Title: Continental-scale hotspots of pelagic fish abundance inferred from commercial catch records

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ABSTRACT

Aim: Protected areas have become pivotal to the modern conservation planning toolbox but a limited understanding of marine macroecology is hampering their efficient design and implementation in pelagic environments. We explored the respective contributions of environmental factors and human impacts in capturing the distribution of an assemblage of commercially valuable, large-bodied, open-water predators (tunas, marlins, mackerels).

Location: Western Australia.

Methods: We compiled ten years of commercial fishing records from the *Sea Around Us Project* and derived relative abundance indices from standardised catch rates while accounting for confounding effects of effort, year, gear type and body mass. We used these indices to map pelagic "hotspots" over a 0.5°-resolution grid, and we built random forests to estimate the importance of 29 geophysical, oceanographic and anthropogenic predictors in explaining their locations. We additionally examined the spatial congruence between inferred hotspots and an extensive network of marine reserves, and determined whether patterns of co-occurrence deviated from random expectations using null model simulations.

Results: (1) We identify three regional pelagic hotspots off the coast of Western Australia. (2) Geomorphometrics alone explained more than 50% of the variance in relative abundance of pelagic fish, and submarine canyon presence ranked as the most influential variable in the North bioregion. Seafloor rugosity and fractal dimension, salinity, ocean energy, current strength and human impacts were also identified as important predictors. (3) The spatial overlap between hotspots and marine reserves was limited, with most high-abundance areas primarily found in zones where anthropogenic activities are subject to few regulations.

Main conclusions: This study reveals that geomorphometrics are potentially valuable indicators of the distribution of mobile fish species and highlights the relevance of harnessing static topography as a blueprint for ocean zoning and spatial management.

INTRODUCTION

The past decades have seen unprecedented changes in the abundance of marine living resources. Overexploitation since the 1950s (Pauly, 2012; Pauly & Zeller, 2016) is widely accepted as a catalyst of modern declines in elasmobranchs (sharks, skates and rays) and teleosts globally (e.g. Collette *et al.*, 2011; Juan-Jordá *et al.*, 2011; Letessier *et al.*, In press), despite diverging perspectives on the present status and future prospects of the world's fisheries (Hampton *et al.*, 2005; Daan *et al.*, 2011; Froese *et al.*, 2012; Cook, 2013; Froese *et al.*, 2013; Grubbs *et al.*, 2016), Rebuilding efforts are now underway in several ecosystems (Worm *et al.*, 2009), however their success to date remains relatively modest as insufficient control on current exploitation rates often precludes recovery, even for resilient stocks that may have adapted to moderate levels of extractive pressure (Murawski, 2010; Neubauer *et al.*, 2013).

In this context, a new generation of multilateral environmental treaties has emerged to mitigate overfishing and potentially forestall large-scale erosion of biodiversity. The United Nations Convention on Biological Diversity (CBD, http://www.cbd.int/) is perhaps one of the best-known examples, and presently binds 190 countries to take legislative and policy action to protect at least 10% of the oceans by 2020. In coastal systems, the main strategy adopted to meet this objective entails the implementation of regulatory frameworks such as marine reserves (MRs), whose ecological and socio-economic merits are well established (e.g. Mosquera *et al.*, 2000; Russ *et al.*, 2008; Angulo-Valdés & Hatcher, 2010; Kerwath *et al.*, 2013; Costello, 2014; Mellin *et al.*, 2016). By contrast, the utility of MRs in pelagic environments is more contentious, to some degree due to the widespread perception that far-ranging species require protection over too large a geographic space to be logistically, politically or financially practical to implement or enforce (Game *et al.*, 2009; Kaplan *et al.*, 2010; Wilhelm *et al.*, 2014). Such assumptions, however, rarely account for heterogeneous population structuring (e.g. Grewe *et al.*, 2015), partial migration, residency, site fidelity, philopatry (Chapman *et al.*, 2015) or predictable aggregative behaviour in upper-trophic level organisms (Hueter *et al.*, 2005; Barnett *et al.*, 2012; Fontes *et al.*, 2014; Kessel *et al.*, 2014; Werry *et al.*, 2014; Queiroz *et al.*, 2016). There is now a growing consensus that even mobile predators with extensive home ranges such as seabirds (Young *et al.*, 2015), cetaceans (Gormley *et al.*, 2012), turtles (Scott *et al.*, 2012), fishes (Kerwath *et al.*, 2009) and sharks

(Salinas de León *et al.*, 2016) can benefit from spatial closures (Claudet *et al.*, 2010; Jensen *et al.*, 2010; Breen *et al.*, 2015), especially where these strategically encompass core habitat areas or sites where key life-cycle events perennially occur (Diamond *et al.*, 2010; Breen *et al.*, 2015; Graham *et al.*, 2016).

Sparse ecological data in remote offshore waters (Butler *et al.*, 2010; Webb *et al.*, 2010) make the direct identification of such hotspots difficult, and call for robust surrogates of biological diversity to predict, delineate and prioritise candidate sites for zoning (Harris & Whiteway, 2009; McArthur *et al.*, 2010). Complex topography has been recognised as a determinant of wildlife dynamics across numerous taxa (Bouchet *et al.*, 2015; Lawler *et al.*, 2015), which suggests that locating protected areas over sites of rugged terrain could yield a range of conservation gains (Harris & Whiteway, 2009; Michael *et al.*, 2014). Worm et al. (2003), Morato et al. (2008) and Morato *et al.* (2010) illustrated this possibility in the open ocean by showing that North Atlantic and Pacific seamounts were important centres of taxonomic richness of special interest for the management of threatened vertebrates. The idea that static topography could be used as a blueprint for ocean planning may be widely applicable but has yet to be investigated in other ocean basins and for different types of geomorphologies. Submarine canyons, for instance, are prominent and commonly occurring physical seabed features throughout the world's oceans. While their role as drivers of primary productivity, plankton abundance and benthic biomass is well documented (e.g. Genin, 2004), our understanding of their importance to pelagic megafauna remains nascent, and somewhat skewed towards mammalian vertebrates (Hooker *et al.*, 1999; Fiori *et al.*, 2014; Moors-Murphy, 2014).

Here, we combine a long-term fishing dataset from the *Sea Around Us Project* (SAUP, http://www.seaaroundus.org; Pauly, 2007) with a recent reclassification of Australian submarine canyons (Huang *et al.*, 2014) to (1) determine the location of abundance hotspots for a suite of commercially important predatory pelagic fishes within the western part of Australia's exclusive economic zone (hereafter 'wEEZ'); (2) examine associations between these hotspots and an array of abiotic variables (including seabed topography) on a continental scale; and (3) assess their spatial congruence with a subset of Australia's 3.1 million km^2 national network of Commonwealth Marine Reserves (http://www.environment.gov.au/topics/marine/marine-reserves).

METHODS

Nomenclature

Despite urgent calls to expand global MR coverage (O'Leary *et al.*, 2016), a single and universally agreed definition of marine reserves under international law is still lacking (Techera & Troniak, 2009). In practice, virtually any intertidal or subtidal area subject to one or more regulations can qualify as a reserve, and both the label and its acronym are used in contrasting and sometimes opposing ways in different parts of the world (Ballantine, 2014). Confusion is exacerbated by the wide spectrum of activities that are permissible in MRs as well as the increasing establishment of patchwork "multiple-use" reserves in which permanent no-take zones adjoin areas afforded either partial or no protection. This is the template in place in Australia, and accordingly what the term "MR" refers to throughout. Note, however, that at the time of writing statutory management plans for Australian MRs are still in development following an independent scientific review of the national network (https://www.environment.gov.au/marinereservesreview/). The zoning scheme described herein is suspended and subject to change. Importantly, the strictly no-take marine national parks (MNP, IUCN category II) and sanctuaries (IUCN category Ia) currently grant no on-ground protection.

Fish and environmental data

Annual commercial fishing records for the wEEZ were extracted from the quality-checked databases compiled by SAUP. Landings (in tonnes) originated primarily from yearly catch reports (corrected for discarded bycatch) produced by the Food and Agriculture Organization (FAO) (Watson *et al.*, 2005; see Appendix S1 in Supplementary Information). Effort statistics were obtained from an array of public domain sources (Watson *et al.*, 2013) and were standardised to a common unit of vessel engine power and operation time (kilowatt sea days*, kwsd*), following Anticamara *et al.* (2011). Both catch and effort were disaggregated into a grid system of 0.5° (latitude) x 0.5° (longitude) spatial cells using a rule-based algorithm (see Watson *et al.* (2004) and Watson *et al.* (2013) for technical details). The full dataset spanned the period 1950-2006 and comprised 5,640,222 entries from 111 species and taxa, representing a total catch of 3.11 million tonnes extracted over 3.35 million km^2 of the eastern Indian Ocean between 93-129°E and 8-39°S.

We also collated a biophysical dataset composed of 51 variables computed over the same half-degree square cells as the fisheries data (Tables 1 & S1 in Supporting Information). We chose variables that (i) are thought or known to be functionally or ecologically relevant to mobile pelagic fishes and (ii) exhibited low levels of multicollinearity (Spearman rank coefficient $|\rho| < 0.75$, see Fig. S1 in Supporting Information). The majority of these variables were geomorphometrics (measures of seabed complexity, n=20) assembled from existing archives curated by Geoscience Australia (http://www.ga.gov.au/search), including a newly revised digital catalogue of submarine canyons (Huang *et al.*, 2014). Recognising both the importance of meso-scale hydrographic features to mobile megafauna and the potential for human activities to cause shifts in predator distributions (Maxwell *et al.*, 2013), the dataset also comprised oceanographic factors (n=14; Tables 1 & S1) as well as indices of cumulative anthropogenic stress (n=3; Tables 1 & S1).

Data processing

Our step-wise approach to data preparation and analysis is illustrated in Fig. 1, and a brief description of each step follows below. Analyses were carried out in R 3.0.2 and Matlab 2012a.

Gear matching

We allocated every fishing gear type from the independent catch and effort datasets to one of five discrete and mutually exclusive categories (Fig. S2), and used this classification to pair landings with a corresponding value of effort for all combinations of *year x grid cell* (Appendix S1).

Filtering

We filtered the data to generate a time series spanning the period 1997-2006 as we surmised that catch reporting was likely more transparent and less prone to bias in recent years. We also excluded grid cells situated outside the continental wEEZ (i.e. those surrounding Christmas Island and the Cocos Keeling

Islands), and all demersal or bentho-pelagic animals (Appendix S1 and Table S2). Unidentified records were discarded, and those for families and genera were reapportioned to confirmed species in proportion to their relative contribution to the total family- or genus-specific catch. Finally, gears contributing less than 5% of total landings were omitted, effectively removing all benthic fishing from our study area. Clear outliers, including particularly small coastal grid cells and exaggerated estimates of effort, were also excluded (Appendix S1, Table S2).

Geographic partitioning

Spatial non-stationarity can be problematic in statistical models of broad-scale ecological phenomena as species-environment relationships, and by extension model parameters, may not be constant across space (Miller, 2012). To control for spatial non-stationarity, we subdivided the consolidated data into four contiguous bioregions: North, Gascoyne, West and South. These broadly reflected homogeneous environmental conditions and biological assets (Fig. S3), consistent with management boundaries recognised by the Western Australian Department of Fisheries (WA DoF, 2013).

Imputation of missing effort data

Addressing missing data has been a long-standing issue in fisheries science, as gaps may distort the relative trends inferred from catch rate tables (Carruthers *et al.*, 2011). Although the filtered landings achieved full temporal and spatial coverage with a positive catch value for each *grid cell x year* combination, available effort estimates were incomplete and required reconstructing in locations where none existed (Fig. S4). Watson *et al.* (2013) proposed a forwards-backwards imputation method where the average of the five preceding/subsequent years is used, but the underlying assumption that each ocean square is "independent" of its nearest neighbour is somewhat limiting in a habitat modelling context as both fishing effort and resource distributions are likely to be spatially and temporally auto-correlated. To circumvent issues of independence, we gap-filled the effort matrix using the *smoothn* package (http://www.biomecardio.com/matlab/smoothn.html) introduced by Garcia (2010), which applies penalised regression to smooth evenly-gridded data in multi-dimensional space. The algorithm was executed on a 3D space-time cube (*year x latitude x longitude*) of effort values, summed across fishing gear types due to data scarcity in some grid cells (Fig. S5). After imputation, effort predictions were re-allocated to all gears proportionally to their original usage rate in (i) each *cell x year* (when cell-level data existed) or (ii) the bioregion as a whole (when cell-level data were missing).

Catch rate standardisation

Landings only reflect the portion of a stock that is vulnerable to capture, and a complex suite of factors may affect catchability, directly (e.g. crew number, in-hull storage capacity, fleet composition, gear efficiency and saturation, species life-histories and age or size-related vulnerability) or indirectly (e.g. climatic forcing, information sharing between fishers) (Salthaug & Aanes, 2003; Killen *et al.*, 2015). The use of fisheries-dependent data for ecological inference thus hinges on standardising catch rates to control for confounding elements that may obscure underlying population signals. We constructed lognormal generalised linear models (GLMs) to standardise total catch values for each bioregion across year, fishing gear category, species body mass, and grid cell (Fig. S6). A subset of nine plausible models was considered and competing formulations ranked based on their second-order (corrected) Akaike's information criterion scores (AICc, Table 2). Cell terms were fixed as explanatory variables but their interaction with *year* was not considered owing to the paucity of records on a per year and cell basis. Finally, individual grid cell effects (their coefficients) from the model with lowest AICc were converted to canonical form (Francis, 1999) and exponentiated to extract relative abundance indices.

Random forests

We gauged quantitative relationships between predictor variables and abundance indices using random forests (Breiman, 2001). This machine learning technique has been proven to have superior predictive performance relative to traditional regression models of biota distributions (e.g. Huang *et al.*, 2011) due to its capacity to handle complex nonlinear trends, especially when the number of predictors (p) is relatively large compared to the number of samples (n). We used the *party* R package to construct nt = 10,000 unbiased conditional inference trees of fish abundance in each bioregion (Strobl *et al.*, 2007). Owing to the nature of the available environmental data, the relative importance of each predictor was evaluated by unconditional permutation. Whilst such an approach is not optimal, it can be shown that the greater the number of splitting variables (*mtry*) available at each node, the more the behaviour of the standard measure of importance resembles that of the conditional and more robust version (Strobl *et al.*, 2008). We ran models using both (i) the full environmental dataset and (ii) the geomorphometrics dataset only, with $mtry \approx p/2$, and verified the stability of the algorithm by comparing the outputs from three runs with different seeds for the random number generator (Strobl, personal communication). We also developed partial dependence plots to visualise the effects of the top-scoring predictors using package *edarf* (https://github.com/zmjones/edarf).

Hotspot detection and mapping

Bartolino *et al.* (2011) describe how a 45° tangent to the cumulative relative frequency distribution of a variable of interest can be drawn to mark its corresponding hotspot areas. Instead of empirically approximating tangents from pairs of adjacent points, we adapted this approach by fitting the parametric non-linear species-area functions described by Tjørve, 2003 and Dengler (2009) (Appendix S1) to the abundance indices and deriving tangent intersections by numerically solving the curves' first derivative equations (Fig. S7). Asymptotes were fixed at a value of one in all scenarios (as per theoretical requirements), and the model with the lowest AICc was selected as the best model (Table S3).

Finally, we matched hotspots with individual MRs and measured their spatial congruence using Jaccard's similarity coefficient J (Real & Vargas, 1996; Warman *et al.*, 2004), which ranges from 0 (complete dissimilarity) to 1 (complete match) and is down-weighted by the size of non-overlap areas such that $J = A/(A+B+C)$, with A the number of hotspot cells within reserves, B the number of reserve cells empty of hotspots, and C the number of hotspot cells outside reserves. We used null models to determine the probability of obtaining these patterns by chance, with the null expectation that hotspots could occur anywhere within each bioregion (Tittensor *et al.*, 2010). Following Leroux *et al.* (2007), we randomly selected without replacement the same number of grid cells as identified hotspots, calculated J and reiterated this permutation 10,000 times. We then compared the simulated distribution of Jaccard indices to the corresponding observed values via Z-tests. The same steps were followed to quantify overlap with MNPs.

RESULTS

Fish landings and abundance indices

The catch data consisted of 22 pelagic species (21 teleosts, one elasmobranch), of which 12 are highly migratory (Annex I of the 1982 Convention on the Law of the Sea, Table S4). Mackerels and tunas dominated, with six species (*Katsuwonus pelamis*, skipjack tuna; *Thunnus maccoyii*, southern bluefin tuna; *Thunnus albacares*, yellowfin tuna; *Thunnus obesus,* bigeye tuna; *Scomberomorus commerson*, narrow-banded Spanish mackerel; and *Trachurus declivis,* greenback horse mackerel) making up nearly 75% of all landings over the ten years of the study. Northern fisheries contributed nearly twice as much to total catches (37%) as those operating in other bioregions (18% Gascoyne, 23% West, 22% South).

Catch standardisation models for the North and South bioregions returned the highest adjusted R^2 (0.355 and 0.391 respectively), while models for the Gascoyne and West bioregions explained less of the deviance (adjusted R^2 of 0.263 and 0.173, respectively) (Table 2). Relative abundance indices ranged from 0.00802 to 28.25, with maximum values reported in the North bioregion (interquartile range ca. twice as high as elsewhere in the wEEZ).

Pelagic hotspots

Three regions of elevated fish abundances (i.e. clusters of hotspot cells) could be reliably identified (Fig. 2). One region was situated in the north, starting at Barrow Island, branching south along the Ningaloo Reef peninsula down to Shark Bay, and stretching in a north-east direction across part of the Exmouth Plateau, along the Rowley Terrace and Wombat Plateau. A second was identified in the south-west, extending from the Perth Canyon north to Jurien Bay and south to Geographe Bay and Cape Leeuwin, as well as over some parts of the Naturaliste Plateau. The third was located along the south coast from the Bremer Basin east to the western half of the Great Australian Bight.

Random forest models built on the full set of biophysical predictors explained between 64-82% of the out-of-bag variance (R^2) in fish abundances (Appendix S1 and Table 3). Narrowing the set of splitting variables to geomorphometrics led to little loss of predictive power, with the reduced models still accounting for more than 50% of the variance. The important environmental predictors identified by the models also varied across bioregions (Fig. 3). For example, canyon distribution (i.e. canyon presence in both focal cells, CAN, and neighbouring cells, CANadj) was the top-ranked parameter in the North bioregion and among the first five variables in the South bioregion. However, it had a negligible effect in the clearly oceanography-driven systems of the West and Gascoyne bioregions where salinity (SAL) and ocean energy (L3) emerged as the most influential pair (Fig. 3). Likewise, canyon heads (CANhead) and canyon size (CANpercent) were poor predictors of fish abundance in regions other than the North, and geodiversity (FEATCOUNT) only received a high importance score in the West bioregion. Despite these discrepancies, however, measures of static topographic complexity (including canyon attributes) comprised 35% of the top 10 splitting variables on average, with some metrics such as rugosity (RUG), dominant geomorphic feature (FEATdom) and to a lesser extent fractal dimension (FRD) and contour index (CI) appearing in recurrently prominent positions. By contrast, the frequency of chlorophyll peak index (FCPI) was of trivial importance in all bioregions, and rarely even selected. Human presence indicators (Hi, Him, and Hir) were especially dominant in the West, South and Gascoyne bioregions.

Spatial overlap

Hotspots occupied an area of 484,340 km^2 (n=178 cells, i.e. 19.5% of total) and were most abundant in the South (31% of the cumulative number of hotspots in the entire wEEZ) but most prevalent in Gascoyne (29% of the number of grid cells in the bioregion) (Fig. 2). In comparison, MR coverage was 796,110 km^2 (n=316 cells) and was more prominent in the North (32% of the cumulative number of reserve cells in the entire wEEZ) but widest in the West (39% of the number of grid cells in the bioregion). The South bioregion, 25% of which comprises suspended no-take zones, made the largest contribution to national park area (56% of cumulative total). Congruence was highest in the North bioregion although Jaccard scores remained generally low (<0.3), suggesting that a substantial proportion of the MR network does not intersect hotspots (Fig. 4). All Z-tests were significant (null permutation models, $p < 0.01$), and hotspots coincided with reserves less frequently than expected by chance alone in all bioregions but the North. As a whole, overlap with marine national parks was significantly lower than with the wider MRs.

DISCUSSION

Our study offers quantitative insights into the occurrence patterns of an assemblage of highly mobile, pelagic predatory fishes in the eastern Indian Ocean. Prediction maps revealed three large-scale fish hotspots along the northern, southwestern and southern continental shelves of Western Australia broadly consistent with findings from previous research. For example, tuna and billfish species richness peaks in similar parts of the North and Gascoyne bioregions (Trebilco *et al.*, 2011), as does the behavioural activity of some tiger sharks (*Galeocerdo cuvier*, Ferreira *et al.*, 2015) and pygmy blue whales (*Balaenoptera musculus brevicauda,* Double *et al.*, 2014). These congruent spatial patterns suggest a potentially common basis to hotspot formation across multiple taxa (Bouchet *et al.*, 2015). Higher relative abundance was also inferred at a number of discrete sites, confirming their importance to marine megafauna. These included (i) the seasonally productive Bremer basin, a known foraging ground for white sharks (*Carcharodon carcharias*) and killer whales (*Orcinus orca*), (ii) the waters adjacent to Shark Bay (Letessier *et al.*, 2013) and (iii) the Ningaloo Reef peninsula (Sleeman *et al.*, 2007).

Importantly, we add to a growing body of literature demonstrating that mobile top predators congregate at discrete and sometimes perennial sites (Wingfield *et al.*, 2011). As international support for expanding the world's marine reserve coverage continues to rise (Singleton & Roberts, 2014), the hotspot concept may become particularly appropriate in guiding long-term MR placement and focusing research attention and resources on regions of persistently high ecological value for mobile species whilst conferring maximum conservation benefits per dollar invested (Myers *et al.*, 2000). Such information will be crucial as designing reserves is a notoriously difficult task constrained by both the costs of sampling vast swaths of ocean (Letessier *et al.*, In press), as well as by the necessity to address a broad gamut of socio-economic and geopolitical interests. Thus far, most extant pelagic MRs have been established opportunistically (i.e. without a defined scientific basis; Roberts, 2000) and/or residually (i.e. where there is little perceived conflict with resource users; Devillers *et al.*, 2015). In many information-poor settings such as offshore waters, surrogate-based approaches may thus be the only viable option for improvement (McArthur *et al.*, 2010). If so, the main difficulty will then lie in identifying both (i) a universally accepted operational definition of what constitutes a hotspot, an exercise so far thwarted by mixed interpretations (Bouchet *et al.*, 2015; Marchese, 2015), and (ii) reliable proxies that can predict hotspot locations and possibly their change through time.

Conflicting results from empirical studies have fuelled controversy about the application of abiotic surrogates to conservation planning scenarios (e.g. Stevens & Connolly, 2004 vs. Rees *et al.*, 2014). These discrepancies likely stem from unresolved questions regarding the spatial and temporal stability of surrogate relationships or the effects of data quality and availability on indicator performance (Mellin, 2015). However, as efforts to test the validity of explanatory variables continue, it will become easier to draw generalisations and identify those that perform consistently better across ecosystems, regions and scales (Beier *et al.*, 2015b; Sutcliffe *et al.*, 2015). Geomorphometrics have generally remained broadly unvalidated proxies of oceanic biodiversity (though see Worm *et al.* (2003) and Morato *et al.* (2010)) because large portions of the seafloor are yet to be fully mapped and the majority of submarine canyons around the world are still poorly explored (Huvenne & Davies, 2014). This suggests that weak correlations between static topography and predator hotspots may, at least historically, more likely reflect sporadic and uneven sampling than the absence of genuine wildlife-habitat relationships. Syntheses are also beginning to emerge that highlight the value of using geodiversity to prioritise areas for biological conservation (Beier *et al.*, 2015a). We confirmed this by showing that geomorphometry can be a good predictor of fish abundance on a macro-ecological scale, and highlighting several indices of topographic complexity with robust associations with pelagic biodiversity. That said, not all geomorphometrics were equally important. For instance, consistent with Huang *et al.* (2014)'s observations that the Australian margin is both physically and morphologically heterogeneous, submarine canyon metrics were outperformed in some bioregions but not others. We see two possible explanations for this. Firstly, the formation and maintenance of open-ocean hotspots may demand a suite of interacting oceanographic and bio-physical forces that are not associated with all canyons (e.g. upwellings, eddies, physical retention of prey; Hazen *et al.*, 2013). Secondly, some canyons may only provide favourable conditions for pelagic fish species episodically. If the latter is true, the relatively coarse temporal and spatial resolution of our data may not have been sufficient to reveal such variable relationships. This could be the case for canyon heads, which were not retained in our analysis but are typically reported as biodiversity hotspots sustained by cyclical upwelling events (Rennie *et al.*, 2009). Similarly, the Oceanic Shoals Commonwealth Marine Reserve (11.5°S, 128.5°E) was here a cold spot of fish abundance despite records of seasonally elevated pelagic diversity (Nichol *et al.*, 2013). In order to fully explore the hotspot spectrum and more robustly prioritise candidate areas for protection, a conceptual shift is warranted whereby hotspots are no longer defined in purely geographical terms, but are rather mapped in three (latitude, longitude and time) or even four (latitude, longitude, time and depth) dimensions, with explicit evaluations of their levels of persistence and intra/inter-annual variability (Diamond *et al.*, 2010; Santora & Veit, 2013).

Assessing the processes underpinning the environmental preferences of wildlife species is a major challenge in the pelagic realm (Robinson *et al.*, 2011). The trophodynamics and habitat usage of tunas, billfishes and their relatives prove complex, dynamic and niche-dependent such that species occupying temperate or tropical eco-regions may exhibit contrasting tolerance for, and responses to, similar environmental signals (Arrizabalaga *et al.*, 2015). Such non-stationarity is illustrated in the contrasting partial dependence plots of Fig. 3, and may be mediated, and further complicated. by biotic interactions of varying intensity and direction across latitudes (Schemske *et al.*, 2009). This helps explain why temperature, kinetic energy, oxygen and salinity are often seen as important predictors of biogeographic range but a mechanistic understanding of their influence is often missing in the literature. For example, the role of salinity, the variable that was the most important in Gascoyne and in the West bioregions, in determining the occurrence of pelagic species is particularly obscure albeit some evidence exists that haline fronts may be indirectly linked with reproductive success (e.g. Alvarez-Berastegui *et al.*, 2014), prey density and therefore favourable foraging areas (e.g. Maury *et al.*, 2001). Remotely-sensed measurements of ocean colour and their derivatives, such as FCPI, are more readily interpretable, but may lack explanatory power if the target organisms sit several trophic levels above primary producers

(Grémillet *et al.*, 2008) and/or track productivity at depth by following the deep scattering layer or chlorophyll maxima. The prevalence of cumulative human impact measures in the West is unsurprising as the city of Perth (31.95° S, 115.86°E) concentrates most of the state's human population. The positive relationship with fish abundance, however, does point to the susceptibility of pelagic vertebrates to the global anthropogenic footprint. Indeed, distributional shifts caused by climate change or overfishing have been documented in several species (Fromentin *et al.*, 2014; Hill *et al.*, 2015), and disentangling the respective contributions of oceanographic conditions, migratory behaviour, density-dependence, exploitation levels and population structure to habitat selection will necessitate finer inspections of catch time series.

Against a backdrop of limited global ocean protection (i.e. presently less than 1% of the world's seas has been set aside in no-take sanctuaries; http://www.protectplanetocean.org/)(Costello & Ballantine, 2015), Australia recently scaled up its marine spatial management framework by declaring a national network of Commonwealth Marine Reserves that occupies more than a third of its entire jurisdiction (ca. 3.1 million km^2). This areal coverage is exceptional by international standards, however the reserve system, in its current form, provides relatively low levels of protection equality across habitats and bathymetric classes (Barr & Possingham, 2013). For instance, albeit 36% of Australian canyons now intersect the network (wholly or in part, Huang *et al.*, 2014), merely 10% overlap (wholly or in part) sanctuary/national park areas and are therefore at least only partially safeguarded from anthropogenic activities. In the wEEZ, this equates to 11 small (i.e. average centreline length ± 1SD of 13.2 ± 6.0 km) and remote (i.e. average distance from coastline of 291.9 ± 166.5 km) canyons being fully enclosed within national parks out of a total of 272. Our analysis demonstrates that other natural assets, namely hotspots of mobile predatory wildlife, are also significantly under-represented. Whilst the declaration of the network has been a milestone in Australia's ecosystem-based approach to conservation, work remains to be done to ensure the framework in place is ecologically coherent and enables rapid progress towards the new target set by the International Union for the Conservation of Nature (IUCN) 2014 Sydney World Parks Congress to have at least 30% of ocean environments afforded strict protection within the next fifteen years. Of course, marine reserves are just one piece in the conservation jigsaw and do not constitute a blanket solution to the problem of declining fish populations and biodiversity loss. However, they complement management efforts focused on setting and enforcing sustainable exploitation levels, controlling illegal fishing, mitigating pollution, decreasing reliance on destructive gear, and reducing bycatch rates (Allison *et al.*, 1998; Breen *et al.*, 2015). We also recognise that the mission statement of the world's protected area portfolio has expanded far beyond the original objectives the first reserves were created to fulfil in the early 1900s. Today, MRs are not only promoted as a means of preserving iconic wildlife/seascapes, but also help bolster national economies, increase tourism, support the livelihood of local communities, replenish depleted stocks, and provide resilience in the face of environmental change (Watson *et al.*, 2014). The relevance of MRs for pelagic species will therefore need to be balanced against these and numerous other goals.

CONCLUDING STATEMENT

We provided empirical evidence that geomorphometrics can be meaningful proxies of macro-ecological patterns in pelagic marine species, a notion long suspected to be true but seldom comprehensively tested (with some exceptions; e.g. Worm *et al.*, 2003; Morato *et al.*, 2010). We also added to a body of literature suggesting that landing statistics can be instructive in a biogeographical context (Zainuddin *et al.*, 2006; Froese *et al.*, 2012; Reygondeau *et al.*, 2012), provided they are handled with care, transparency, and a thorough understanding of their theoretical and practical limitations. This is critical as these data represent some of the most spatially and temporally extensive sources of information in existence for a majority of marine organisms (Maunder *et al.*, 2006), making them relevant as an input to spatial planning within the data-limited pelagic ocean. Importantly, we showed that significant opportunities to advance existing conservation frameworks await within national waters. The establishment of a global "hotspot repository" (Hazen *et al.*, 2013), in particular, constitutes an essential step in developing a robust and flexible system of ocean management. When harnessed in combination with topographic data, historical fishing records may be useful for mapping such hotspots at broad resolutions, and subsequently guiding smaller-scale, dedicated surveys that can assist the effective placement and designation of marine reserves.

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SUPPLEMENTARY MATERIALS

Appendix S1. Supplementary methods.

Appendix S2. Supplementary figures.

Figure S1. Correlation matrix between the retained environmental variables.

Figure S2. Fishing gear classification key.

Figure S3. Bioregions recognised by the WA Department of Fisheries.

Figure S4. Patterns of missing data across the fishing effort time series.

Figure S5. Fishing effort imputation in the North bioregion.

Figure S6. Diagnostic plots from the catch standardisation GLMs.

Figure S7. Frequency distribution curves used for hotspot identification.

Appendix S3. Supplementary tables.

Table S1. Predictor variables used in models of pelagic fish hotspots.

Table S2. Filtering statistics for the Sea Around Us Project catch data.

Table S3. Summary of the non-linear models used in hotspot detection.

Table S4. Biological and life-history parameters of pelagic fishes.

Appendix S4. Calculation of the frequency of chlorophyll peak index (FCPI).

BIOSKETCH

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TABLES

Table 1. Summary of explanatory variables. Only the top 15 random forest predictors from each bioregion are shown (Fig. 3). See Table S1 in the Supplementary Information for the full list. Geomorphometrics encompass both "bathymetric / topographic" and "geologic" parameters.

VARIABLE	NAME	UNIT	STATE	ECOLOGICAL INTERPRETATION
Bathymetric / topographic				
CI	Contour index	d.u.	Static	Vertical circulation and mixing, eddy formation, prey refugia, prey entrapment
CRS	Cross-sectional curvature	rad.m^{-1}	Static	Vertical circulation and mixing, eddy formation, prey refugia, prey entrapment
FRD	Fractal dimension	d.u.	Static	Vertical circulation and mixing, eddy formation, prey refugia, prey entrapment
LSRI	Land surface ruggedness index	d.u.	Static	Vertical circulation and mixing, eddy formation, prey refugia, prey entrapment
RUG	Rugosity	d.u.	Static	Vertical circulation and mixing, eddy formation, prey refugia, prey entrapment
Geologic				
CAN	Presence/absence of one or more submarine canyons	d.u.	Static	Breeding/spawning habitat, migration cue, prey availability
CANpercent	Percentage of grid cell area occupied by submarine canyons	%	Static	Breeding/spawning habitat, migration cue, prey availability

CANhead	Presence/absence of one or more canyon heads	d.u.	Static	Productivity (upwelling), food availability, feeding ground
CANadj	Number of adjacent cells containing submarine canyons	d.u.	Static	Population connectivity, larval dispersal
CANdepth	Maximum canyon depth within a cell	m	Static	Prey availability, breeding/spawning habitat
FEATcount	Number of distinct geomorphic features within a cell	d.u.	Static	Prey and habitat diversity
FEATdom	Dominant geomorphic feature class	d.u.	Static	Prey availability, breeding/spawning habitat
Oceanographic				
CUREW	East-west current velocity	$m.s^{-1}$	Dynamic	Nutrient inputs, oxygenation, enhanced productivity, larval drift and juvenile recruitment
CURNS	North-south current velocity	$m.s^{-1}$	Dynamic	Nutrient inputs, oxygenation, enhanced productivity, larval drift and juvenile recruitment
FFD	Daily sea surface temperature frontal frequency	%	Dynamic	Food availability, migration cue
L2	Regional circulation regimes	d.u.	Dynamic	Eddy formation, enhanced primary and secondary production
L3	Ocean energy	d.u.	Dynamic	Prey availability, breeding habitat, feeding success, larval growth rates
MIX	Mixed layer depth	m	Dynamic	Prey availability, physiological tolerance, oxygen availability
PP	Annual mean primary production	$mg\ C.m^{-2}.d^{-1}$	Dynamic	Prey availability

PPstd	Standard deviation of annual mean primary production	mg C.m^{-2}.d^{-1}	Dynamic	Prey availability
SAL	Annual mean salinity at the surface	PSU	Dynamic	Prey availability, physiological tolerance, hatching rate
SSTstd	Standard deviation of sea surface temperature	°C	Dynamic	Spawning cue, breeding habitat, metabolic stress
WAT	Water mass at surface	d.u.	Dynamic	Prey availability, physiological tolerance
Anthropogenic				
Hi	Mean cumulative human impact	d.u.	Dynamic	Mortality, sub-lethal disturbance, displacement
Hir	Range of cumulative human impacts	d.u.	Dynamic	Mortality, sub-lethal disturbance, displacement
Him	Maximum cumulative human impact	d.u.	Dynamic	Mortality, sub-lethal disturbance, displacement

Table 2. Model selection summary from the GLM standardisation of pelagic fish catch rates. The best model (with minimum second-order Akaike Information Criterion AICc and maximum adjusted R^2) is shown in bold. ΔAICc quantifies the difference in AICc score between the current and best models. α is the intercept, ε is the residual variation, log(E) and log(A) are offset terms for fishing effort and water surface area respectively, and the standard notation 'x' represents all covariate main effects and their associated interactions. Weights are the species-specific values reported in Table S4.

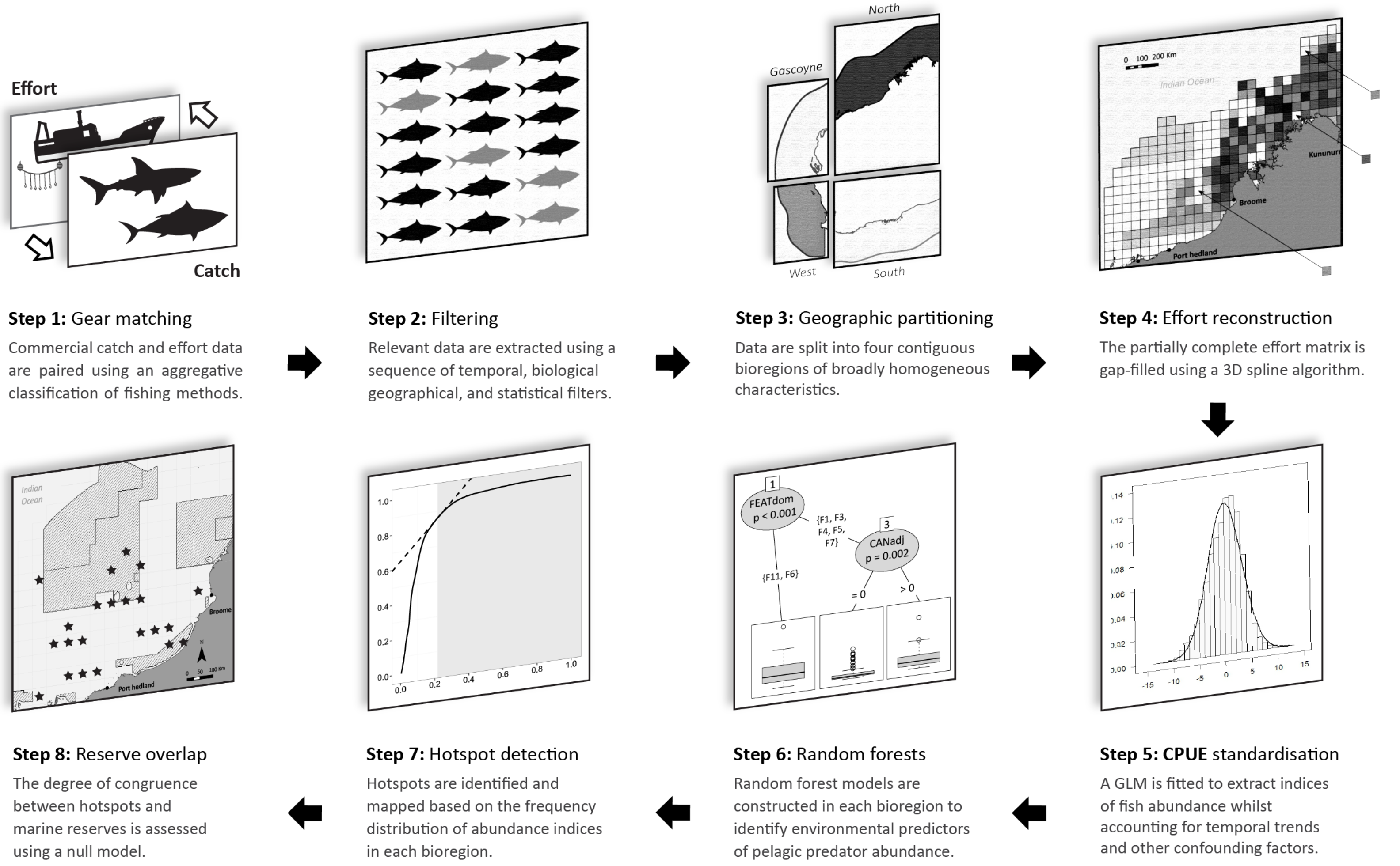
Model formulation	North		Gascoyne		West		South	
	ΔAICc	Adj. R^2	ΔAICc	Adj. R^2	ΔAICc	Adj. R^2	ΔAICc	Adj. R^2
log(Catch) ~ α + Cell + Year x Gear x Weight + log(E) + log(A) + ε	**0**	**0.355**	**0**	**0.263**	**0**	**0.173**	**0**	**0.391**
log(Catch) ~ α + Cell + Year + Gear x Weight + log(E) + log(A) + ε	3,866	0.324	980	0.228	880	0.14	480	0.374
log(Catch) ~ α + Cell + Year x Gear + Weight + Dport + log(E) + log(A) + ε	4,164	0.321	647	0.24	631	0.149	180	0.384
log(Catch) ~ α + Cell + Year x Dport + Gear + Weight + log(E) + log(A) + ε	5,065	0.314	854	0.233	969	0.137	459	0.375
log(Catch) ~ α + Cell + Year + Gear + Weight + log(E) + log(A) + ε	5,690	0.309	1,112	0.223	1,050	0.134	535	0.372
log(Catch) ~ α + Cell + Year + Gear + Weight + Dport + log(E) + log(A) + ε	5,690	0.309	1,112	0.223	1,050	0.134	535	0.372
log(Catch) ~ α + Cell + Year + Gear x Dport + log(E) + log(A) + ε	12,293	0.3	2,523	0.232	3,410	0.128	6,517	0.196
log(Catch) ~ α + Cell + Year + Gear + log(E) + log(A) + ε	12,437	0.299	2,800	0.222	3,617	0.12	6,532	0.196
log(Catch) ~ α + Cell + Year + log(E) + log(A) + ε	26,663	0.169	4,855	0.146	3,738	0.116	9,110	0.073

Table 3. Predictive accuracy of the random forest models of pelagic fish abundance. Performance is evaluated on the out-of-bag data (see Appendix S1). RMSE stands for the root mean squared error, and R^2 represents the percentage of variance explained.

Input	**Performance metric**	**Bioregions**			
		North	Gascoyne	West	South
All variables	RMSE	2.051	0.385	0.559	0.351
All variables	R^2	0.644	0.804	0.722	0.823
Geomorphometrics	RMSE	2.321	0.528	0.723	0.50
Geomorphometrics	R^2	0.530	0.666	0.516	0.628

FIGURES

Figure 1. Graphic representation of the grooming and analysis of the *Sea Around Us* Project (SAUP) data.



Step 1: Gear matching

Commercial catch and effort data are paired using an aggregative classification of fishing methods.

Step 2: Filtering

Relevant data are extracted using a sequence of temporal, biological geographical, and statistical filters.

Step 3: Geographic partitioning

Data are split into four contiguous bioregions of broadly homogeneous characteristics.

Step 4: Effort reconstruction

The partially complete effort matrix is gap-filled using a 3D spline algorithm.

Step 5: CPUE standardisation

A GLM is fitted to extract indices of fish abundance whilst accounting for temporal trends and other confounding factors.

Step 6: Random forests

Random forest models are constructed in each bioregion to identify environmental predictors of pelagic predator abundance.

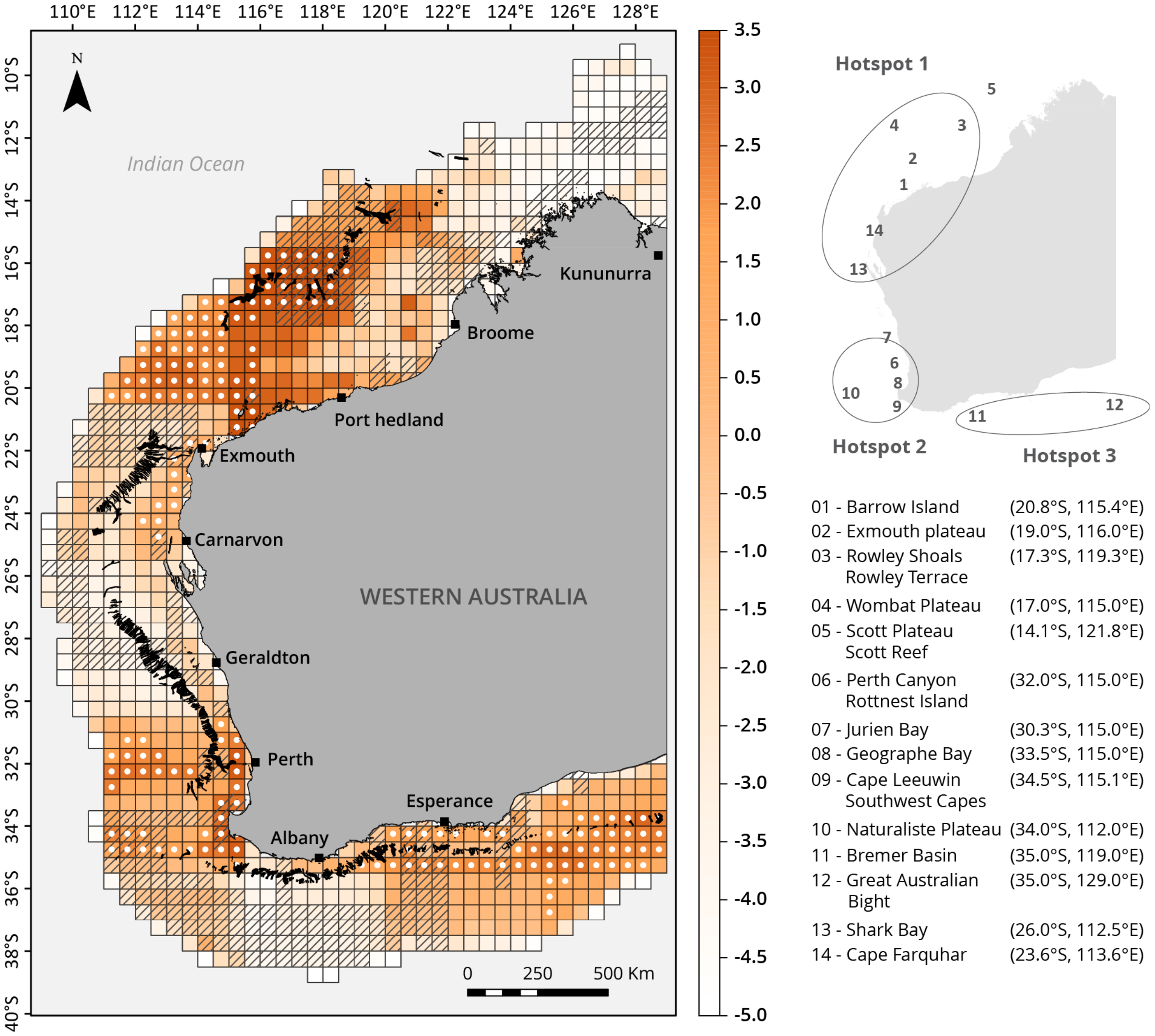
Step 7: Hotspot detection

Hotspots are identified and mapped based on the frequency distribution of abundance indices in each bioregion.

Step 8: Reserve overlap

The degree of congruence between hotspots and marine reserves is assessed using a null model.

Figure 2. Pelagic fish hotspots derived from the SAUP data. Submarine canyons (Huang *et al.*, 2014; in black) are overlaid on the predicted spatial patterns in fish relative abundance (displayed on the log scale). Hotspot locations are marked with white circles and shown relative to the distribution of Commonwealth Marine Reserves (striped fill).



01 - Barrow Island	(20.8°S, 115.4°E)
02 - Exmouth plateau	(19.0°S, 116.0°E)
03 - Rowley Shoals Rowley Terrace	(17.3°S, 119.3°E)
04 - Wombat Plateau	(17.0°S, 115.0°E)
05 - Scott Plateau Scott Reef	(14.1°S, 121.8°E)
06 - Perth Canyon Rottnest Island	(32.0°S, 115.0°E)
07 - Jurien Bay	(30.3°S, 115.0°E)
08 - Geographe Bay	(33.5°S, 115.0°E)
09 - Cape Leeuwin Southwest Capes	(34.5°S, 115.1°E)
10 - Naturaliste Plateau	(34.0°S, 112.0°E)
11 - Bremer Basin	(35.0°S, 119.0°E)
12 - Great Australian Bight	(35.0°S, 129.0°E)
13 - Shark Bay	(26.0°S, 112.5°E)
14 - Cape Farquhar	(23.6°S, 113.6°E)

Figure 3. Top 10 environmental predictors of highest relative importance in the random forest models. Canyon attributes appear in black, topographic variables in grey and all remaining predictors in white (left). Also shown are the corresponding partial dependence plots for the three most influential variables (right). These display the marginal effects that each term exerts on the response (here normalised to the [0-1] range in each bioregion to facilitate interpretation) whilst holding all other input variables constant at their average values. A full list of variable abbreviations is provided in Table 1.

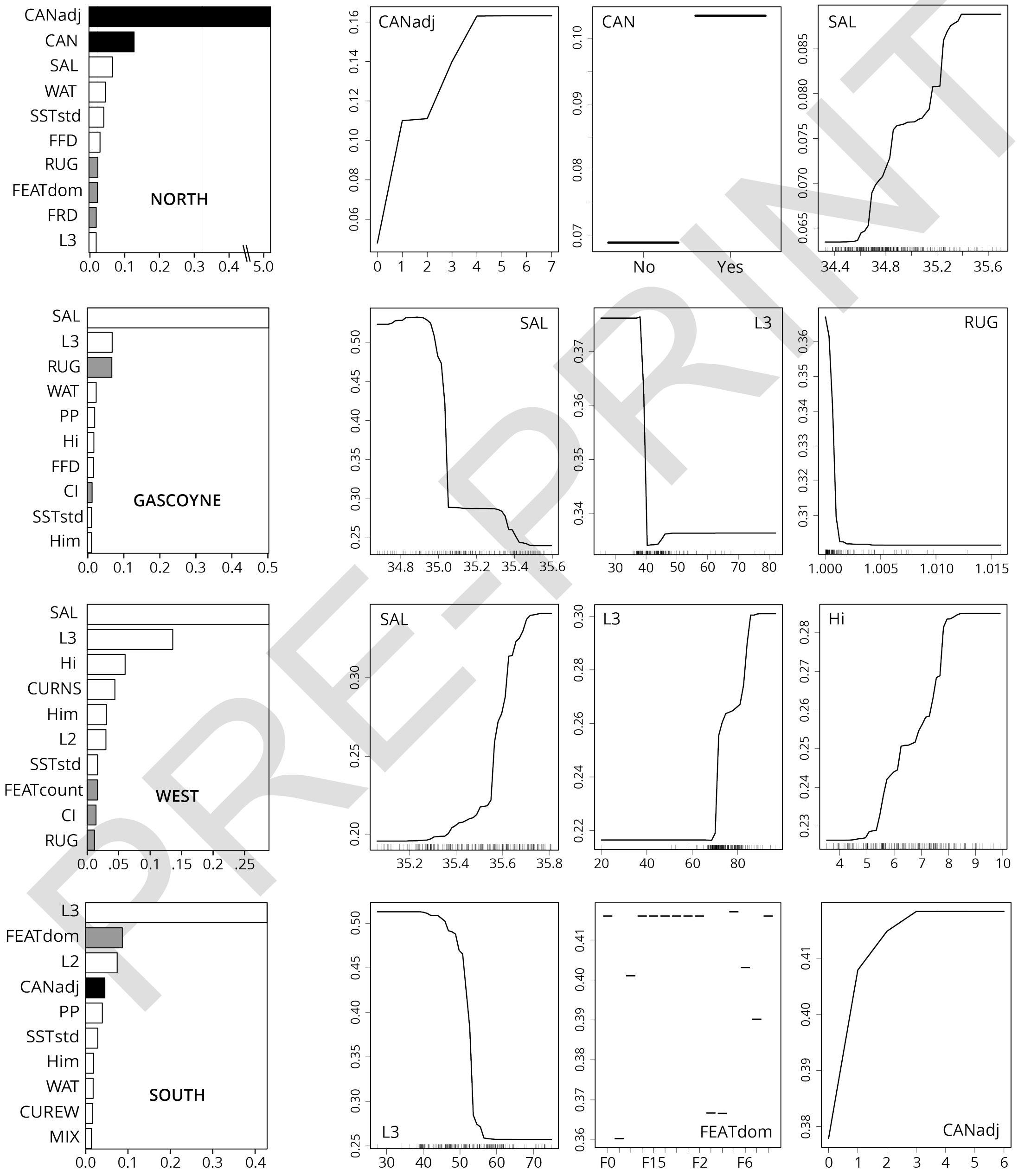


Figure 4. Congruence between pelagic fish hotspots and marine reserves. Overlap is measured via the Jaccard similarity coefficient J, which ranges from 0 (no overlap) to 1 (complete congruence) and can be written as J=A/(A+B+C), with A the area of overlap, B the cumulative hotspot area in a given bioregion, and C the cumulative area occupied by marine reserves. Observed values are shown as filled circles, and boxplots capture the distribution of values under a random null model (n=10,000). CMR: Commonwealth Marine Reserves (all zones), MNP = Marine National Parks (no-take zones only).