator for overall pelagic species richness (Worm et al., 2005; Tittensor et al., 2010).

The impact driver layers selected for consideration in our study were: (i) Pelagic fishing (millions of tons caught per half degree cell per year divided into high and low bycatch categories by Halpern et al., 2008, originally from the Sea Around Us Project). This variable included all reported fish catch from 1999–2003, on the basis of FAO and other sources (Pauly, 2007; Watson et al., 2004). (ii) SST increase (the change in the frequency of positive temperature anomalies in 1km^2 grid cells that exceed the standard deviation for that location and week of the year between 1985–1990 and

2000–2005, derived by Halpern et al. (2008) from NOAA Advanced Very High Resolution Radiometer Pathfinder Version 5.0 data). Impact driver data layers were obtained as geoTIFF images, and values were averaged over five degree grid cells using the raster arithmetic program StarSpan (Rueda et al., 2005) to enable comparison with the biodiversity datasets.

Fishing was considered because it is widely recognized as a primary driver of changes in marine biodiversity (Halpern et al., 2007; Myers and Worm, 2003; Pauly, 2007; Roberts, 2003; Sala and Knowlton, 2006). Fishing was divided into high and low bycatch categories by Halpern et al. (2008) on the basis of gear type with the low-bycatch category including: troll lines, hook and line, handlines, pilks or jigs, nets other than gill nets, and seines; and the high-bycatch category including: gillnets, set lines, drift lines and mid-water trawls. The high-bycatch category was primarily concentrated in shelf waters, and only accounted for a small proportion of fishing activity.

SST has been recognized as the dominant oceanographic correlate of pelagic biodiversity across many pelagic species groups (Boyce et al., 2008; Rutherford et al., 1999; Tittensor et al., 2010; Whitehead et al., 2008; Worm et al., 2005) as well as primary production (Boyce et al., 2010). By capturing the change in frequency of large positive anomalies, the metric developed by Halpern et al. (2008) is likely to provide a good indication of the ecosystem impact of contemporary increases in SST because it accounts for local variation (to which species are likely adapted) and it focuses on the frequency anomalies which are likely stressful to a broad range of species. Frequency of extreme events is well recognized as a major determinant of biogeographic patterns (Jentsch et al., 2007).

2.2. Analysis

A regression tree was fitted to the data to examine those factors most closely associated with the error structure in the species richness data. Regression trees are an exploratory technique that fit models by binary recursive partitioning, with results displayed as a dendrogram. The data are successively split into increasingly more homogeneous subsets until it is unfeasible to continue (Clark and Pregibon, 1996). While some predictive applications have been developed using regression trees, the method does not assume any causal association between predictors and response variables. Regression tree analysis is thus appropriate in this context, as we are interested in associations between species richness and impact drivers but are not inferring causality. The tree was constructed using the R package *rpart* (Therneau and Grambsch, 1997). The overall model was *species richness* ~ *ocean* + *pelagic low-bycatch fishing pressure* + *pelagic high-bycatch fishing pressure* + *SST rise.* All predictor variables were numeric except *ocean*, which was defined as a three-level un-ordered factor (Atlantic, Indian or Pacific). The tree was simplified to reduce over-fitting using cross-validation cost-complexity pruning (Clark and Pregibon, 1996).

Generalised Additive Models (GAMs) are a nonparametric extension of Generalised Linear Models (GLMs) in which part of the linear predictor is specified in terms of a sum of smoothed functions of predictor variables (Wood, 2006). We used GAMs to investigate the relationship between species richness and impact drivers for two major reasons: (1) they are subject to less restrictive distributional assumptions than linear methods (Hastie and Tibshirani, 1990), and (2) they provide a powerful and flexible approach to describing non-linear relationships. GAMs were constructed using the R package *mgcv* (Wood, 2006). Continuous predictors were smoothed using thin plate regression splines (denoted by $s(x)$ in model formulae). Models using tensor product smoothing were also tested as they can perform well in representing smooth interactions of quantities measured in different units (Wood, 2006), but they resulted in poorer fits, and did not change the overall form of smoothed relationships. An overall model relating species richness to all impact drivers across all oceans was constructed: *species richness* ~ *ocean* + *s(pelagic low-bycatch fishing pressure)* + *s(pelagic* high-bycatch fishing pressure) + *s(SST rise)*; in addition to individual models relating species richness to impact drivers within oceans: *species richness* ~ *s(pelagic low-bycatch fishing pressure)* + *s(pelagic* high-bycatch fishing pressure) + *s(SST rise).*

2.3. Grid cell coverage and hotspots

Only grid cells in which both species richness and impact driver data were available were considered in the analyses. It is important to note that, as our index of biodiversity was derived from Japanese longline logbook data, only some of the world's EEZs were within the scope of the original data; these included countries such as Australia, New Zealand and other Pacific nations that granted coastal access to Japanese vessels through joint agreements. However, coverage was improved by averaging at the 5° scale. This yielded 833 individual 5° × 5° grid cells. We followed Worm et al. (2005) in defining species richness hotpots as the 50 cells with the highest values for species richness. We also followed this definition in identifying threat hotspots for each of the selected impact drivers (i.e. the top 50 cells for each of SST increase, low-bycatch fishing, and high-bycatch fishing, respectively).

3. Results

3.1. Distribution of species richness

Of the 833 grid cells considered, 238 fall within the Atlantic Ocean, 189 in the Indian and 406 in the Pacific. We note the following species richness patterns in tuna and billfish: consistent peaks at intermediate latitudes (15° to 30° N or S); lower toward the poles and equator; higher richness in the west than in the east in the Atlantic and Indian Oceans; hotspots of species richness clustered mostly in the subtropics – off the US and Australian east coasts, south of the Hawaiian Islands chain, east of Sri Lanka, and most prominently in the south-eastern Pacific. We further note that the distribution of species richness values for grid cells differs between oceans, with a greater frequency of low-richness cells in the Indian and Atlantic than in the Pacific (Fig. 1). The Pacific Ocean contains most richness hotspots, both in terms of total number of hotspot cells (30 compared with 10 in each of the Atlantic and Indian Oceans), and as a percentage of grid cells (7.4% compared with 3.7% in the Atlantic and 4.5% in the Indian).

Twenty-seven nations have EEZs that overlap with one or more richness hotspot grid cells. These nations include Australia, the Bahamas, Brazil, Chile, China, Colombia, Costa Rica, El Salvador, Fiji, France, India, Japan, Kenya, Kiribati, Korea (joint regime with Japan), Mauritius, Mozambique, New Zealand, Nicaragua, Panama, Russia, Somalia, Sri Lanka, Taiwan (disputed with China and Japan), Tanzania, the United Kingdom and the United States. Of these, part of the Australian, French, Indian, UK and US EEZs overlap with two or more hotspot grid cells.

3.2. Model results: associations between drivers and biodiversity

The Generalised Additive Model that compares all oceans indicates that the relationship between species richness and impact drivers is ocean-specific (Table 1, Fig. 2). It also indicates that the relationship between species richness and impact drivers is not significantly different between the Atlantic and Indian Oceans, while the Pacific Ocean is distinct from both. This was confirmed by the results of the regression tree, which split the Pacific Ocean

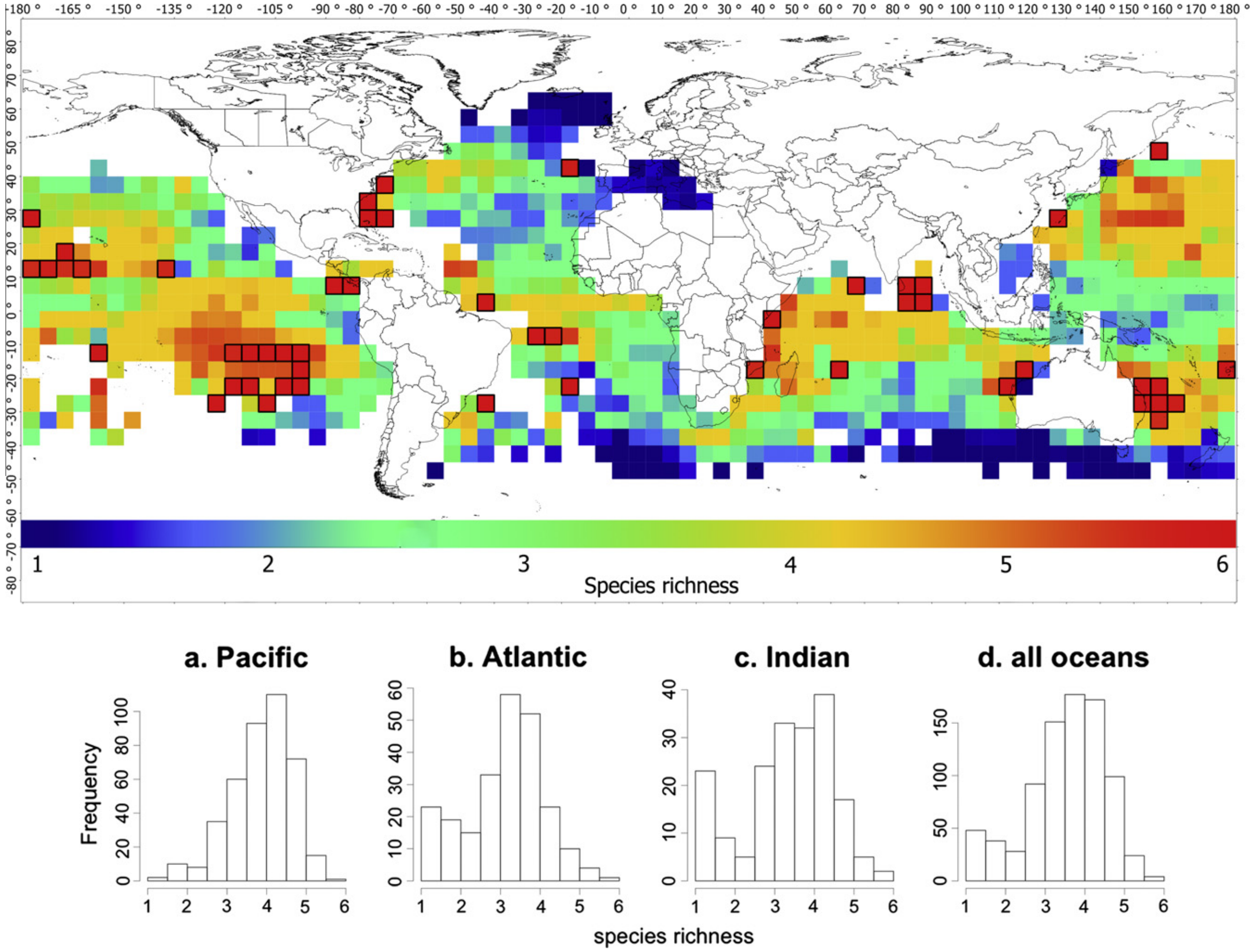

Fig. 1. Tuna and billfish species richness. Colours refer to the expected number of species per 50 randomly sampled landed fish, estimated by rarefaction and expressed on a 5° × 5° grid. The 50 cells with the highest species richness are indicated with dark outlines. Histograms illustrate the distribution of species richness in individual ocean basins and all oceans combined. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Generalised additive model results: (a) overall goodness of fit statistics and (b) statistics for individual smoothed parameters (GCV score = the minimized generalised cross-validation score of the model; scale estimate = estimated scale parameter; edf = estimated degrees of freedom of model terms).

(a)	All oceans	Atlantic	Indian	Pacific
N	833	238	189	406
R^2 (adjusted)	0.26	0.27	0.26	0.20
GCV score	0.74	0.81	0.98	0.49
Deviance explained	0.28	0.32	0.29	0.23
Scale estimate	0.72	0.76	0.93	0.47

(b)	Parameter	*edf*	*F*	*t*	*P*
All oceans	Ocean: Indian			1.70	0.09
	Ocean: Pacific			7.81	0.00
	s(low-bycatch)	6.89	6.14		0.00
	s(high bycatch)	4.05	8.15		0.00
	s(sst increase)	7.82	9.14		0.00
Atlantic	s(low-bycatch)	1.00	1.11		0.29
	s(high bycatch)	7.42	5.00		0.00
	s(sst increase)	5.30	6.63		0.00
Indian	s(low-bycatch)	3.10	12.55		0.00
	s(high bycatch)	3.31	6.27		0.00
	s(sst increase)	1.00	0.02		0.89
Pacific	s(low-bycatch)	8.02	6.07		0.00
	s(high bycatch)	3.80	1.44		0.22
	s(sst increase)	4.47	5.39		0.00

from the Indian and Atlantic at the first branch (Supplementary Fig. 1). Therefore, separate GAMs were constructed for each ocean.

Results indicate a significant association between species richness and one or both of the high or low-bycatch categories of fishing pressure for all oceans. In the Indian Ocean, there was a significant association between species richness and fishing pressure in both categories, while in the Atlantic, only the high-bycatch category showed a significant association with species richness, and in the Pacific only the low-bycatch category showed a significant association with species richness. In the Pacific, the relationship between species richness and the low-bycatch fishing category was broadly u-shaped, with higher species richness in grid cells with very low or very high low-bycatch fishing pressure, and lower species richness in those grid cells with intermediate low-bycatch fishing pressure (Fig. 2). In the Indian Ocean the relationship between species richness and fishing pressure in the low-bycatch category was monotonic and positive, whereas for the high-bycatch fishing category, species richness generally peaked at moderate levels of fishing pressure. In the Atlantic, there was a slight trend for higher species richness to be associated with higher fishing pressure in the high-bycatch category. Again, these results were confirmed in the regression tree results, which split the data on the basis of high-bycatch fishing pressure, low-bycatch fishing pressure then SST increase in the Atlantic and Indian Oceans.

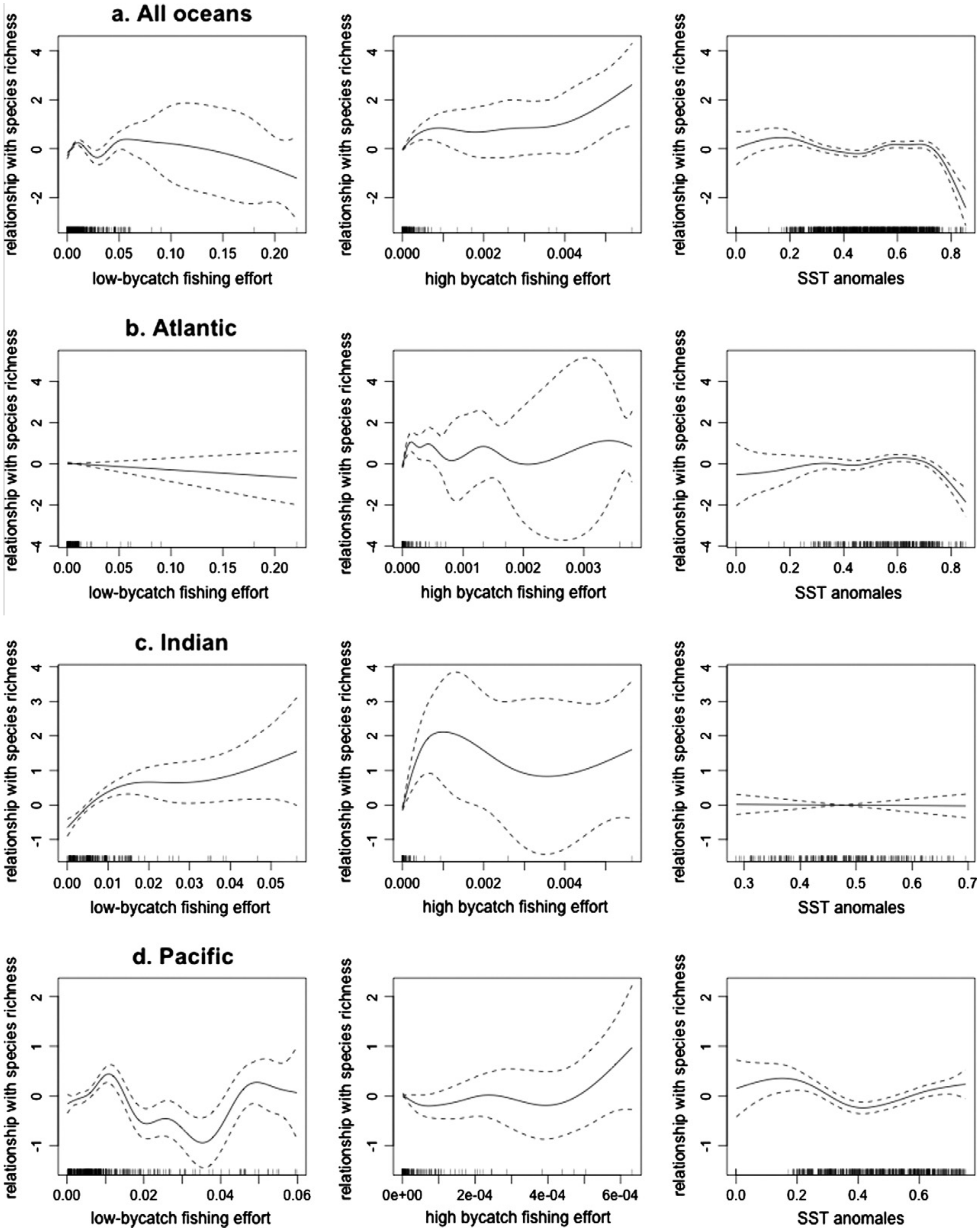

Fig. 2. Relationships between impact drivers and species richness estimated by Generalised Additive Models: (a) for all oceans considered together, with ocean included in the model as a categorical variable, and for the (b) Atlantic, (c) Indian and (d) Pacific oceans individually. Dashed lines illustrate Bayesian credible intervals. 'Rug plots' along the bottom of each plot show the values of the covariates of each smooth function.

The change in frequency of large positive SST displayed a significant association with species richness in both the Pacific and the Atlantic Oceans. In the Pacific, there was a small but significant trend for higher species richness in those areas that had the seen either the lowest or the highest levels of SST increase, with lower species richness in cells that showed intermediate levels of SST increase. In the Atlantic, species richness was relatively uniform across low to intermediate levels of SST increase, with the cells with the highest level of SST increase generally having lower species richness. The SST increase term was not significant in the GAM for the Indian Ocean, indicating that there was no significant association between species richness and the degree of SST increase for Indian ocean grid cells (Table 1, Fig. 2).

3.3. Hotspots of species richness and impact drivers

In total, there were twelve grid cells that were hotspots for both species richness and one or more of the impact drivers, constituting 24% of species richness hotspots and 1.4% of all 833 grid cells analysed here. Ten of these grid cells overlapped with EEZs, of nations including Australia, Brazil, China, Costa Rica, El Salvador, India, Japan, Kenya, Nicaragua, Somalia, Sri Lanka and Tanzania.

Fishing pressure in the low-bycatch category is most notably concentrated in the western and central Pacific (Fig. 3), with 33 of the 50 hotspot cells for this fishing category falling within the Pacific Ocean. However, there is only one grid cell in the Pacific that is a hotspot for both species richness and low-bycatch fishing pressure. This cell is located in the central Pacific. Regions of notably high low-bycatch fishing pressure also occur around Nova Scotia and Iceland in the North Atlantic, and around the Maldives and Sri Lanka in the Indian Ocean. There are overlapping hotspots of species richness and low-bycatch fishing pressure in the latter two regions in the Indian Ocean.

Overall, the Atlantic Ocean had the greatest number of hotspots for the high-bycatch fishing category (primarily concentrated in continental shelf areas), but the region with the highest pressure for this category was in the Indian Ocean, near Sri Lanka (Fig. 3). Other highly impacted grid cells occurred near Taiwan, off the Northwest coast of Australia, and around the coasts of Africa, Mexico and Brazil (Fig. 3). The high-impact area off Sri Lanka was concordant with a species richness hotspot in the same region, and the greatest number of cells that were hotspots for both species richness and high-bycatch fishing pressure occur in the Indian Ocean (four cells, compared with two cells in each of the Atlantic and Pacific).

High levels of SST increase were generally most pronounced at mid to high latitudes, particularly in the north Atlantic and North Pacific (Fig. 3). Areas of relatively high SST increase were also evident around the southern coast of the African continent, and to the East of South America. The majority of the hotspot cells for SST increase were in the Atlantic, with none of the warming hotspot cells occurring in the Indian Ocean. While only 17 hotspots for SST increase were seen in the Pacific, one of these cells was also a hotspot for species richness.

3.4. Hotspots of species richness with little impact

Areas where low levels of fishing pressure in the low-bycatch category coincided with richness hotspots were notable off North-western (NW) Australia, in the Tasman Sea (off Eastern Australia), and off Florida. Isolated grid cells in this category also occurred around Fiji, off Mozambique, near the Baja California Peninsula, around the North-western Hawaiian Islands, and in the South-central Pacific (Fig. 3a). As impact in the high-bycatch category was concentrated over continental shelves, the deep-sea hotspots in all oceans represented high richness/low impact areas for this driver (Fig. 3b). Richness hotpots with the lowest levels of SST increase were evident in the Eastern-central Pacific (to the Southwest of Galapagos), and the richness hotspots of NW Australia, in the Tasman Sea, off Africa, off the Baja Peninsula and off central Brazil (Fig. 3c).

Of these low impact/high richness areas, grid cells off NW Australia, in the Tasman Sea and off Mozambique are particularly notable in that they have low levels of impact for all of the drivers, but very high richness.

4. Discussion

Our results illustrate a significant but spatially limited overlap between tuna and billfish species richness and two important human impact drivers in the open oceans. Notably, 35 of the top 50 richness hotspot grid cells overlapped with EEZs and only 24% of hotspot cells for species richness were also hotspots of human impact. There were a large number of richness hotspots that had low levels of impact for each of the drivers. These areas may be worthy of attention, because they may involve only limited displacement of fishing effort.

Fishing pressure had a more consistent association with species richness than did SST increase. Obviously, the former can be managed using protected areas, whereas the latter cannot. Ten out of 12 combined richness and impact hotspot cells overlapped with EEZs. Importantly, this suggests that both opportunities and challenges for richness-based conservation strategies lie within the realm of national jurisdictions.

In addition to these general patterns, we found that relationships between individual drivers and diversity can be complex and non-linear. For example, in the Pacific Ocean, fishing pressure in the low-bycatch category, which accounts for the majority of the fishing pressure in the open oceans, is generally highest in areas of intermediate species richness. This relationship was not significant for the Atlantic and Indian Oceans, although results suggest that there may be a trend for higher species richness in areas with greater low-bycatch fishing pressure in the Indian Ocean. For fishing pressure in the high-bycatch category, which is concentrated in continental shelf waters, the areas of higher impact generally coincide with areas of high species richness for all oceans. SST increase generally exhibited a dome-shaped relationship with species richness, with the highest species richness areas generally associated with intermediate levels of SST increase.

Areas with particularly notable overlap between high species richness and human impact (category 1) included (by ocean, alphabetically): (i) off the east coast of the US (high-bycatch fishing pressure); (ii) to the southeast of Sri Lanka (high fishing pressure in both categories), (ii) surrounding Mauritius (high low-bycatch fishing pressure); and (iii) in the vicinity of Easter Island (large SST increase). While species richness and impact drivers overlapped in these areas, there were very few combined hotspots for species richness and impact drivers over all (12 out of 833 grid cells), and many areas with high species richness and more limited fishing or SST rise impact.

Richness hotspots that are associated with low human impacts (category 2) occur around the East Pacific, off NW Australia, in the Tasman Sea (east of Australia), in the mid-Western Indian Ocean and near the East coast of Africa. The most notable example of an area with high impacts and lower richness (category 3) is the North Atlantic, which harbours low species richness, high levels of fishing pressure, and high levels of SST increase. Such an area may be expected to have low resilience and therefore may not be able to sustain high levels of fishing pressure into the future (see for example Beaugrand et al., 2003). (Beaugrand et al., 2003).

Seventy percent of species richness hotspot cells, and 83% of cells that were hotspots for both species richness and threat, overlapped with EEZ areas. This implies that protection of considerable pelagic biodiversity value may be achievable by establishing protected areas within EEZs, and with minimal displacement of fishing effort. A similar point was made by Worm et al. (2003), but based on more limited data.

Of the combined hotspot (category 1) cells, those where fishing in the high-bycatch category overlap with biodiversity rank especially highly in warranting further attention as the gear types (gill nets, set lines, drift lines and mid-water trawls) in the

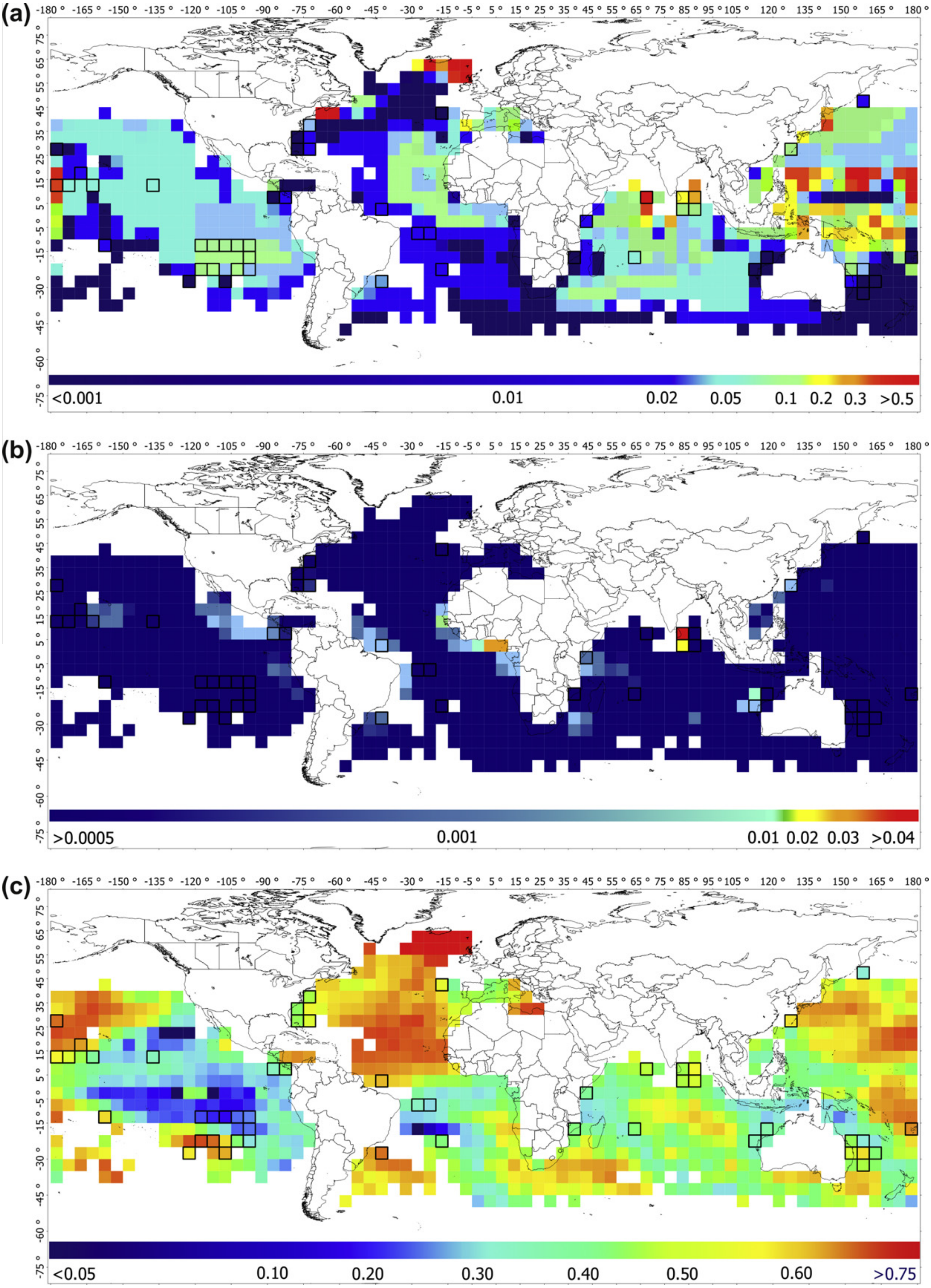

Fig. 3. Distribution of impact drivers expressed on a 5° × 5° grid: (a) and (b) show average pelagic fishing pressure (catch in tons × 10^5/half degree/year) for low-bycatch and high bycatch fisheries respectively (*sensu* Halpern et al., 2008); (c) shows the average SST increase (average increase in frequency of positive temperature anomalies from 1985–1990 and 2000–2005). In each map, the 50 cells with the highest species richness are indicated with dark outlines.

high-bycatch fishing category may be expected to be particularly damaging to biodiversity. In cases where these are in EEZs, this may simplify the establishment and enforcement of protection. It should, however, be noted that it is problematic to use our results to prescribe which EEZ areas are most deserving of conservation attention globally. A more targeted and detailed consideration of biodiversity values, human impacts, and social and economic considerations in the worlds' EEZ areas would be a useful approach for future research.

Isolated hotspots of species richness could also be important, for example if they represent migratory "bottlenecks". Such a hotspot is notable, for example near the mouth of the Mediterranean. This hotspot also coincides with moderate SST increase. The patterns and relationships described here should prove informative for developing first-order priorities for conservation efforts and in guiding future research. We emphasise that relationships will require further attention at finer spatial scales, ideally incorporating information on conservation costs.

Our analyses illustrate how Regression Trees and GAMs can be used to investigate complex non-linear relationships in a conservation context. This approach allowed us to examine the relationships between species richness and several covariates simultaneously and to assess the nature and strength of the relationships. We also note with interest the apparent differences in the frequency distributions of species richness within grid cells between ocean basins (Fig. 1). Investigating these differences in more detail, including determining how and whether they change with different spatial resolution, could be an interesting avenue for future research aimed at identifying hotspots of species richness. If these patterns are general, it will also be interesting to elucidate what ecological (or historical) processes may be responsible for creating observed differences in the distribution of biodiversity. A recent publication by Tittensor et al. (2010) has begun to address these questions but there is still great scope for further research.

Experience with global conservation prioritisation schemes on land has illustrated that no single scheme can capture all the factors that need to be considered in developing global priorities for conservation spending. Instead, multiple sources of information should be considered together in making informed decisions on the allocation of conservation funding (Whittaker et al., 2005). We hope that the patterns identified here will be useful to practitioners and researchers alike in helping to guide the evolution of large-scale pelagic conservation strategies.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.02.024.

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