

#### True blue: Temporal and spatial stability of pelagic wildlife at a submarine canyon

Forrest, J. A. H.; Bouchet, P. J.; Barley, S. C.; McLennan, A. G.; Meeuwig, J. J.

#### **Ecosphere**

DOI: 10.1002/ecs2.3423

Published: 30/03/2021

Publisher's PDF, also known as Version of record

Cyswllt i'r cyhoeddiad / Link to publication

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA): Forrest, J. A. H., Bouchet, P. J., Barley, S. C., McLennan, A. G., & Meeuwig, J. J. (2021). True blue: Temporal and spatial stability of pelagic wildlife at a submarine canyon. *Ecosphere*, *12*(3), Article e03423. https://doi.org/10.1002/ecs2.3423

Hawliau Cyffredinol / General rights Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

• Users may download and print one copy of any publication from the public portal for the purpose of private study or research.

- You may not further distribute the material or use it for any profit-making activity or commercial gain
  You may freely distribute the URL identifying the publication in the public portal ?

Take down policy If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

#### esa

## ECOSPHERE

### COASTAL AND MARINE ECOLOGY

# True blue: Temporal and spatial stability of pelagic wildlife at a submarine canyon

J. A. H. Forrest,<sup>1</sup> P. J. BOUCHET,<sup>1,2</sup> S. C. BARLEY<sup>(D)</sup>,<sup>1</sup>,<sup>†</sup> A. G. MCLENNAN,<sup>1</sup> AND J. J. MEEUWIG<sup>1</sup>

<sup>1</sup>School of Biological Sciences, University of Western Australia, 35 Stirling Hwy, Crawley, Perth 6009 Australia <sup>2</sup>School of Ocean Sciences, Bangor University, LL59 5AB Menai Bridge, Bangor, UK

Citation: Forrest, J. A. H., P. J. Bouchet, S. C. Barley, A. G. McLennan, and J. J. Meeuwig. 2021. True blue: Temporal and spatial stability of pelagic wildlife at a submarine canyon. Ecosphere 12(3):e03423. 10.1002/ecs2.3423

**Abstract.** In coastal systems, marine-protected areas (MPAs) have been shown to increase the diversity, abundance, and biomass of wildlife assemblages as well as their resilience to climate change. The effectiveness of pelagic MPAs is less clear, with arguments against their establishment typically based on the highly mobile nature of pelagic taxa. We used mid-water stereo-baited remote underwater video systems (stereo-BRUVS) and spatial predictive models to characterize the pelagic wildlife assemblage at the head of the Perth Canyon, one of the largest submarine canyons in Australia, over a 7-yr period (2013–2019). The total number of unique taxa and mean values of taxonomic richness, abundance, fork length, and biomass demonstrated strong interannual stability, although mean taxonomic richness and abundance were significantly lower in 2018 relative to other years. Seasonal variability was absent in 2016, but in 2018, taxonomic richness and abundance were three times greater in the Austral spring than in the autumn. Some mobile megafauna were only recorded at the Perth Canyon Marine Park (PCMP) in the autumn, suggesting a seasonal component to their occurrence. The fine-scale distribution of pelagic taxa at the canyon head was largely stable over time, with many areas of higher relative probability of presence located outside protected zones. Despite a degree of variability that may relate to the effect of the El Niño Southern Oscillation on the Leeuwin Current, the PCMP assemblage demonstrates a relatively high degree of spatiotemporal stability. Stronger protection of the PCMP (IUCN II or higher) would potentially improve conservation outcomes for many species of pelagic wildlife.

**Key words:** annual and seasonal variability; mid-water stereo-BRUVS; marine-protected areas; pelagic fish and sharks; Perth Canyon; Western Australia.

Received 20 April 2020; revised 24 September 2020; accepted 17 October 2020; final version received 13 January 2021. Corresponding Editor: Sean P. Powers.

**Copyright:** © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited. † **E-mail:** shanta.barley@gmail.com

#### INTRODUCTION

The pelagic zone is one of the least protected ecosystems on Earth, and its sharks and rays are among the most at risk vertebrates, with almost a quarter of species designated as endangered, vulnerable, or near threatened by the International Union for Conservation of Nature (IUCN) Red List (Dulvy 2014, Dulvy et al. 2017). Top pelagic predators such as the hammerhead shark *Sphyrna* sp. have been reduced in abundance to 2–10% of pre-industrial fishing levels, and few spatial refuges remain (Myers et al. 2007, Letessier et al. 2019, Queiroz et al. 2019). The inherent noisiness of fisheries data, a lack of standardized and/or species level data and widespread lack of transparency in some parts of the fishing industry, means that the magnitude of these declines remains debated (Beddington et al. 2007). However, the cross-taxa nature of the downward

population trajectories of sharks, tuna, and other pelagic predators is clear (Juan-Jordá et al. 2011, Dulvy 2014, Palomares et al. 2020). Efforts to manage and/or reverse these declines have largely failed thus far (Pauly 2018), with only few exceptions (Neilson et al. 2013).

There is now strong evidence that coastal MPAs increase the density and biomass of sharks (Bond et al. 2012, Frisch and Rizzari 2019) and other marine taxa (Lester and Halpern 2008, Marshall et al. 2019), including mobile species (Kerwath et al. 2008). MPAs also create spillover effects that boost adjacent fisheries and biodiversity (Kerwath et al. 2013, Di Lorenzo et al. 2016), and increase ecological resilience to climate change (Bates et al. 2013, Davies et al. 2017, Roberts et al. 2017). There is some evidence that pelagic MPAs, similarly, can benefit mobile species (Jensen et al. 2010, Boerder et al. 2017, Doherty et al. 2017), although this is still debated (Le Quesne and Codling 2009, Sibert et al. 2012). Small, strategically placed MPAs can benefit mobile species, especially when local fishing pressures are high (Kerwath et al. 2008, Mee et al. 2017) and large pelagic MPAs such as the British Indian Ocean Territory MPA have been shown to encompass the activity spaces of blue marlin Makaira nigricans, sailfish Istiophorus platypterus, silky sharks Carcharhinus falciformis, and yellowfin tuna Thunnus albacares (Carlisle et al. 2019).

A traditional argument against the implementation of pelagic MPAs is that they are difficult and/or prohibitively expensive to enforce (Game et al. 2009, Kaplan et al. 2010). Moreover, many pelagic species are highly mobile and often follow spatially dynamic hydrographic features such as fronts, traveling up to thousands of kilometers in a year (Kaplan et al. 2010, Runge et al. 2014). Thus, pelagic MPAs may only protect a fraction of a species' life cycle, and it has been argued that dynamic pelagic MPAs would have greater conservation benefits than traditional, static MPAs (Hobday et al. 2014, Garcia-Rojas et al. 2018, Gilman et al. 2019). However, pelagic megafauna also display broad predictability in their movement patterns. Sharks and other pelagic wildlife such as the black marlin Istiompax indica may display natal or regional philopatry, revisiting the same locations over time (Jorgensen et al. 2010, Howey-Jordan et al. 2013, Rogers et al. 2015). Mobile species also tend to migrate along prescribed highways (Horton et al. 2017, Sequeira et al. 2018) and use submarine canyons and other locations of topographical complexity as reliable and predictable foraging grounds (Bouchet et al. 2017, Boerder et al. 2019, Gilman et al. 2019).

Despite being one of the least explored ecosystems on the planet (Matos et al. 2018), submarine canyons are keystone structures that strongly influence the distribution of pelagic wildlife (Vetter et al. 2010, Santora et al. 2018). Submarine canyons provide refugia from predators in otherwise homogeneous and exposed shelf and slope environments (Fernandez-Arcaya et al. 2017, Jones et al. 2019). Their complex bathymetry interacts with currents to generate upwellings, fronts, internal waves, and sub-surface eddies that inject nutrients into the euphotic zone, creating primary production hotspots that concentrate krill and other small prey for larger, mobile predators (Bax and Hedge 2015, Huang et al. 2018, Santora et al. 2018). Shelf-incising submarine canyons are of particular ecological importance because they allow the direct transfer of cold, nutrient-rich water into the neritic zone (Santora et al. 2018).

One example of such a submarine canyon is the Perth Canyon in Western Australia. Carved over 100 million years ago by an ancient river in Western Australia, the 4683 m deep Perth Canyon is the second largest submarine canyon on Australia's continental margin (Huang et al. 2014). Over 75% of the canyon's depth range lies in darkness and its vertical cliffs, 600 m tall in places, support a diverse range of invertebrates and coral graveyards dating to the last ice age (Trotter et al. 2019). The head of the Perth Canyon lies approximately 60 km west of Perth, which is the capital and largest regional population center of Western Australia. At the canyon head, which lies in 281 m of water, ROV surveys have revealed a benthos dominated by crabs, polychaete tube worms, glass sponges, and lobsters while grenadiers and deep-sea dories are the most common demersal fish species (Trotter et al. 2019).

The water column of the Perth Canyon consists of several major water masses, including the Leeuwin Current, a warm (16–24°C) surface layer, the Leeuwin Undercurrent, a deeper, northward-flowing and nutrient-rich layer, and Upper Circumpolar Deep Water, a 2 km deep

ECOSPHERE **\*** www.esajournals.org

water mass that originates in Antarctica (Rennie et al. 2009, Trotter et al. 2019). Inter-current shear and a strong interaction between the canyon and the Leeuwin Undercurrent generate deep cyclonic eddies and internal waves, causing upwelling, the formation of a high-productivity, subsurface layer (Rennie et al. 2009, Huang et al. 2014), and aggregations of pygmy blue whales Balaenoptera musculus brevicauda and other mobile megafauna (Rennie et al. 2009, Erbe et al. 2015, Bouchet et al. 2017, Trotter et al. 2019). Moreover, this upwelling occurs throughout the year to some extent, such that the Perth Canyon may act as a year-round foraging ground for some species (Pattiaratchi and Buchan 1991, Feng et al. 2009, Rennie et al. 2009, Nanson et al. 2018).

In 2012, almost 2.4 million km<sup>2</sup>, or 36% of Australia's ocean, was given marine park status, including the 7409 km<sup>2</sup> Perth Canyon Marine Park (PCMP). However, in 2013, the newly elected government suspended the marine parks plan and commissioned an independent review that was eventually published in 2016. When the management plans were finally implemented in July 2018, the level of protection afforded to the head of the Perth Canyon had been downgraded from the originally planned IUCN II (i.e. no fishing) zoning to IUCN IV zoning which allows both recreational and commercial fishing and limits protection to the sea floor habitat.

Mid-water stereo-baited remote underwater video systems (stereo-BRUVS) are increasingly used to document pelagic assemblages as an alternative to lethal, fisheries-based sampling, particularly in MPAs (Letessier et al. 2019, Bouchet et al. 2020). Here, we use a long-term stereo-BRUVS dataset collected between 2013 and 2019 to assess the potential conservation value of the area in terms of the predictability of its aggregations of wildlife. Specifically, we test the hypothesis that the assemblage at PCMP does not display significant variation in total unique taxa, taxonomic richness, abundance, biomass, and size between years, that is, displays sufficient spatiotemporal stability to warrant stronger protection (Fig. 1). We also model the probability of occurrence of pelagic taxa at the canyon head, predicting that fine-scale spatial trends are largely consistent over time.

The study builds on an initial analysis at this location that predicted the probability of

FORREST ET AL.

occurrence of pelagic taxa in and around the canyon head (Bouchet and Meeuwig 2015), with the aim of establishing whether current levels of protection are commensurate to the conservation importance of this site to pelagic taxa. Our hypothesis that the PCMP would display temporal stability in these characteristics was underpinned by evidence that (1) upwelling, and therefore, potentially favorable prey conditions likely occur year-round at the canyon (Pattiaratchi and Buchan 1991, Rennie et al. 2009, Nanson et al. 2018), and (2) Perth Canyon is used as a foraging ground and/or navigational marker by several iconic marine megafauna, including cetaceans and shark species such as the tiger shark Galeocerdo cuvier and the shortfin mako Isurus oxyrinchus (Ferreira et al. 2015, Corrigan et al. 2018).

#### **M**ETHODS

#### Mid-water stereo-BRUVS

Mid-water stereo-BRUVS were deployed in strings of five rigs, with each rig on a string separated by 200 m of line (Appendix S1: Fig. S1; Bouchet et al. 2018). The data from 2013 were sourced from Bouchet and Meeuwig (2015), although in that study the rigs were not joined in longline configurations but still drifted largely in parallel. String is defined as the sampling unit, noting that individual rigs are not statistically independent because they are deployed from a single point of entry. The longline configuration, or string, simplifies retrieval and minimizes loss of equipment. Rigs were deployed for a minimum of two hours and then retrieved. The surveys were conducted from the vessels RV Whale Song, Thalanyji, and NEGU under an exemption from the Australian Marine Safety Authority (EX2016/A185; EX2017/A007A). All fieldwork was approved under ethics permit RA/3/100/ 1484.

#### Field sampling design

Sampling sites were chosen based on a generalized random tessellation stratified design (Fig. 1), with a focus on the area of the PCMP that lies in and adjacent to the canyon head. Austral autumn was considered to span the period between April and June, with Austral spring occurring between October and December



Fig. 1. Deployments of mid-water stereo-BRUVS at the head of Perth Canyon in autumn 2013 (white), autumn 2016 (light gray), spring 2016 (light green), autumn 2018 (dark gray), spring 2018 (dark green), and autumn 2019 (black) with the internal yellow shaded box representing the boundary of the current IUCN IV zone and the larger, gray box representing the outer perimeter of the PCMP (IUCN VI).

(Sequeira et al. 2012). Replicating the autumn 2013 survey conducted by Bouchet and Meeuwig (2015), surveys were conducted in the autumn of 2016, 2018, and 2019 while spring surveys occurred in 2016 and 2018. The spring 2018 and autumn 2019 surveys were the only ones to be conducted after enforcement of the MPA began in July 2018. A total of 398 rigs were deployed as part of 78 strings, with an average of 13 strings deployed per survey across seabed depths ranging from 172 to 1550 m (Appendix S1: Table S1). Because the 2013 rigs largely drifted together from the point of deployment, group deployments were treated as strings. All sampling was undertaken during daylight hours between 7:00 and 17:00 to minimize any effects of crepuscular and nocturnal behavior on fishes (Axenrot et al. 2004), which may bias our interpretation of results.

#### Image analysis

Videos were imported into the Event Measure software package (SeaGIS Pty) for processing. Processing commenced once the rig stabilized at a depth of 10 m below the sea surface and ended after two hours. Animals were identified to species level where possible and to genus or family otherwise. We estimated relative abundance as the maximum number of individuals of a given taxa in a single frame (Cappo et al. 2006; MaxN). We also took fork length measurements that generated estimates of distance of individual animals from the rig. Lengths were converted to weight using taxa-specific length-weight relationships derived from FishBase (Froese and Pauly 2020) and then summed to estimate biomass. Image analysis included independent checks on taxa identifications performed by experienced analysts.

#### Data analysis

Taxonomic richness, abundance, biomass, and fork length.-A taxa accumulation curve was calculated for combined surveys using string as the sampling unit and the Michaelis-Menten model to estimate the pool size and the number of samples needed to record 50% of the taxa (Keating and Quinn 1998). The total unique number of taxa observed on a string  $(TR_U)$  was calculated as the sum of taxa found on any given rig across a string. Taxonomic richness (TR), total abundance (TA), total biomass (TB; kg; excluding three common minke whales Balaenoptera acutorostrata), and mean fork length (FL; cm) were calculated for each rig, with TA, TB, and FL then log-10transformed to meet the assumption of homoscedasticity (Zar 2010). Finally, TR, logTA, logTB, and logFL were averaged to generate mean values for each string as the sampling unit.

Interannual and seasonal variation in TR<sub>U</sub>, TR, TA, TB, and FL was tested using permutational analysis of variance (PERMANOVA) based on unrestricted permutations, with survey as the fixed factor (Zar 2010, Anderson 2017). All analyses were conducted using software Primer v.7 (Clarke and Gorley 2020). For each univariate variable, a Euclidean distance matrix was calculated. The multivariate taxa abundance data were square-root-transformed and a Bray-Curtis resemblance matrix then calculated. The Bray-Curtis resemblance matrix was chosen as it is not influenced by joint-zeros (Anderson 1997), which reduces the influence of samples with no observations. For both the univariate and multivariate data, one-way PERMANOVA was used to test for an effect of year on TR<sub>U</sub>, TR, TA, TB, and FL. As the surveys were imbalanced (four autumnal vs. two spring surveys), only the autumn data from the four years were used to control for seasonal effects. Where one-way PERMANOVA results were significant, pairwise tests were used to determine which years were responsible for the differences.

Two-way PERMANOVA was used to test the effect of year and season on the same assemblage variables listed above, based on the balanced autumn and spring data for 2016 and 2018. Where the interaction was insignificant, it was removed and the PERMANOVA recalculated (Zar 2010). No pairwise tests were necessary as each factor only had two levels. For the

taxonomic assemblage data, a canonical analysis of principal co-ordinates (CAP) was also used to visualize the distinctiveness of the pelagic taxa in multivariate space (Anderson 2008).

#### Fine-scale spatial and temporal stability

To determine whether the spatial distribution of taxa was consistent in time, we built presenceonly maximum entropy (MaxEnt) models of wildlife occurrence (Phillips et al. 2006, Bouchet and Meeuwig 2015) in statistical software package R v3.4.3 (R Core Team 2019). We considered an identical set of candidate explanatory variables (depth, aspect northing, rugosity, longitudinal curvature, cross-sectional curvature, slope, slope variance, topographic position index, fractal dimension, and sea surface temperature mean and variance), in addition to daytime remotesensed chlorophyll a (mg/m<sup>3</sup>), derived from 8day AQUA MODIS composite images available at 4 km resolution (Bouchet and Meeuwig 2015). Rugosity was included as a variable due to its well-understood influence on surface productivity and prey availability, via upwelling, eddy formation, and diurnally migrating species (Rennie et al. 2009, Bouchet et al. 2017, Maggs et al. 2019). Temperature and chlorophyll *a* values were sourced from the Environmental Data Connector (http://www.pfeg.noaa.gov/products/EDC/) and both seasonal means and variances calculated.

Observations of pelagic taxa were pooled and thinned to reduce the effects of spatial auto-correlation and improve potential model performance (Verbruggen et al. 2013). We used the ENMEval package (Muscarella et al. 2014) for tuning, allowing optimal feature classes (linear vs. quadratic) and regularization multipliers ( $\beta$ , from 1 to 8 in one-unit increments) to be chosen automatically according to Akaike's secondorder information criterion score (AIC<sub>c</sub>; Sequeira et al. 2012). We then identified the most relevant predictors using iterative functions from the MaxentVariableSelection package (Jueterbock et al. 2016), run at a contribution threshold of 5%. Reduced models were implemented using the R package dismo (Hijman et al. 2016), using 1000 background (pseudo-absence) points, randomly extracted based on a custom bias grid as defined by Bouchet and Meeuwig (2015) and rescaled to range between 1 and 20 (Elith et al. 2010). Models were trained on 75% random partitions of the data (repeated n = 50 times), reserving the remaining 25% for performance evaluation based on the true skill statistic (Allouche et al. 2006). We interpreted MaxEnt's logistic output as a measure of relative occurrence probability and mapped final predictions across the region of study.

To ensure robust comparisons of spatial patterns across time periods, we truncated model predictions made in areas characterized by novel conditions relative to the training data, using the multivariate environmental similarity surface (MESS) tool (Elith et al. 2011). This tool quantifies the distance in environmental space between each prediction pixel and the set of reference points contained in the original sample (Dormann et al. 2007, Fitzpatrick and Hargrove 2009). To improve the credibility of the model predictions, we computed MESS indices for each survey, and only retained those intersecting grid cells that yielded positive MESS values in all years (Elith et al. 2011, Verbruggen et al. 2013). We then compared maps based on a structural similarity index (SSIM, ranging from -1 to +1), with SSIM values typically used qualitatively rather than in the context of explicit thresholds (Robertson et al. 2014, Jones et al. 2016). A value of -1 indicates complete dissimilarity between the spatial structure of the maps, 0 indicates that species distributions are independent and 1 shows that the maps are identical (Robertson et al. 2014, Jones et al. 2016).

#### Results

# Taxonomic richness, abundance, biomass, and fork length

The taxa accumulation curve for the combined survey data based on 78 strings indicated a taxonomic pool of 40, with 16 samples required to capture 50% of the pool. In total, 1,467 individuals representing 32 taxa and 19 families or classes were recorded. We also recorded 105 unidentified teleost juvenile fishes (defined as translucent and typically <2 cm in fork length), noting that accurate identification of most larval fish species based on morphology is largely impossible during early life stages (Ko et al. 2013). The most common observed taxa included the following: Decapterus scad *Decapterus* sp. (31% of total mean abundance), jacks Carangidae sp. (20%), common dolphinfish *Coryphaena hippurus* (9%), and juveniles (9%). Observed fishes ranged in size from 0.5-cm-long juveniles to a 5.3-m-long northern minke whale (Tables 1, 2).

One-way PERMANOVA demonstrated that the autumnal assemblage in the study area did not vary between years in terms of TR<sub>U</sub>, TB, or FL (Fig. 2; Table 3). However, both TR (pseudo-F = 4.49, P = 0.009) and logged TA differed

Table 1. Family, scientific name, and common name for pelagic taxa recorded in the PCMP across all surveys, ordered alphabetically by family.

Family	Scientific name	Common name			
Balaenopteridae	Balaenoptera acutorostrata	Northern minke whale			
Carangidae	Carangidae sp	Jacks			
	Decapterus sp	Decapterus scad			
	Naucrates ductor	Pilotfish			
	Seriola lalandi	Yellowtail amberjack			
Carcharhinidae	Carcharhinus brachyurus	Copper shark			
	Carcharhinus falciformis	Silky shark			
	Carcharhinus sp	Requiem shark			
	Galeocerdo cuvier	Tiger shark			
	Prionace glauca	Blue shark			
Hydrozoa (class)	Hydrozoa sp	Sea jellies			
Coryphaenidae	Coryphaena equiselis	Pompano dolphinfish			
	Coryphaena hippurus	Common dolphinfish			
Delphinidae	Delphinus delphis	Common dolphin			
Echeneidae	Echeneis naucrates	Live sharksucker			
	Remora remora	Shark sucker			
Fistulariidae	<i>Fistularia</i> sp	Cornetfish			
Istiophoridae	Istiompax indica	Black marlin			
Lamnidae	Isurus oxyrinchus	Shortfin mako			
Molidae	Mola mola	Ocean sunfish			
Monacanthidae	Aluterus monoceros	Unicorn leatherjacket filefish			
	Monacanthidae sp	Leatherjackets			
Myliobatidae	Mobula sp	Mobula ray			
Nomeidae	Psenes sp	Psenes driftfish			
Scombridae	Acanthocybium solandri	Wahoo			
	Katsuwonus pelamis	Skipjack tuna			
	Thunnus maccoyii	Southern bluefin tuna			
	Thunnus sp	Thunnus tuna			
Sphyraenidae	Sphyraena sp	Barracudas			
Sphyrnidae	Sphyrna mokarran	Great hammerhead			
Syngnathidae	Syngnathidae sp	Pipefishes			
Tetraodontidae	Arothron firmamentum	Starry toado			
Juvenile	Juvenile sp	Juvenile			

#### COASTAL AND MARINE ECOLOGY

Table 2. Common names for pelagic taxa recorded in the PCMP across all surveys, with total number of sight-
ings (n), mean number of sightings per string (n mean), and average fork lengths (FL; cm), ordered alphabeti-
cally by common name. Ellipses indicate where no observations of a taxa were recorded.

	Autumn							Spring					
	2	2013		2016		2018		2019		2016	1	2018	
Common name	п	<i>n</i> mean	n	<i>n</i> mean	n	<i>n</i> mean	n	<i>n</i> mean	n	<i>n</i> mean	n	<i>n</i> mean	FL (cm)
Barracuda	1	0.11											
Black marlin		-							1	0.09			198.2
Blue shark	1	0.11											272.9
Common dolphin					7	0.41							204.9
Common dolphinfish	48	5.33	21	2.10	19	1.12	102	5.37	8	0.73	12	1.00	68.6
Copper shark					2	0.12	7	0.37					196.6
Cornetfish			2	0.20	1	0.06	1	0.05					18.8
Decapterus scad	199	22.11	81	8.10	19	1.12	151	7.95	38	3.45	118	9.83	5.78
Great hammerhead					1	0.06							270
Jacks	4	0.44			30	1.76							3.26
Juvenile			62	6.20	5	0.29	3	0.16	35	3.18	-	-	2.9
Leatherjackets									4	0.36	5	0.42	3.21
Live sharksucker					1	0.06							
Mobula rav									1	0.09			
Northern minke whale			3	0.30									470
Ocean sunfish	2	0.22											
Pilotfish	36	4.00	4	0.40	2	0.12	4	0.21	2	0.18	1	0.08	13.2
Pipefishes									1	0.09			
Pompano dolphinfish					2	0.12							
Psenes driftfish	4	0.44							3	0.27	1	0.08	12.3
Requiem shark											1	0.08	
Sea jellies					1	0.06					-		
Shark sucker	6	0.67			-	0.00							
Shortfin mako	1	0.11							3	0.27			140.9
Silky shark	1	0.11							0	0			204.9
Skipiack tuna	-	0.11	2	0.20	-	-	13	0.68					45
Southern bluefin tuna			-	0.20	15	0.88	18	0.00					36.8
Starry toado					10	0.00	3	0.16					38.5
Thunnus tuna		0.89	•••				U	0.10					00.0
Tiger shark	0	0.07	•••				2	0.11					191.4
Unicorn leatherjacket					1	0.06							28.6
Wahaa									2	0.18			202
Vallowtail ambariack			•••						4	0.10	 22	1.83	44.1
renowian aniberjack	•••	•••	• • •	•••		•••		•••		•••	22	1.05	44.1

between years (pseudo-F = 5.39, P = 0.002). Pairwise comparisons (Appendix S1: Table S2) confirmed that 2018 differed from all other years for both TR (2013 t = 3.27, P = 0.005; 2016 t = 3.13, P = 0.005; 2019 t = 2.92, P = 0.006) and logged TA (2013 t = 3.76, P = 0.001; 2016 t = 3.2, P = 0.004; 2019 t = 3.78, P = 0.003), and in both cases, TR and TA values in 2018 were on average roughly 50% of those in the other years. Mean TR, for example, was 0.6 taxa per survey  $\pm 0.10$ 

in 2018, compared to  $1.29\pm0.21$  in 2013,  $1.34\pm0.24$  in 2016, and  $1.1\pm0.13$  in 2019 (Appendix S1: Table S3).

Autumn and spring surveys differed significantly in terms of  $TR_U$  (pseudo-F = 4.29, P = 0.048), TR (pseudo-F = 11.4, P = 0.001), TA (pseudo-F = 17.2, P = 0.001), and FL (pseudo-F = 5.46, P = 0.034). There was an interaction between year and season for all variables except TR<sub>U</sub> (Table 3, Fig. 2). Spring was always



Fig. 2. Interannual (left) and seasonal (right) variation in (a) total unique taxonomic richness (TR<sub>U</sub>), (b) mean taxonomic richness (TR), (c) mean logged total abundance (TA; no.), (d) mean logged total biomass (TB; kg),

ECOSPHERE **\*** www.esajournals.org

#### (Fig. 2. Continued)

excluding a single minke whale *Balaenoptera acutorostrata* in autumn 2016, and (e) mean logged fork length (FL; mean  $\log_{10}$  cm), with standard error bars. There was a significant effect of year on TR and TA, while seasonal differences were significant for TR<sub>U</sub>, TR, TA, and FL, with an interaction between year and season present for TR, TA, and FL. See Table 3 and Appendix S1: Table S2 for *P* values.

associated with higher TR<sub>U</sub> values than autumn, regardless of year. Seasonal differences in terms of TR and logged TA were minimal in 2016 but marked in 2018, when these measures were on average 2.7 times higher in spring compared to autumn. Mean logged FL showed the opposite trend, with a mean value in spring 2018 that was half that in the autumn (0.73  $\pm$  0.084 vs. 1.41  $\pm$  0.14 per survey).

#### Species composition

Multivariate PERMANOVA indicated that the composition of the assemblages differed between years ( $P \le 0.00001$ ) and by season ( $P \le 0.00001$ ; Table 4). The CAP visualization of the multi-year autumnal logged abundance data showed separation of taxa along year gradients, although there was overlap between the assemblages in 2018 and 2019 (Fig. 3). Taxa that contributed the most to dissimilarity between years are shown using vector plots and included southern bluefin tuna Thunnus maccoyii, which was strongly associated with 2018, pilotfish Naucrates ductor and Decapterus scad (2013) and juvenile fishes (2016). CAP visualization of abundance data in 2016 and 2018 revealed significant seasonal shifts, with the spring surveys not only overlapping in space but also clearly distinct from the autumn assemblages. Spring assemblages were strongly associated with jacks and Decapterus scad, autumn 2016 with pilotfish, juvenile fishes, and wahoo and autumn 2018 with southern bluefin tuna.

Mobile megafauna were primarily observed in autumn and included southern bluefin tuna (n = 33; 2018/2019), common dolphin *Delphinus delphis* (n = 7; 2018), copper shark *Carcharhinus brachyurus* (n = 9; 2018/2019), northern minke whale *Balaenoptera acutorostrata* (n = 3; 2016), tiger shark (n = 2; 2019), and blue shark *Prionace glauca* (n = 1; 2013). In contrast, some megafauna were primarily or only observed in spring, including shortfin mako shark *Isurus oxyrinchus* (n = 3, spring 2016; n = 1, autumn 2013) and wahoo *Acanthocybium solandri* (n = 2; 2016).

#### Fine-scale spatial and temporal stability

Spatial comparisons of model predictions between the six surveys suggest that the fine-scale habitat usage patterns of pelagic taxa within the study area largely did not differ either between seasons or years (Fig. 4; Appendix S1: Fig. S2). Thirteen of the 15 SSIM values were positive, with 11 of these comparisons suggestive of relatively strong positive spatial correlation (0.1 < SSIM < 0.6) and three comparisons more consistent with spatial independence (-0.1 < SSIM < 0.1). Only one comparison (autumn/spring 2016) displayed a notably negative SSIM value (-0.2) consistent with seasonal partitioning.

#### Discussion

Many pelagic taxa are nomadic, displaying plastic migratory schedules and long-distance (>1000s kms) movements influenced by dynamic oceanographic features (Game et al. 2009, Briscoe et al. 2016, Braun et al. 2019). A perennial criticism of pelagic MPAs remains that they are ill-suited to the life histories of the species that they purport to conserve (Le Quesne and Codling 2009, Graham et al. 2012, Gilman et al. 2019). We found that a pelagic assemblage associated with a major Indian Ocean bathymetric feature, the Perth Canyon, demonstrated temporal stability across a sevenyear period, with no effect of year on total number of unique taxa, mean biomass, and mean size. Moreover, even though variation was recorded between years in taxonomic richness and abundance, pairwise comparisons confirmed that the variability was due to 2018 alone, with these values stable between the remaining sampled years.

These results add to growing evidence that Perth Canyon is a habitat that supports relatively high abundances of pelagic fishes (Bouchet et al. 2017) and aggregations of wildlife, including the pygmy and Endangered Antarctic blue whale *Balaenoptera musculus intermedia* (Double et al. 2014, Nanson et al. 2018). Our finding that the Perth Canyon pelagic assemblage is relatively

Table 3. Results of PERMANOVAs testing the effect of (A) year on total unique number of taxa (TR<sub>U</sub>), mean taxonomic richness (TR), mean total abundance (TA), mean total biomass (TB; kg), and mean fork length (FL; cm) (one-way PERMANOVA) and (B) year and season on the same variables (two-way PERMANOVA).

Variable	df	SS	MS	Pseudo-F	Р	perms	
A							
TRu							
Survey	3	6.50	2.17	1.08	0.371	800	
Res	50	100.80	2.02				
Total	53	107.30					
TR							
Survey	3	4.46	1.49	4.49	0.009	999	
Res	50	16.57	0.33				
Total	53	21.03					
TA							
Survey	3	1.11	0.37	5.39	0.002	999	
Res	50	3.44	0.07				
Total	53	4.55					
ТВ							
Survey	3	4.76	1.59	1.38	0.238	999	
Res	50	57.55	1.15				
Total	53	62.30					
FL							
Survey	3	0.79	0.26	1.32	0 291	998	
Res	47	9.30	0.20	1.01	0.271	,,,,	
Total	50	10.08	0.20				
B	00	10.00					
TRu							
Season	1	9 37	9 37	1 29	0.048	33	
Rec	17	102 59	2.18	4.27	0.040	55	
Total	18	111.06	2.10				
TP	40	111.90					
Concor	1	2.05	2.05	11.02	0.002	005	
Vear	1	0.54	5.05	1.02	0.002	995	
fear SauVa	1	0.54	0.54	1.95	0.175	990	
Sex re	1	5.14 10.44	3.14	11.56	0.001	995	
Kes	45	12.44	0.28				
Iotal	48	20.57					
IA		0 = 1	0.74	45.00	0.000	~~~	
Season	1	0.74	0.74	15.00	0.002	997	
Year	1	0.01	0.01	0.24	0.624	997	
YexSe	1	0.85	0.85	17.20	0.001	996	
Res	45	2.23	0.05				
Total	48	4.12					
TB							
Season	1	0.79	0.79	1.15	0.276	997	
Res	47	32.27	0.69				
Total	48	33.06					
FL							
Season	1	1.34	1.34	11.05	0.003	995	
Year	1	0.12	0.12	0.96	0.318	995	
SexYe	1	0.66	0.66	5.46	0.034	998	
Res	41	4.96	0.12				
Total	44	7.48					

*Notes:* Mean values were calculated across samples on a given string and a single minke whale *Balaenoptera acutoros-trata* was excluded from TB in autumn 2016. Significant *P* values have been formatted in bold.

spatiotemporally stable adds to the location's ecological importance and suggests that strong, year-round protection (i.e., IUCN II or above) could have major conservation outcomes for pelagic wildlife.

In 2016, levels of taxonomic richness, abundance, and biomass remained high throughout the year, with a seasonal signature effectively absent. Oceanographic variability in the vicinity of the Perth Canyon is driven by the Leeuwin Current, a 100 km wide, ~300 m deep current of warm water that runs south along the coast of Western Australia. In autumn, a strong Leeuwin Current suppresses upwelling, yet cooling and storm activity destratify the water column, allowing deep, nutrient-rich water to reach the surface and cause sporadic peaks in primary productivity (Lourey et al. 2006, Koslow et al. 2008). In the spring, however, southerly winds weaken the Leeuwin Current, allowing upwelling (Rennie et al. 2009), such that the submarine canyon's attractiveness as a feeding ground for mobile megafauna may remain high throughout the year (Pattiaratchi and Buchan 1991, Feng et al. 2009, Rennie et al. 2009, Nanson et al. 2018). Indeed, our results suggest that the Perth Canyon may act as an important stopover for a range of migratory species, regardless of season. Many megafauna species, including the tiger shark, common dolphin, and southern bluefin tuna, were recorded within the study area in autumn, despite overall abundance and diversity typically being higher in spring.

The more pronounced seasonality observed in 2018, in addition to the anomalously low levels of taxonomic richness and abundance observed in this year compared to others, may reflect interactions between the Leeuwin Current and easterly wind anomalies in the equatorial Pacific (i.e., ENSO). Unlike the other sampled years, autumn 2018 was associated with an unexpected La Niña event (Zhang et al. 2019). La Niña strengthens the Leeuwin Current's flow, driving marine heatwaves, the tropicalization of temperate communities, and changes in productivity (Feng et al. 2013, Pearce and Feng 2013, Pearce et al. 2016, Hewitt et al. 2018). For example, the 2011 La Niña event raised temperatures by over 4°C and reduced chlorophyll concentrations from 1 to <0.25 mg/m<sup>3</sup> (Chen et al. 2019). As such, the 2018 La Niña may have affected the productivity and

ECOSPHERE **\*** www.esajournals.org

Table 4. Results of (A) one-way multivariate PERMANOVA testing the effect of year on relative abundances of pelagic taxa at the PCMP and (B) two-way multivariate PERMANOVA testing for the effect of both year and season.

	df	SS	MS	Pseudo-F	Р	perms	
A							
Year	3	15802	5267.2	4.53	0.000001	569156	
Res	50	58079	1161.6				
Total	53	73881					
В							
Year	1	6511.3	6511.3	7.1537	0.00001	95235	
Season	1	11205	11205	12.311	0.00001	95193	
YexSe	1	4740.8	4740.8	5.2085	0.0005	95046	
Res	45	40959	910.2				
Total	48	64497					



Fig. 3. Canonical analysis of principal (CAP) co-ordinates visualizing differences in taxonomic composition between (left) autumn in different years and (right) seasons in 2016 and 2018, based on a square-root-transform of abundance data and Bray-Curtis similarity matrix. Species with strong associations include the following: Decapterus scad *Decapterus* sp., jacks Carangidae sp., pilotfish *Naucrates ductor*, and southern bluefin tuna *Thunnus maccoyii*.

other characteristics of the Perth Canyon, with knock-on effects on taxonomic richness and abundance.

We also found some evidence for spatial stability in the fine-scale predicted distribution of pelagic wildlife at the head of Perth Canyon. The vast majority of the 15 SSIM values were positive, suggesting that taxa are likely to occur in the same habitats regardless of season or year. Areas of greater probability of presence were associated with the southern and eastern borders of the IUCN IV box in addition to the less protected



Fig. 4. Structural similarity (SSIM) index values for compared surveys. SSIM values vary between 1 and -1, with these indicating, respectively, positive and negative spatial correlations.

southern rim of the canyon tip, where depth-integrated primary production levels are highest and krill corralled by upwellings and eddies attract foraging pygmy blue whales (Rennie et al. 2009). The only clear exception to the trend was the autumn-spring 2016 comparison, which displayed a negative SSIM value of  $\sim -0.2$  and was more consistent with mild inter-seasonal spatial partitioning. This anomaly is plausibly related to the occurrence in the first half of 2016 of a strong El Niño event, which has been shown to weaken the Leeuwin Current and reduce prey availability in the eastern Indian Ocean, forcing mobile predators to shift offshore (Crocker et al. 2006, Koslow et al. 2008, Hill et al. 2016, Sprogis et al. 2018). The high abundance and taxonomic richness values observed in the canyon head in 2016 are also consistent with it potentially having an ecological function as a megafauna refuge during environmentally challenging years (Yoklavich et al. 2000).

The strong interannual stability demonstrated by the pelagic assemblage at the Perth Canyon head appears to have masked underlying changes in taxonomic composition. For example, pilotfish and Decapterus scad were strongly associated with 2013 and 2019, whereas juvenile fishes were more closely associated with 2016 and southern bluefin tuna with 2018. The CAP plots were also consistent with high seasonal turnover in taxa composition, with clear separation between spring and autumn assemblages and strong, seasonal associations of jacks and Decapterus scads with spring. Autumns were primarily associated with southern bluefin tuna and juvenile fishes, consistent with previous studies suggesting that recruitment increases with strong Leeuwin Current flows (Pearce et al. 2016). While a degree of taxonomic turnover at this pelagic hotspot is consistent with prey patchiness as an important pelagic influence on predator abundance (Benoit-Bird et al. 2013, Ainley et al. 2017),

ECOSPHERE **\*** www.esajournals.org

we note that our results also demonstrated interannual stability in the total unique number of taxa at the PCMP. As such, it appears that the canyon head remains a pelagic biodiversity hotspot despite changes in the dominant taxa from year to year.

A caveat to our results is that our sampling design was limited to the Austral autumn and spring and thus can only provide seasonal snapshots of the PCMP assemblage. While these snapshots were compiled over a relatively long time period and focused on a datadeficient area, monthly sampling would have enabled a more robust understanding of seasonal variability. Moreover, although mid-water stereo-BRUVS are an effective, non-destructive methodology available to quantify remote, patchy pelagic assemblages (Letessier et al. 2015), their ability to detect is a function of deployment depth and bait type, with the biases surrounding the use of BRUVS described in detail in Bouchet and Meeuwig (2015). Thus, interpretation of our MaxEnt results is vulnerable to issues surrounding imperfect detectability, such that the failure to detect a species does not necessarily equate to true absence (Bouchet and Meeuwig 2015, Jones et al. 2019). Our surveys will not have detected all taxonomic groups present at the canyon, particularly rare or low-abundance species; however, the taxa accumulation curve suggests that all major groups are likely represented.

Another potential criticism of our study may be that our sampling effort was insufficient to detect differences between seasons and years; however, we conducted post hoc power analyses, following Cohen (1988). We note that in the case of total number of unique taxa, which had the least significant *P* value (0.39) for the between-year ANOVA, the effect size, *f*, was 0.14, indicating that our detectable effect size was closer to small (f = 0.1) than medium (f = 0.25; Cohen 1988) given the sample sizes and variances in each survey. As such, the stability observed was unlikely to be a type II error where we failed to see interannual and seasonal differences.

There are over 9000 submarine canyons globally, measuring over 25,000 km in cumulative length (Huang et al. 2014, Fernandez-Arcaya et al. 2017). In Australia alone, there are 713 submarine canyons, 95 of which are shelf-incising (Huang et al. 2014). Despite their ecological importance, it was estimated in 2014 that just 8% of submarine canyons in southeastern and southwestern Australia were protected by Australian Marine Parks (AMPs), declining to 1% in the north (Huang et al. 2014). Protection of these keystone structures is dwindling rather than increasing: In 2018, the main Perth Canyon head was stripped of its IUCN II status and downgraded to IUCN IV in order to "improve access to important fishing areas," with the original IUCN II zone transplanted to a smaller head approximately 40 km further offshore (Southwest Marine Parks Network Management Plan 2018).

Strengthening protection within the PCMP could improve conservation outcomes for a range of pelagic wildlife. Many species appear to use the canyon both across seasons and years, with the Critically Endangered southern bluefin tuna, for example, observed in both 2018 and 2019, while pygmy blue whales have been observed for durations of roughly a month during the summer (Double et al. 2014, Nanson et al. 2018). Yet the region around Perth is subject to high levels of recreational fishing relative to other parts of the Western Australian coast, and the PCMP is the target of a growing charterbased fishing industry (Ryan et al. 2015). Strengthening protection at the PCMP would therefore protect associated wildlife from areaspecific stressors, consistent with Kerwath et al. (2008).

Moreover, many migratory species in the region experience multiple stressors along their ranges, including acoustic pollution from shipping (i.e., Double et al. 2014), thus improved protection at the PCMP may provide a haven from cumulative, sub-lethal threats, consistent with Game et al. (2009). Lastly, there is evidence that large MPAs such as the British Indian Ocean Territory MPA (BIOT; 640,000 km<sup>2</sup>) and the proposed Sea of the Hebrides MPA (10,325 km<sup>2</sup>) encompass the majority of the activity ranges of some mobile species (Doherty et al. 2017, Richardson et al. 2018, Carlisle et al. 2019). Although the PCMP (7409 km<sup>2</sup>) is not as large as BIOT MPA, it is similar in size to the Sea of Hebrides MPA and may therefore provide some protection for some mobile species with limited movement rates.

Spatial modeling showed that areas of greater probability of presence occurred not just in the IUCN VI zone but also in the least protected (IUCN V) waters at the southern rim of the canyon. This finding indicates that the current zoning plan may be incommensurate with the conservation value of the PCMP to pelagic wildlife populations, and suggests that IUCN II zoning should be reinstated to the majority of the canyon head. The precautionary principle states that conservative action is prudent when uncertainty levels are high (Falcy 2016). Although we did not examine the broader PCMP assemblage directly, it could be argued that the entire length of the submarine canyon extending to the EEZ should also receive higher levels of protection. This is especially true as despite strong fisheries governance in Australia, targeted fish populations have declined by one third in a decade (Edgar et al. 2018) and pelagic sharks have declined by over 70-90% in 50 yr (Roff et al. 2018). Stronger protection of locations predictably used by ocean wildlife is necessary to protect all life stages along their transoceanic journeys (Boerder et al. 2019). Submarine canyons such as the PCMP are clear candidates for strong protection if we are to halt and reverse declines in pelagic wildlife.

#### **A**CKNOWLEDGMENTS

The authors acknowledge Nikki DeCampe, Claire Raphael, Vyv Summers, Adam Jolly, and Hanna Jabour Christ, for their contributions to logistics, fieldwork, and data management. This research was funded through the Ian Potter Foundation and the first author.

## LITERATURE CITED

- Ainley, D. G., K. Lindke, G. Ballard, P. O. Lyver, S. Jennings, V. Toniolo, J. Pennycook, M. Massaro, and J. A. Santora. 2017. Spatio-temporal occurrence patterns of cetaceans near Ross Island, Antarctica, 2002–2015: implications for food web dynamics. Polar Biology 40:1761–1775.
- Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43:1223–1232.
- Anderson, M. J. 2008. Animal-sediment relationships re-visited: characterising species' distributions

along an environmental gradient using canonical analysis and quantile regression splines. Journal of Experimental Marine Biology and Ecology 366:16– 27.

- Anderson, M. J. 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley Stats-Ref: Statistics Reference Online 1–15.
- Anderson, T. W. 1997. An introduction to multivariate statistical analysis. Third edition. John Wiley & Sons, Stanford, California, USA.
- Axenrot, T., T. Didrikas, C. Danielsson, and S. Hansson. 2004. Diel patterns in pelagic fish behaviour and distribution observed from a stationary, bottom-mounted, and upward-facing transducer. Journal of Marine Science 61:1100–1104.
- Bates, A. E., N. S. Barrett, R. D. Stuart-Smith, N. J. Holbrook, P. A. Thompson, and G. J. Edgar. 2013. Resilience and signatures of tropicalization in protected reef fish communities. Nature Climate Change 4:62–67.
- Bax, N., and P. Hedge. 2015. NERP Marine Biodiversity Hub Final Report 2011–2015. Report to Department of the Environment. Canberra, Australia.
- Beddington, J. R., D. J. Agnew, and C. W. Clark. 2007. Current problems in the management of marine fisheries. Science Magazine 316:1713–1716.
- Benoit-Bird, K. J., et al. 2013. Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. PLOS ONE 8:e53348.
- Boerder, K., A. Bryndum-Buchholz, and B. Wom. 2017. Interactions of tuna fisheries with the Galapagos marine reserve. Marine Ecology Progress Series 585:1–15.
- Boerder, K., L. Schiller, and B. Worm. 2019. Not all who wander are lost: improving spatial protection for large pelagic fishes. Marine Policy 105:80–90.
- Bond, M. E., E. A. Babcock, E. K. Pikitch, D. L. Abercrombie, N. F. Lamb, and D. D. Chapman. 2012. Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier reef. PLOS ONE 7:e32983.
- Bouchet, P. J., T. B. Letessier, M. J. Caley, S. L. Nichol, J. M. Hemmi, and J. J. Meeuwig. 2020. Submerged carbonate banks aggregate pelagic megafauna in offshore tropical Australia. Frontiers in Marine Science 7:1–14.
- Bouchet, P. J., and J. J. Meeuwig. 2015. Drifting baited stereo-videography: a novel sampling tool for surveying pelagic wildlife in offshore marine reserves. Ecosphere 6:1–29.
- Bouchet, P. J., J. J. Meeuwig, Z. Huang, T. B. Letessier, S. L. Nichol, M. J. Caley, and R. A. Watson. 2017. Continental-scale hotspots of pelagic fish abundance inferred from commercial catch records. Global Ecology and Biogeography 26:1098–1111.

- Bouchet, P., C. Phillips, Z. Huang, J. Meeuwig, S. Foster, and R. Przesławski. 2018. Comparative assessment of pelagic sampling methods used in marine monitoring. Report to the National Environmental Science Programme, Marine Biodiversity Hub.
- Braun, C. D., P. Gaube, T. H. Sinclair-Taylor, G. B. Skomal, and S. R. Thorrold. 2019. Mesoscale eddies release pelagic sharks from thermal constraints to foraging in the ocean twilight zone. Proceedings of the National Academy of Sciences of the United States of America 116:17187–17192.
- Briscoe, D. K., S. M. Maxwell, R. Kudela, L. B. Crowder, and D. Croll. 2016. Are we missing important areas in pelagic marine conservation? Redefining conservation hotspots in the ocean. Endangered Species Research 29:229–237.
- Cappo, M., E. Harvey, and M. Shortis. 2006. Counting and measuring fish with baited video techniques an overview. Australian Society for Fish Biology Workshop Proceedings 101–114.
- Carlisle, A. B., D. Tickler, J. J. Dale, F. Ferretti, D. J. Curnick, T. K. Chapple, R. J. Schallert, M. Castleton, and B. A. Block. 2019. Estimating space use of mobile fishes in a large marine protected area with methodological considerations in acoustic array design. Frontiers in Marine Science, 6.
- Chen, M., C. B. Pattiaratchi, A. Ghadouani, and C. Hanson. 2019. Seasonal and inter-annual variability of water column properties along the Rottnest continental shelf, south-west Australia. Ocean Science 15:333–348.
- Clarke, K., and R. Gorley. 2020. PRIMER v7: user Manual/Tutorial. PRIMER-E, Plymouth, Auckland, New Zealand.
- Cohen, J. 1988. Statistical power analysis for the behavioral sciences. Second edition. Lawrence Erlbaum Associates, Hillsdale, New Jersey, USA.
- Corrigan, S., et al. 2018. Population connectivity of the highly migratory shortfin mako (*Isurus oxyrinchus* Rafinesque 1810) and implications for management in the Southern Hemisphere. Frontiers in Ecology and Evolution 6:1–15.
- Crocker, D., D. P. Costa, B. J. Le Boeuf, P. M. Webb, and D. S. Houser. 2006. Impact of El Niño on the foraging behavior of female northern elephant seals. Marine Ecology Progress Series 2:1–10.
- Davies, T. E., S. M. Maxwell, K. Kaschner, C. Garilao, and N. C. Ban. 2017. Large marine protected areas represent biodiversity now and under climate change. Scientific Reports 7:1–7.
- Di Lorenzo, M., J. Claudet, and P. Guidetti. 2016. Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component. Journal for Nature Conservation 32:62–66.

- Doherty, P. D., et al. 2017. Testing the boundaries: seasonal residency and inter-annual site fidelity of basking sharks in a proposed Marine Protected Area. Biological Conservation 209:68–75.
- Double, M. C., V. Andrews-Goff, K. C. S. Jenner, M. N. Jenner, S. M. Laverick, T. A. Branch, and N. J. Gales. 2014. Migratory movements of pygmy blue whales (*Balaenoptera musculus brevicauda*) between Australia and Indonesia as revealed by satellite telemetry. PLOS ONE 9:e93578.
- Dulvy, N. K., et al. 2014. Extinction risk and conservation of the world's sharks and rays. eLife 3:1–34.
- Dulvy, N. K., C. A. Simpfendorfer, L. N. K. Davidson, S. V. Fordham, A. Bräutigam, G. Sant, and D. J. Welch. 2017. Challenges and priorities in shark and ray conservation. Current Biology 27:565–572.
- Edgar, G. J., T. J. Ward, and R. D. Stuart-Smith. 2018. Rapid declines across Australian fishery stocks indicate global sustainability targets will not be achieved without an expanded network of "nofishing" reserves. Aquatic Conservation: Marine and Freshwater Ecosystems 28:1–14.
- Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. Methods in Ecology and Evolution 1:330–342.
- Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43–57.
- Erbe, C., A. Verma, R. McCauley, A. Gavrilov, and I. Parnum. 2015. The marine soundscape of the Perth Canyon. Progress in Oceanography 137:38– 51.
- F. Dormann, C., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609– 628.
- Falcy, M. R. 2016. Conservation decision making: integrating the precautionary principle with uncertainty. Frontiers in Ecology and the Environment 14:499–504.
- Feng, M., M. J. McPhaden, S. P. Xie, and J. Hafner. 2013. La Niña forces unprecedented Leeuwin Current warming in 2011. Scientific Reports 3:1–9.
- Feng, M., E. Weller, and K. Hill. 2009. The Leeuwin current. Pages 1–11 in E. S. Poloczanska, A. J. Hobday, and A. J. Richardson, editors. A Marine climate change impacts and adaptation report card for Australia 2009. NCCARF, Perth.
- Fernandez-Arcaya, U., et al. 2017. Ecological role of submarine canyons and need for canyon conservation: a review. Frontiers in Marine Science 4:1–26.
- Ferreira, L. C., M. Thums, J. J. Meeuwig, G. M. S. Vianna, J. Stevens, R. McAuley, and M. G. Meekan.

15

March 2021 **\*** Volume 12(3) **\*** Article e03423

2015. Crossing latitudes: long-distance tracking of an apex predator. PLOS ONE 10:1–17.

- Fitzpatrick, M. C., and W. W. Hargrove. 2009. The projection of species distribution models and the problem of non-analog climate. Biodiversity and Conservation 18:2255–2261.
- Frisch, A. J., and J. R. Rizzari. 2019. Parks for sharks: Human exclusion areas outperform no-take marine reserves. Frontiers in Ecology and the Environment 1–6.
- Froese, R., and D. Pauly. 2020. FishBase. www.fishba se.org
- Game, E. T., H. S. Grantham, A. J. Hobday, R. L. Pressey, A. T. Lombard, L. E. Beckley, K. Gjerde, R. Bustamante, H. P. Possingham, and A. J. Richardson. 2009. Pelagic protected areas: the missing dimension in ocean conservation. Trends in Ecology and Evolution 24:360–369.
- Garcia-Rojas, M. I., K. C. S. Jenner, P. C. Gill, M. N. M. Jenner, A. L. Sutton, and R. D. McCauley. 2018. Environmental evidence for a pygmy blue whale aggregation area in the Subtropical Convergence Zone south of Australia. Marine Mammal Science 34:901–923.
- Gilman, E., M. J. Kaiser, and M. Chaloupka. 2019. Do static and dynamic marine protected areas that restrict pelagic fishing achieve ecological objectives? Ecosphere 10:1–38.
- Graham, R. T., M. J. Witt, D. W. Castellanos, F. Remolina, S. Maxwell, B. J. Godley, and L. A. Hawkes. 2012. Satellite tracking of manta rays highlights challenges to their conservation. PLOS ONE 7: e36834.
- Hewitt, M. J., M. Hourston, and J. I. McDonald. 2018. A long way from home: biosecurity lessons learnt from the impact of La Niña on the transportation and establishment of tropical portunid species. PLOS ONE 13:e0202766.
- Hijman, R. J., S. J. Phillips, J. R. Leathwick, and J. Elith. 2016. Dismo. R package ver. 1.0-15. https://cran. r-project.org/web/packages/dismo/dismo.pdf
- Hill, N. J., A. J. Tobin, A. E. Reside, J. G. Pepperell, and T. C. L. Bridge. 2016. Dynamic habitat suitability modelling reveals rapid poleward distribution shift in a mobile apex predator. Global Change Biology 22:1086–1096.
- Hobday, A. J., et al. 2014. Dynamic ocean management: integrating scientific and technological capacity with law, policy and management. Stanford Environmental Law Journal 33:125–165.
- Horton, T. W., et al. 2017. Route fidelity during marine megafauna migration. Frontiers in Marine Science 4:422.
- Howey-Jordan, L. A., E. J. Brooks, D. L. Abercrombie, L. K. B. B. Jordan, A. Brooks, S. Williams, E.

Gospodarczyk, and D. D. Chapman. 2013. Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the Western North Atlantic. PLOS ONE 8:e56588.

- Huang, Z., S. L. Nichol, P. T. Harris, and M. J. Caley. 2014. Classification of submarine canyons of the Australian continental margin. Marine Geology 357:362–383.
- Huang, Z., T. A. Schlacher, S. Nichol, A. Williams, F. Althaus, and R. Kloser. 2018. A conceptual surrogacy framework to evaluate the habitat potential of submarine canyons. Progress in Oceanography 169:199–213.
- Jensen, O. P., S. Ortega-Garcia, S. J. D. Martell, R. N. M. Ahrens, M. L. Domeier, C. J. Walters, and J. F. Kitchell. 2010. Local management of a "Highly migratory species": the effects of long-line closures and recreational catch-and-release for Baja California striped marlin fisheries. Progress in Oceanography 86:176–186.
- Jones, A., E. Bruce, K. P. Davies, M. Blewitt, and S. Sheehan. 2019. Assessing potential environmental influences on killer whale (*Orcinus orca*) distribution patterns in the Bremer Canyon, south-west Australia. Australian Geographer 50:381–405.
- Jones, E. L., L. Rendell, E. Pirotta, and J. A. Long. 2016. Novel application of a quantitative spatial comparison tool to species distribution data. Ecological Indicators 70:67–76.
- Jorgensen, S. J., C. A. Reeb, T. K. Chapple, S. Anderson, C. Perle, S. R. Van Sommeran, C. Fritz-Cope, A. C. Brown, A. Peter Klimley, and B. A. Block. 2010. Philopatry and migration of Pacific white sharks. Proceedings of the Royal Society B: Biological Sciences 277:679–688.
- Juan-Jordá, M. J., I. Mosqueira, A. B. Cooper, J. Freire, and N. K. Dulvy. 2011. Global population trajectories of tunas and their relatives. Proceedings of the National Academy of Sciences of the United States of America 108:20650–20655.
- Jueterbock, A., I. Smolina, J. A. Coyer, and G. Hoarau. 2016. The fate of the Arctic seaweed *Fucus distichus* under climate change: an ecological niche modeling approach. Ecology and Evolution 6:1712–1724.
- Kaplan, D. M., E. Chassot, A. Gruss, and A. Fonteneau. 2010. Pelagic MPAs: The devil is in the details. Evolution 25:62–63.
- Keating, K. A., and J. F. Quinn. 1998. Estimating species richness: the Michaelis-Menten model revisited. Nordic Society Oikos 81:411–416.
- Kerwath, S. E., E. B. Thorstad, T. F. Naesje, P. D. Cowley, F. Økland, C. Wilke, and C. G. Attwood. 2008. Crossing invisible boundaries: the effectiveness of the langebaan lagoon marine protected area as a

harvest refuge for a migratory fish species in South Africa. Conservation Biology 23:653–661.

- Kerwath, S. E., H. Winker, A. Götz, and C. G. Attwood. 2013. Marine protected area improves yield without disadvantaging fishers. Nature Communications 4:1–6.
- Ko, H. L., Y. T. Wang, T. S. Chiu, M. A. Lee, M. Y. Leu, K. Z. Chang, W.-Y. Chen, and K. T. Shao. 2013. Evaluating the accuracy of morphological identification of larval fishes by applying DNA barcoding. PLOS ONE 8:e53451.
- Koslow, J. A., S. Pesant, M. Feng, A. Pearce, P. Fearns, T. Moore, R. Matear, and A. Waite. 2008. The effect of the Leeuwin Current on phytoplankton biomass and production off Southwestern Australia. Journal of Geophysical Research: Oceans 113:1–19.
- Le Quesne, W. J. F., and E. A. Codling. 2009. Managing mobile species with MPAs: the effects of mobility, larval dispersal, and fishing mortality on closure size. ICES Journal of Marine Science 66:122–131.
- Lester, S. E., and B. S. Halpern. 2008. Biological responses in marine no-take reserves versus partially protected areas. Marine Ecology Progress Series 367:49–56.
- Letessier, T. B., et al. 2019. Remote reefs and seamounts are the last refuges for marine predators across the Indo-Pacific. PLOS Biology 17:e3000366.
- Letessier, T. B., P. J. Bouchet, J. Reisser, and J. J. Meeuwig. 2015. Baited videography reveals remote foraging and migration behaviour of sea turtles. Marine Biodiversity 45:609–610.
- Lourey, M. J., J. R. Dunn, and J. Waring. 2006. A mixed-layer nutrient climatology of Leeuwin Current and Western Australian shelf waters: seasonal nutrient dynamics and biomass. Journal of Marine Systems 59:25–51.
- Maggs, J. Q., P. D. Cowley, S. N. Porter, and A. R. Childs. 2019. Should I stay or should I go? Intrapopulation variability in movement behaviour of wide-ranging and resident coastal fishes. Marine Ecology Progress Series 619:111–124.
- Marshall, D. J., S. Gaines, R. Warner, D. R. Barneche, and M. Bode. 2019. Underestimating the benefits of marine protected areas for the replenishment of fished populations. Frontiers in Ecology and the Environment 17:407–413.
- Matos, F. L., S. W. Ross, V. Huvenne, J. S. Davies, and M. R. Cunha. 2018. Canyons pride and prejudice: exploring the submarine canyon research landscape, a history of geographic and thematic bias. Progress in Oceanography 169:6–19.
- Mee, J. A., S. P. Otto, and D. Pauly. 2017. Evolution of movement rate increases the effectiveness of marine reserves for the conservation of pelagic fishes. Evolutionary Applications 10:444–461.

- Muscarella, R., P. J. Galante, M. Soley-Guardia, R. A. Boria, J. M. Kass, M. Uriarte, and R. P. Anderson. 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods in Ecology and Evolution 5:1198– 1205.
- Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315:1846–1850.
- Nanson, R., Z. Huang, P. Bouchet, S. Nichol, and K. Miller. 2018. An eco-narrative of Perth Canyon Marine Park - South-west marine region. Report to the National Environmental Science Programme, Marine Biodiversity Hub, Perth, Western Australia, Australia.
- Neilson, J., F. Arocha, S. Cass-Calay, J. Mejuto, M. Ortiz, G. Scott, C. Smith, P. Travassos, G. Tserpes, and I. Andrushchenko. 2013. The Recovery of Atlantic Swordfish: the Comparative Roles of the Regional Fisheries Management Organization and Species Biology. Reviews in Fisheries Science 21:59–97.
- Palomares, M. L. D., R. Froese, B. Derrick, J. J. Meeuwig, S. L. Nöel, G. Tsui, J. Woroniak, D. Zeller, and D. Pauly. 2020. Fishery biomass trends of exploited fish populations in marine ecoregions, climatic zones and ocean basins. Estuarine, Coastal and Shelf Science 243:1–10.
- Pattiaratchi, C., and S. J. Buchan. 1991. Implications of long-term climate change for the Leeuwin Current. Journal of the Royal Society of Western Australia 74:133–140.
- Pauly, D. 2018. A vision for marine fisheries in a global blue economy. Marine Policy 87:371–374.
- Pearce, A. F., and M. Feng. 2013. The rise and fall of the "marine heat wave" off Western Australia during the summer of 2010/2011. Journal of Marine Systems 112:139–156.
- Pearce, A., B. Hutchins, A. Hosch, and P. Fearns. 2016. Record high damselfish recruitment at Rottnest Island, Western Australia, and the potential for climate-induced range extension. Regional Studies in Marine Science 8:77–88.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231–259.
- Queiroz, N., et al. 2019. Global spatial risk assessment of sharks under the footprint of fisheries. Nature 572:461–466.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Austria, Vienna.

ECOSPHERE **\*** www.esajournals.org

17

March 2021 **\*** Volume 12(3) **\*** Article e03423

- Rennie, S. J., C. E. Hanson, R. D. McCauley, C. Pattiaratchi, C. Burton, J. Bannister, C. Jenner, and M. N. Jenner. 2009. Physical properties and processes in the Perth Canyon, Western Australia: links to water column production and seasonal pygmy blue whale abundance. Journal of Marine Systems 77:21–44.
- Richardson, A. J., K. J. Downes, E. T. Nolan, P. Brickle, J. Brown, N. Weber, and S. B. Weber. 2018. Residency and reproductive status of yellowfin tuna in a proposed large-scale pelagic marine protected area. Aquatic Conservation: Marine and Freshwater Ecosystems 28:1308–1316.
- Roberts, C. M., et al. 2017. Marine reserves can mitigate and promote adaptation to climate change. Proceedings of the National Academy of Sciences of the United States of America 114:6167–6175.
- Robertson, C., J. A. Long, F. S. Nathoo, T. A. Nelson, and C. C. F. Plouffe. 2014. Assessing quality of spatial models using the structural similarity index and posterior predictive checks. Geographical Analysis 46:53–74.
- Roff, A. G., C. J. Brown, M. A. Priest, and P. J. Mumby. 2018. Decline of coastal apex shark populations over the past half century. Communications Biology 1:1–11.
- Rogers, P. J., C. Huveneers, B. Page, S. D. Goldsworthy, M. Coyne, A. D. Lowther, J. G. Mitchell, and L. Seuront. 2015. Living on the continental shelf edge: habitat use of juvenile shortfin makos *Isurus oxyrinchus* in the Great Australian Bight, southern Australia. Fisheries Oceanography 24:205–218.
- Runge, C. A., T. G. Martin, H. P. Possingham, S. G. Willis, and R. A. Fuller. 2014. Conserving mobile species. Frontiers in Ecology and the Environment 12:395–402.
- Ryan, K. L., N. G. Hall, E. K. Lai, C. B. Smallwood, S. M. Taylor, and B. S. Wise. 2015. State-wide survey of boat-based recreational fishing in Western Australia 2013/14: fisheries Research Report No. 268. Department of Primary Industries and Regional Development, Perth, Western Australia, Australia.
- Santora, J. A., R. Zeno, J. G. Dorman, and W. J. Sydeman. 2018. Submarine canyons represent an essential habitat network for krill hotspots in a Large Marine Ecosystem. Scientific Reports 8:1–9.
- Sequeira, A. M. M., et al. 2018. Convergence of marine megafauna movement patterns in coastal and open

oceans. Proceedings of the National Academy of Sciences of the United States of America 115:3072–3077.

- Sequeira, A., C. Mellin, D. Rowat, M. Meekan, and C. Bradshaw. 2012. Ocean-scale prediction of whale shark distribution. Diversity and Distributions 18:504–518.
- Sibert, J., I. Senina, P. Lehodey, and J. Hampton. 2012. Shifting from marine reserves to maritime zoning for conservation of Pacific bigeye tuna (*Thunnus obesus*). Proceedings of the National Academy of Sciences of the United States of America 109:18221–18225.
- South-west marine parks network management plan. 2018. Australian Government, Canberra, Australian Capital Territory, Australia.
- Sprogis, K. R., F. Christiansen, M. Wandres, and L. Bejder. 2018. El Niño Southern Oscillation influences the abundance and movements of a marine top predator in coastal waters. Global Change Biology 24:1085–1096.
- Trotter, J. A., et al. 2019. First ROV exploration of the perth canyon: canyon setting, faunal observations, and anthropogenic impacts. Frontiers in Marine Science 6:1–24.
- Verbruggen, H., L. Tyberghein, G. S. Belton, F. Mineur, A. Jueterbock, G. Hoarau, C. F. D. Gurgel, and O. De Clerck. 2013. Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. PLOS ONE 8:1–13.
- Vetter, E. W., C. R. Smith, and F. C. De Leo. 2010. Hawaiian hotspots: enhanced megafaunal abundance and diversity in submarine canyons on the oceanic islands of Hawaii. Marine Ecology 31:183–199.
- Yoklavich, M. M., H. G. Greene, G. M. Cailliet, D. E. Sullivan, R. N. Lea, and M. S. Love. 2000. Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. Fishery Bulletin 98:625–641.
- Zar, J. H. 2010. Biostatistical analysis. Fifth edition. Pearson Education, Upper Saddle River, New Jersey, USA.
- Zhang, C., J. Luo, and S. Li. 2019. Impacts of tropical Indian and Atlantic ocean warming on the occurrence of the 2017/2018 La Niña. Geophysical Research Letters 46:3435–3445.

#### SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2. 3423/full