Drifting baited stereo-videography: a novel sampling tool for surveying pelagic wildlife in offshore marine reserves

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Abstract.   We present a novel system of drifting pelagic baited stereo-video cameras that operate in deep-water, topographically complex environments typically considered inaccessible for sampling. The instruments are portable, semi-autonomous and inexpensive, allowing the recording of high-definition video footage in near-real time and over broad stretches of ocean space. We illustrate their benefits and potential as non-extractive monitoring tools for offshore marine reserves with a pilot study conducted within the newly established Perth Canyon Commonwealth Marine Reserve, southwestern Australia (32° S, 115° E). Using occupancy and maximum entropy models, we predict the distribution of midwater fishes and sharks and show that their most suitable habitat encompasses a wider fraction of the canyon head than is covered by park boundaries. Our proof-of-concept study demonstrates that drifting pelagic stereo-video cameras can serve as appropriate field platforms for the construction of species distribution models with implications for ocean zoning and conservation planning efforts.

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INTRODUCTION

In response to dwindling fish stocks and concerns over the footprint of anthropogenic activities on biodiversity (Maxwell et al. 2013, Worm et al. 2013), marine protected areas (MPAs) have undergone exponential growth on a global scale (Wood et al. 2008). In the last 10 years alone, the MPA coverage of the world's oceans has indeed nearly tripled (IUCN-UNEP 2014), an expansion mostly catalyzed by the emergence of super-sized or "giant" (>100,000 km²) offshore (>200 m depth) no-take reserves (termed "VLMPAs" by Singleton and Roberts 2014) and networks thereof (Sheppard et al. 2012,

Dulvy 2013, Toonen et al. 2013). The rapid spread of spatial planning on the high seas (Ardron et al. 2008, O'Leary et al. 2012) has however outpaced the development of field technologies that can yield the ecological data necessary for assessing the value of zoning schemes on increasingly broader scales (Pala 2013). This divergence raises questions about the benefits of giant MPAs and fuels a need for the effective sampling of vagile and elusive wildlife in the remote and relatively inaccessible open ocean (Kaplan et al. 2013).

Stereo-videography is a promising candidate for the in situ monitoring of marine species. Initially pioneered for use with submersibles in the abyssal zone (Priede et al. 1994), baited

remote underwater video systems (BRUVS) have become a staple of observational studies in both tropical and temperate environments (Mallet and Pelletier 2014), where they have been employed as a non-invasive and affordable way of detecting declines in recreationally and commercially important fish populations (e.g., McLean et al. 2011), assessing wildlife distributions along climatic gradients (e.g., Langlois et al. 2012), developing predictive models for conservation planning (e.g., Moore et al. 2010, Malcolm et al. 2012), refining benthic habitat maps (e.g., Malcolm et al. 2011), documenting the extent of illegal, unreported and unregulated (IUU) fishing (Field et al. 2009), or measuring the benefits of areal closures (e.g., Harvey et al. 2012a) with identical or superior efficiency to classical extractive methods such as traps (Harvey et al. 2012c) or longlines (Santana-Garcon et al. 2014a). As demersal instruments, conventional BRUVS are nonetheless unable to function in epipelagic waters, a layer of ocean in which many data-deficient species subject to high extinction risk (e.g., large-bodied migratory sharks) are primarily confined (Priede et al. 2006, Dulvy et al. 2014). In an effort to fill this methodological gap, Heagney et al. (2007), Letessier et al. (2013) and Santana-Garcon et al. (2014b) recently tailored BRUVS to work in the water column, however their designs hinge on the use of an anchoring system, with persisting constraints on maximum operational seabed depth (ca. 120 m, typically). In their current form, pelagic stereo-BRUVS are therefore inadequate for offshore MPA applications, which commonly demand that deployments occur in depths and seabed terrains where moorings quickly become too cumbersome. Finding ways of sampling these topographically complex areas is of critical importance as there is growing evidence that seamounts, submarines canyons and other prominent geomorphic structures predictably attract mobile megafauna and may hence provide a useful blueprint for marine conservation planning (Harris and Whiteway 2009, Morato et al. 2010, Aïssi et al. 2014, Moors-Murphy 2014, Bouchet et al. 2015).

The Perth Canyon in south-western Australia (32° S, 115° E) is a compelling example of a major seafloor feature that has received surprisingly little pelagic research attention, despite showing significant levels of overlap between human (e.g.,

industrial shipping, commercial fishing, military exercises; McCauley et al. 2004) and animal (e.g., seasonal aggregations of endangered charismatic megafauna such as pygmy blue whales, *Balaenoptera musculus brevicauda*; Rennie et al. 2009a, Double et al. 2014) activity. In 2013, the Australian Government declared the establishment of two marine national parks within the Perth Canyon system as part of its strategy to implement a nation-wide network of Commonwealth Marine Reserves (CMRs, http://www.environment.gov.au/topics/marine/marine-reserves) which, at 3.1 million km^2, is currently the world's largest. This new development provided a unique opportunity to test both (1) the relevance of mid-water stereo-videography as a field data collection tool for the monitoring of offshore marine reserves, and (2) the validity of camera-derived sightings as input to species distribution models, a suite of analytical tools in growing demand to support conservation decision-making and aid reserve mapping and management (Guisan et al. 2013, Barker et al. 2014, Marshall et al. 2014). Specifically, we designed a new generation of *drifting* baited pelagic cameras suited for deployment in regions of complex seabed topography and depths greater than 100 m. These were used to document the occurrence of pelagic species within and around the formerly eastern-most national park of the Perth Canyon CMR (hereafter "the eastern park", for brevity; see *Methods: Study area* for details regarding updated zoning arrangements). Our approach relies on a simple modification of existing protocols that adds mobility to the camera systems and enables the dynamic sampling of ocean space over potentially large areas.

METHODS

Study area

Located approximately 60 km west of the Australian mainland, the Perth submarine canyon (or "Rottnest trench") is the second largest such shelf-incising feature on the country's continental margin (von der Borch 1968). It is wide (1820 km^2), deep (> 4000 m), steep, meandering, multi-branched, topographically complex (Huang et al. 2014), and known to interact strongly with the equatorward-flowing Leeuwin undercurrent to encourage the trapping of nutrients and biota, promoting high levels of

seasonal productivity, particularly within the canyon tip (Rennie et al. 2009b). Prior to the suspension of all marine reserve management plans (December 2013), the eastern park was the smaller of two IUCN category II protected areas (i.e., where prohibitions on mining/oil and gas exploration as well as commercial, recreational, or tourism-related fishing are in place; cumulative area = 1107 km^2) nestled inside the wider Perth Canyon CMR. Lying at the head of the canyon, it was embedded inside a multiple-use zone (IUCN category VI; total area = 3733 km^2) where virtually all extractive activities were permitted. A systematic review of the national network is still ongoing at the time of writing, yet this study took place when the former zoning plans were still scheduled to come into effect— and we will accordingly refer to these throughout. Park boundaries extend between 115.05°– 115.13° E and 31.92°–31.98° S, covering a geodesic area of 58.3 km^2 in depths from 635 to 1580 m.

Camera design

Our camera design is an adaptation of the method presented by Letessier et al. (2013) where anchors are no longer required and units float freely within the water column at pre-determined depths of up to 50 m (based on the accredited pressure rating of the camera housings in use), whilst travelling with prevailing currents. Soaking depth is controlled by adjusting the length of the tether line linking individual units to a cluster of surface floats, and each tether is supplemented by a pair of midwater buoys and an elasticized chord to reduce camera shake/bounce from waves and optimize footage quality (Fig. 1a).

Units consist of a central stainless steel frame (full height = 1450 mm) that supports two high definition GoPro HD Hero2 cameras mounted on a cross bar (950 mm) perpendicularly to an adjustable bait arm (1800 mm; Fig. 1b). Cameras are encased in transparent backscatter flat-port underwater housings (adaptable to fit later Hero3–3$^+$–4 models) and placed in a stereo-pair configuration; they are bolted 800 mm apart and converge inwardly at an angle of four degrees, offering a forward visibility of up to 10 m and allowing fish body length measurements to be taken based on three-dimensional trigonometry (Klimley and Brown 1983). Cameras are set to record in wide-FOV (field of view) mode to maximize the area captured in each video frame and improve detection rates. The bait arm serves a double purpose: it (1) holds a bait chamber at a chosen distance from the cameras, and (2) stabilizes the rotational movements of the unit induced by sub-surface current flows (i.e., in the same manner as a rudder), maintaining a downstream field of view. It also supports a 450 mm long perforated PVC pipe bait container that ensures the slow release and diffusion of bait in the water column throughout the duration of the deployment.

Pilchards (also known as sardines, *Sardinops sagax*) are the conventional bait type utilized in video surveys throughout Australasia. They have been validated as an appropriate choice for our region of interest (Dorman et al. 2012), and were therefore used as an attractant in this study. Standard procedures dictate that deployments of (under or up to) one hour in duration should rely on a nominal bait weight of 1 kg (Harvey et al. 2012b). Bait quantity, however, exerts little influence on the patterns of relative abundance and species richness observed in temperate fish assemblages, and larger amounts are only beneficial in allowing longer soak times (Hardinge et al. 2013). To cater for deployments in excess of three hours (as advocated by Letessier et al. 2013), we placed between 2 and 3 kg of fish parts (heads, tails and guts sourced from local factory discards and crushed into a homogenized slurry) in each bait canister.

Units are lightweight (12 kg) and portable and were launched manually (Fig. 1c). This can be done in quick succession and from a variety of platforms types and sizes (from small inflatables to large oceanographic vessels), in a range of weather conditions.

Field protocol

We undertook five trips to the eastern park between March and May 2013. Sampling occurred at nine sites during daylight hours between 07:00 am and 05:00 pm (GMT+8), at least 30 to 60 minutes after sunrise/before sundown to minimize the effects of differential crepuscular behavior in fish (Axenrot et al. 2004, Potts 2009). We deployed six pelagic camera units at each location and spaced them at a minimum distance of 250 m (Fig. 1d) to reduce the likelihood of bait plume overlap and inter-
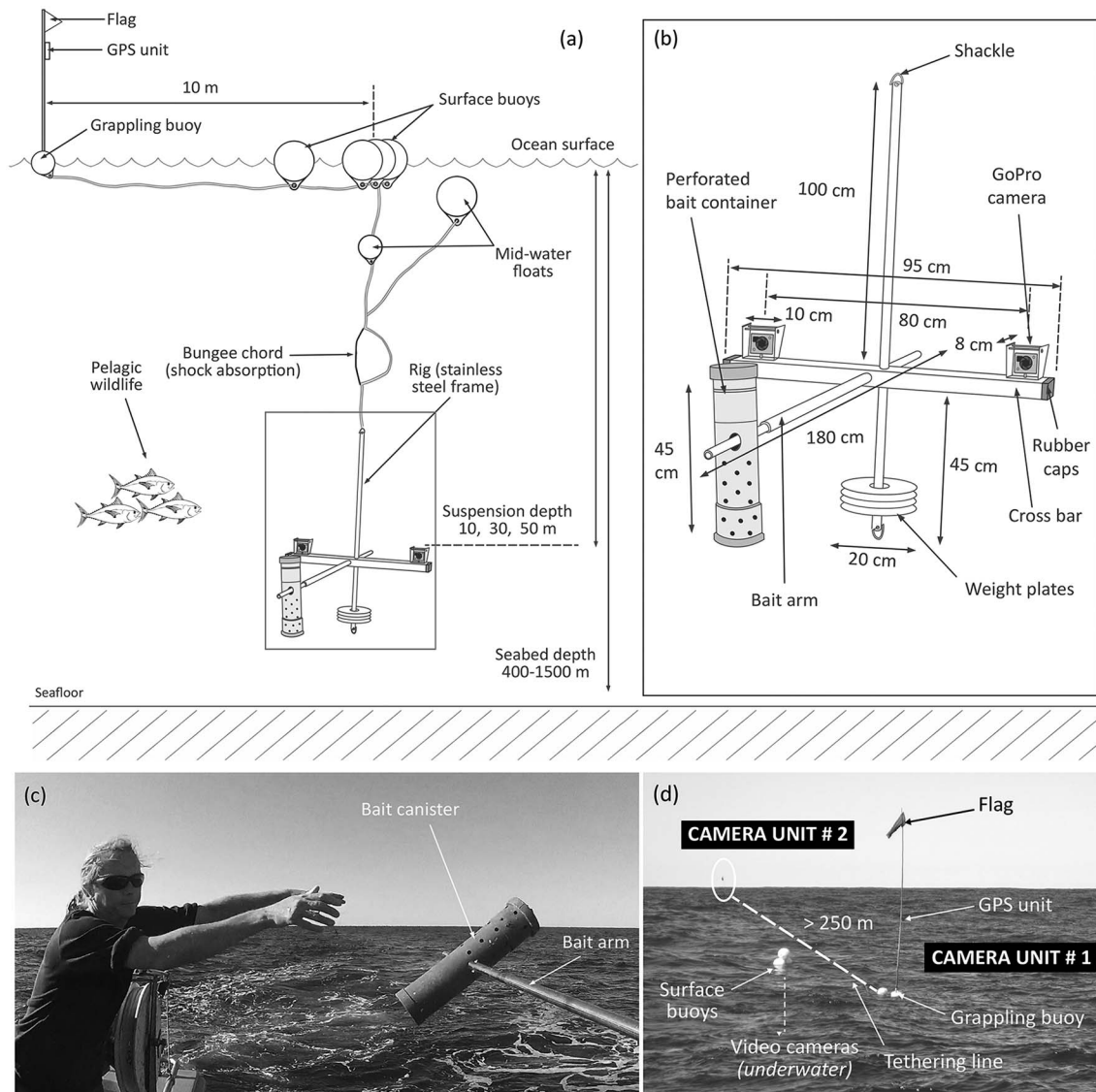
Fig. 1. Drifting baited stereo-videography sampling: (a) schematic diagram of the instruments underwater; (b) annotated blueprint of an individual camera unit; (c) manual deployment by an operator; (d) surface view of the equipment in drift.

camera fish movements (Santana-Garcon et al. 2014b). Sites were chosen according to a generalized random tessellation stratified (GRTS) design (Stevens and Olsen 2004), and spanned a depth range of 1220 m from 360 to 1580 m (Fig. 2). GRTS has become a popular alternative to traditional designs in environmental and landscape-scale surveys as (1) it yields a spatially balanced set of points with good dispersion whilst maintaining the statistical qualities of a random draw (Jiménez-Valencia et al. 2014), (2) it can accommodate unequal inclusion probabilities to allow for some level of stratification based on, say, GIS layers of habitat classes; and (3) it enables dynamic adjustments of sample sizes, thereby providing a framework for the addition of extra (contingency) sites should some be dropped because of, for example, health and safety considerations ensuing from deteriorating weather. Importantly, the integration of GRTS
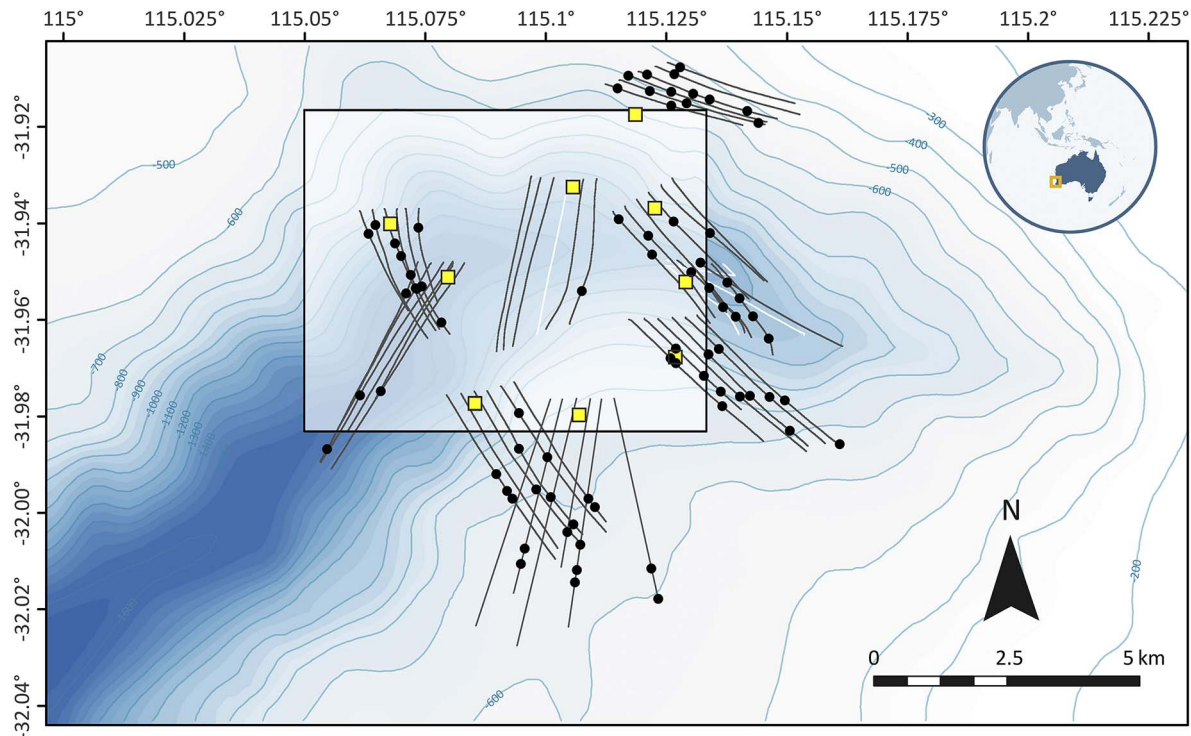
Fig. 2. Visual sampling of the eastern park within the Perth Canyon Commonwealth Marine Reserve (CMR). Study sites are shown as yellow squares and lines represent the trajectories of individual camera units ($n = 54$), color-coded by deployment (grey: full data, $n = 51$; white: no/incomplete data due to camera failure, $n = 3$). Local bathymetry is overlaid in shades of blue. The locations of wildlife sightings (based upon times of first detection) for identified species are shown as black circles. The boundaries of the eastern park appear as a dark grey outline.

with non-extractive baited videography has already been harnessed to monitor other parts of the Australian CMR network (Hill et al. 2014). Units entered the water between 300 m and 1 km upstream of each location to ensure that sampling at the site would take place with little to no human interference, and were suspended at predetermined depths of 10 ($n = 2$), 30 ($n = 2$) and 50 ($n = 2$) m. Cameras soaked for an average duration of 165 min (2.75 hours, i.e., until battery failure or exhaustion of available memory card space) and were fitted with GPS loggers that tracked their position at regular one-second intervals.

Video analysis

Digital image processing proceeded in two stages. First, we scanned individual video files using a custom-built, semi-automated MATLAB 2012a pattern recognition algorithm developed in-house at the University of Western Australia

(currently unreleased; J. Hemmi). The program scans successive frames and contrasts their intensity values with a background image dynamically calculated to reflect the current average background without the presence of objects. The difference image is then lowpass-filtered and thresholded to remove noise and the influence of small isolated objects. The final image highlights discrepancies in pixel content that occur when moving targets (e.g., animals, debris or organic particles) enter the field of view of the cameras. Discrete anomalies are compiled into a time series that can later be reviewed and validated by an operator (who checks for and confirms the presence of animals). Multiple video files can be analyzed simultaneously, leading to drastic improvements of processing times by up to a factor of three (P. Bouchet, *personal observation*). Second, we imported the videos into the EventMeasure software package (SeaGIS Pty Ltd, http://www.seagis.com.au/) for analysis, which

commenced at the point when the rig stabilized at its sampling depth. We identified (to the lowest possible taxonomic level), counted, and marked all validated animal sightings, and we also took stereo-measurements on a subset of observed individuals to yield estimates of body size (data not shown). These measurements required the manual synchronization of camera pairs using a clapperboard immediately before deployment, and were based on independent calibrations undertaken in an enclosed pool environment prior to the survey using software CAL (SeaGIS Pty Ltd) and following the protocols described by Harvey and Shortis (1998).

Spatial modeling

Albeit their practical utility in solving on-ground ecological problems has been chronically under-reported (Addison et al. 2013, Guisan et al. 2013), geographically explicit, correlative species distribution models (SDMs; Elith and Leathwick 2009) that statistically relate records of animal occurrence to environmental attributes have received widespread acclaim as a versatile discipline that can be adopted in aid of spatial planning (Guisan and Thuiller 2005, Cayuela et al. 2009, Azzellino et al. 2012, Syfert et al. 2014). Indeed, the majority of (marine) SDMs are conservation-oriented (Robinson et al. 2011), and numerous examples exist of their potential and/or success in helping to articulate strategic natural resource management schemes across a breadth of conservation scenarios, including protected area delineation (e.g., Cañadas et al. 2005, Varley and Boyce 2006, Kremen et al. 2008, Leathwick et al. 2008, Embling et al. 2010). As Australia's large maritime jurisdiction is, pragmatically, unlikely to be explored in its entirety (Butler et al. 2010), SDMs have an important role to play in facilitating the identification of hotspots of highly vagile and relatively cryptic pelagic predators and guiding the monitoring (and possible refinement) of reserves throughout the network (McGowan et al. 2013, Lavers et al. 2014).

However, despite experiencing explosive growth in the scientific literature, SDMs have some limitations. For instance, few organisms are so conspicuous that they are always observed and in practice detectability (i.e., the probability, p_i, of an individual/species i being captured

conditional on occupying a site) is seldom perfect ($p_i < 1$) (MacKenzie et al. 2002, Martin et al. 2005, Kéry 2011, Chen et al. 2013). This problem, which besets most if not all sampling techniques, including stereo-videography (Bacheler et al. 2014, Espinoza et al. 2014), has long remained neglected in ocean sciences (Monk 2014), with the consequence that modeling studies may have mistaken detection failures for true absences and erroneously skewed predictions towards the *apparent* rather than *true* distribution of their focal species (i.e., inferring where animals are most likely to be *detected*, not *located*; MacKenzie 2005, Kéry and Schmidt 2008, Lahoz-Monfort et al. 2014). Another difficulty is that the array of available SDM techniques is vast and rapidly evolving, necessitating practitioners to clearly understand the appropriateness of a given method for a given biological problem (Thuiller et al. 2009). Even when two (or more) techniques may be deemed equally valid, outputs derived from the same data may diverge. An expanding body of literature advocates the use of "ensembles" or "consensus" (i.e., combinations) of models as a way of overcoming such inter-model variability. By averaging predictions, primary signals of interest (e.g., patterns of distribution) may be disentangled from the noise of individual model errors and inaccuracies (Araújo and New 2007).

With these challenges in mind, and to support monitoring and potential zoning refinement for the Perth Canyon CMR, we took an SDM approach to inferring pelagic wildlife distributions around the eastern park. We contrasted two well-established SDM algorithms: the first, *maximum entropy* (MaxEnt; Phillips et al. 2004, Phillips et al. 2006) attempts to circumvent the issue of false negatives by focusing solely on confirmed presences (Rota et al. 2011), whilst the second, *site-occupancy modeling* (MacKenzie et al. 2002, Tyre et al. 2003), aims to decouple occurrence from detectability based on records of presence/absence (or, termed more correctly, detection/non-detection). Both are widespread, yet to our knowledge there have been limited efforts to make direct comparisons of their performance on "real-world" empirical data (but see Gormley et al. 2011 or Peterman et al. 2013, noting that their purpose was different to ours).

We begin by describing the preparation steps necessary for the implementation of the two models. We then briefly detail their conceptual underpinnings (highlighting their intrinsic discrepancies), before applying them separately to our pilot data. Lastly, we take a hierarchical (two-step) consensus approach whereby all results are first integrated into an ensemble projection *within* each model class, and both ensembles further combined. In doing so, we yield a more robust picture of pelagic wildlife dynamics in the region (Marmion et al. 2009), which we discuss with additional thoughts on the relevance of drifting videography as an open ocean sampling tool.

Data treatments

All data grooming and statistical analyses were carried out in stand-alone programs R v3.1.1 (R Development Core Team 2014), MaxEnt v3.3.3k (http://www.cs.princeton.edu/~schapire/maxent/) and ArcGIS v10.2 (ESRI 2011).

Fish detections.—Conservation planning is seldom directed at individual species, and in many instances, quantitative information about the abundance and distribution of entire guilds is integral to the decision-making process (Manley et al. 2004, Nur et al. 2010, Fitzpatrick et al. 2011, Barker et al. 2014). Much like their demersal, coastal or reef-based analogues (Watson et al. 2010, Fitzpatrick et al. 2012, Hill et al. 2014, Mallet and Pelletier 2014), the pelagic camera systems presented herein focus largely on characterizing entire fish assemblages as opposed to individual animals, and it was therefore a natural step to group all sightings before analysis, particularly given our small overall sample size. In doing so, we not only saved time and resources but also allowed for potentially rarer species to be incorporated when they would typically have been omitted from comparatively data-hungry single-species models (Arponen et al. 2008). Barker et al. (2014) further showed that pooling species *prior to* or *after* model building had a negligible impact on resulting predictions, thereby justifying our approach. Forfeiting species-specific information is an evident drawback, but we deemed it an acceptable one within the context of a pilot study.

To account for soak time heterogeneity, we clipped all individual camera trajectories to reflect the duration of their associated video file (e.g., wherever a unit captured, say, 180 minutes of video footage but was only recovered 210 minutes post-deployment, we discarded the section of its track equating to the last $210 - 180 = 30$ minutes). The cumulative length of transect surveyed in each grid cell was calculated as an explicit measure of sampling effort. We also thinned sighting locations within a distance of 300 m via the "*Spatially rarefy*" command in Brown (2014)'s SDMToolbox add-on (http://sdmtoolbox.org/; equidistant projection: Asia South Equidistant Conic) and checked for the presence of residual spatial auto-correlation using a spline correlogram (Bjørnstad and Falck 2001; as implemented in the *ncf* R package, Bjørnstad 2013).

Environmental correlates.—Following Oppel et al. (2012) and Williams et al. (2006), we generated a grid of cells with a consistent resolution of 1/250th of a degree (ca. 350 m). This grain size roughly matched the distance of separation between individual camera units and was seen as a good compromise between the quality of available covariate layers, the need to mirror the scale of the data-generating mechanism and the need to produce sufficient encounters to yield useable results. A suite of 12 geomorphic and oceanographic covariates (Appendix A) were compiled and linked with each ocean square. Remote-sensed sea surface temperature values were originally only available at 1 km resolution, and were therefore interpolated using ordinary spherical kriging (ESRI 2011).

Multicollinearity between predictors was investigated with variance inflation factors (Fox and Monette 1992) using the *vif* function in the R package *car* (Fox and Weisberg 2011) and a Spearman rank correlation coefficient r_s matrix. When variables were strongly related (that is, $|r_s| > 0.5$ and/or VIF > 2; Appendix B, Dormann et al. 2013), we only retained one from each pair to minimize the possibility of over-fitting.

Maximum entropy

Due to its consistently competitive performance compared to other classical, more established presence-only and machine learning techniques (Elith et al. 2006, Gastón and García-Viñas 2011), MaxEnt has gained prominence in wildlife research and is seeing a rapidly growing number of applications in studies of both

terrestrial and marine mobile mega-vertebrates such as sharks (Dambach and Rödder 2011, Sequeira et al. 2012), seabirds (Friedlaender et al. 2011), turtles (McClellan et al. 2014), dolphins (Thorne et al. 2012, Gomez and Cassini 2015), baleen whales (Bombosch et al. 2014), leopards (McCarthy et al. 2015), falcons (Kassara et al. 2012), owls (Carroll 2010, Isaac et al. 2013), foxes (Cleve et al. 2011), or African wild dogs (Whittington-Jones et al. 2014), among many other examples. MaxEnt is founded "on the bedrock of probability theory" (Brierley et al. 2003), and a complete description of the mechanics underlying the algorithm is given by Elith et al. (2011) and Baldwin (2009). Its fundamental rationale is elementary: if the whereabouts of a species were unknown (i.e., had we not collected any sightings data), we would have no ground to expect that the species prefers any habitat over any other. We could, therefore, do no better than surmise its distribution (in *geographical* space) is uniform and that, by extension, it associates with environmental conditions in proportion to their availability (Elith et al. 2011). It follows that, when modeling habitat preferences, the solution of maximum entropy (i.e., which produces a target distribution that is maximally uninformative) should be selected, so long as it satisfies constraints imposed by the empirical observations (Martínez-Freiría et al. 2008). MaxEnt finds this solution by identifying the probability density of covariates at presence sites that is most similar to that of covariates recorded across the whole ("background") landscape. The main strengths of the method lie in its ability to efficiently handle complex relationships (Phillips and Dudík 2008), its robustness at small sample sizes (Hernandez et al. 2006, Wisz et al. 2008, Williams et al. 2009) and its adaptability to a range of data types and sources, from satellite tracking experiments (Edrén et al. 2010) to visual (Ainley et al. 2012) or acoustic line transects (Brierley et al. 2003). Despite these demonstrated merits, the use of MaxEnt as a conservation instrument has been the subject of an ongoing debate (Hastie and Fithian 2013, Yackulic et al. 2013, Monk 2014), mostly because the accessibility and user-friendly nature of the software seem to have cultivated misconceptions about its limitations and central assumptions. It needs to be clear that:

(1) MaxEnt is not immune to the obstacles posed by imperfect detectability (Dorazio 2012);
(2) contrary to common belief, MaxEnt does not provide measures of occupancy but merely yields *relative* maps of suitability (Phillips et al. 2006);
(3) by default, MaxEnt assumes that all locations on the landscape are equally likely to be sampled.

We are fully aware of (1) yet we note that in the presence of detection heterogeneity, MaxEnt has been suggested as an adequate avenue for analysis for rare and cryptic species at small sample sizes (Rota et al. 2011, Tsai-Yu et al. 2012); it may thus be a reliable option in our case. We further argue that (2), at least so long as it is openly acknowledged, is not necessarily a roadblock, since MaxEnt's relative likelihoods (or rankings of sites) may sometimes suffice from a conservation planning perspective (Guillera-Arroita et al. 2015), and one could post-process them in order to obtain estimates of true occupancy probabilities (Hauser and McCarthy 2009, Guillera-Arroita et al. 2014). Finally, the assumption implicit in (3) does not require a uniformly random sample in *geographic* space but rather in *environmental* space (Merow et al. 2013), and methods of accounting for sampling bias have been proposed accordingly (Phillips et al. 2009, Kramer-Schadt et al. 2013).

Here, the restricted geographical extent of the study region obviated the need for latitudinal bias correction (i.e., the area occupied by a square of ocean did not vary with latitude; Brown 2014) however we created an explicit bias grid reflecting survey intensity throughout the region (log of cumulative length of transect traversed, in km), and applied it as a template for down-weighting the extraction of background ("pseudo-absence") points in zones of intensified search effort (Elith et al. 2010, Syfert et al. 2013, Bombosch et al. 2014, Fourcade et al. 2014).

Halvorsen (2013) and Merow et al. (2013) cautioned against "standard MaxEnt practice", the tendency for authors to uncritically accept regular parameter settings, with strong implications for model quality. One example of this is the regularization multiplier β, a model shrinkage control used to balance the trade-off between

model fit and complexity (i.e., avoid over-fitting) that has a significant influence on MaxEnt's outputs but whose default value is rarely overruled in practice. Accordingly, we employed Warren et al. (2010)'s ENMTools package (http://enmtools.blogspot.com.au/) to perform tuning and variable reduction based on Akaike's information criterion score (corrected for small sample sizes, AICc). This approach has been suggested as a useful option when data are scarce (Warren and Seifert 2010). Model construction was undertaken with restricted settings (i.e., linear and quadratic features only, as per Sequeira et al. 2012), and began with a full covariate set and candidate models with β values ranging from 1 to 10 (in increments of one). As recommended by Warren and Seifert (2010), we excluded models with zero parameters (which may occur with limited sample sizes and elevated β values). Once an optimal β was found (AICc minimized), all possible covariate formulations were tested and ranked, and relative weights (wAICc) computed as a measure of each model's strength of evidence (Link and Barker 2006). Those models within three AICc units were extracted and the contribution of each was weighted according to its wAICc value to build an ensemble prediction. Jack-knife tests were also conducted to infer the relative importance of individual variables.

Site-occupancy

The seminal contributions of MacKenzie et al. (2002) and MacKenzie et al. (2003) overturned conventional belief that the ambiguity surrounding observed zeros in most field settings could not be lifted. The statistical machinery they developed, broadly referred to as *site-occupancy* models, is indeed capable of adjusting for possible non-detections and species misidentification, and has proliferated almost exponentially in the ecological literature of the past decades (for a complete review, see Bailey et al. [2014], and relevant sections in Kellner and Swihart [2014]). The crux of the approach lies in formatting the results of multiple visits to a site into a collection of detection histories that can convey information about the detection process and its inherent error rate (Kéry et al. 2013). Like MaxEnt, however, some authors have been critical of this reasoning for at least three reasons:

(1) Replicated sampling occasions may simply not be logistically realistic as they multiply research and field costs, and within fixed budgetary regimes, imply sacrificing the generality of results by reducing the number of surveyed locations (Lele et al. 2012, Shannon et al. 2014).

(2) Stringent assumptions of population closure, independence and constant occupancy between surveys apply, and are likely untenable in many situations (Rota et al. 2009).

(3) Evidence indicates that the quality of occupancy estimates naturally declines with decreasing sample size and detection probability (McKann et al. 2013), a possible issue with elusive animals such as pelagic fishes and sharks (Kéry 2011).

To address this, we used the *single-visit* algorithm available through the function *svocc* inside the *detect* R package (Sólymos et al. 2014). First introduced by Lele et al. (2012), this framework improves existing occupancy methods by relaxing the aforementioned constraints and allowing the analysis of non-repeated data. It is conceptually tantamount to a zero-inflated binomial regression (later adapted to deal with Poisson-distributed counts; Sólymos et al. 2012) whereby a latent occurrence state (ψ) and an observation process (detection, p, conditional on ψ) are modeled separately as Bernoulli distributions (Kéry 2011). The only requisite is that covariate sets be partially disjoint and contain at least one numeric (non-categorical) term (Lele et al. 2012), conditions that we could easily meet. As in MaxEnt, we examined all possible formulations of environmental predictors, computed relative model weights (wAICc) and used these to combine the predictions of each model (Araújo and New 2007). In all runs, detectability was assumed to be affected by survey effort, taken as the logarithm of the total length of transect traversed in each grid cell.

Predictive performance and model comparison

Acknowledging the shortcomings of the area under the curve of the receiver operating characteristic (AUC) and Cohen's Kappa κ (Cohen 1960) as indices of model discriminatory power (Gwet 2002, Lobo et al. 2008), model

Table 1. Pelagic species observed in the Perth Canyon eastern park, ordered by family.

Family	Scientific name	Common name	n†	MaxN‡	IUCN§
Ariommatidae	*Ariomma indicum*	Indian ocean driftfish	2	3	NE
Carangidae	*Atule mate*	Yellowtail scad	1	1	NE
	Caranx sexfasciatus	Bigeye trevally	1	1	LC
	Decapterus sp.	Scads	36	31	
	Naucrates ductor	Pilot fish	23	7	NE
Carcharhinidae	*Carcharhinus falciformis*	Silky shark	1	1	NT
	Prionace glauca	Blue shark	1	1	NT
Coryphaenidae	*Coryphaena hippurus*	Common dolphinfish	8	47	LC
Echeneidae	*Remora remora*	Sucker fish	2	5	NE
Fistulariidae	*Fistularia* sp.	Cornet fishes	1	1	
Lamnidae	*Isurus oxyrinchus*	Shortfin mako shark	1	1	VU
Molidae	*Mola mola*	Ocean sunfish	2	1	NE
Monacanthidae		Filefishes	1	1	
Scombridae	*Thunnus* sp.	Tunas	1	8	
Sphyraenidae	*Sphyraena* sp.	Barracudas	1	1	

† Total number of sightings per species.
‡ Maximum number of individuals (per species) seen at any one time in a given video frame (conservative estimate of relative abundance).
§ Species conservation status according to the International Union for Conservation of Nature, with Vulnerable (VU) < Near threatened (NT) < Least concern (LC) < Not evaluated (NE).

performance was evaluated in each case based on the true skill statistic (TSS, Allouche et al. 2006), derived from 50 bootstrap replicate runs. Forecasts from the MaxEnt and occupancy ensembles were then weighted by their associated mean TSS value to generate a final predictive map, after translating MaxEnt's raw outputs into true probabilistic space. Guillera-Arroita et al. (2014) provide the correct equations for this, and suggest that an estimate of the required scaling factor (i.e., average species prevalence across the landscape) can be acquired from the ratio of detection counts to sampled sites. We believe, however, that such a value would be negatively biased in a survey subject to incomplete detectability. We therefore transformed MaxEnt results using the average occupancy probability returned by the single-visit models as our estimate.

RESULTS

Underwater footage

A total of 144 hours of underwater video footage was collected over 51 transects spanning a cumulative linear distance of 249.5 km. With an average length per transect of 4.9 km, this equates to a coverage of 3.5% of the surface area of the eastern park, based on an approximate visual search half-width of 10 m either side of the line (Fig. 2). Cameras documented 15 species from 11 families ($n = 84$ sightings), the most diverse being carangids (jacks, pompanos, mack-

erels) and the most abundant being coryphaenids (dolphin fish) (Table 1; Appendices C and D).

The majority of species were observed as singletons, although dolphin fish (*Coryphaena hippurus*), tunas (*Thunnus* sp.) and scads (*Decapterus* sp.) were encountered in medium to large schools (maximum of 47 individuals seen at any one time). Similarly, most species (60%) were only recorded once, with the exception of scads, pilot fish (*Naucrates ductor*) and dolphin fish, which were detected on up to 36 different transects (see Supplement). All sharks sighted were classed as either "vulnerable" or "near-threatened" according to the International Union for Conservation of Nature (IUCN) Red List of endangered species (Table 1), and were at various stages of sexual maturity, as inferred from the stereo-video length measurements (adult male blue shark *Prionace glauca*: 273 cm; sub-adult female shortfin mako shark *Isurus oxyrinchus*: 207 cm; sub-adult female silky shark *Carcharhinus falciformis*: 193 cm; Poisson 2007). Animals were detected on 82% of deployments (42 out of 51), with the number of species ranging from one to four.

Species accumulation

The examination of animal response curves over time (cumulative mean richness and relative abundance (MaxN) over all transects, compiled in 15-minute time intervals as per Santana-Garcon et al. 2014b) revealed little sign of species accumu-
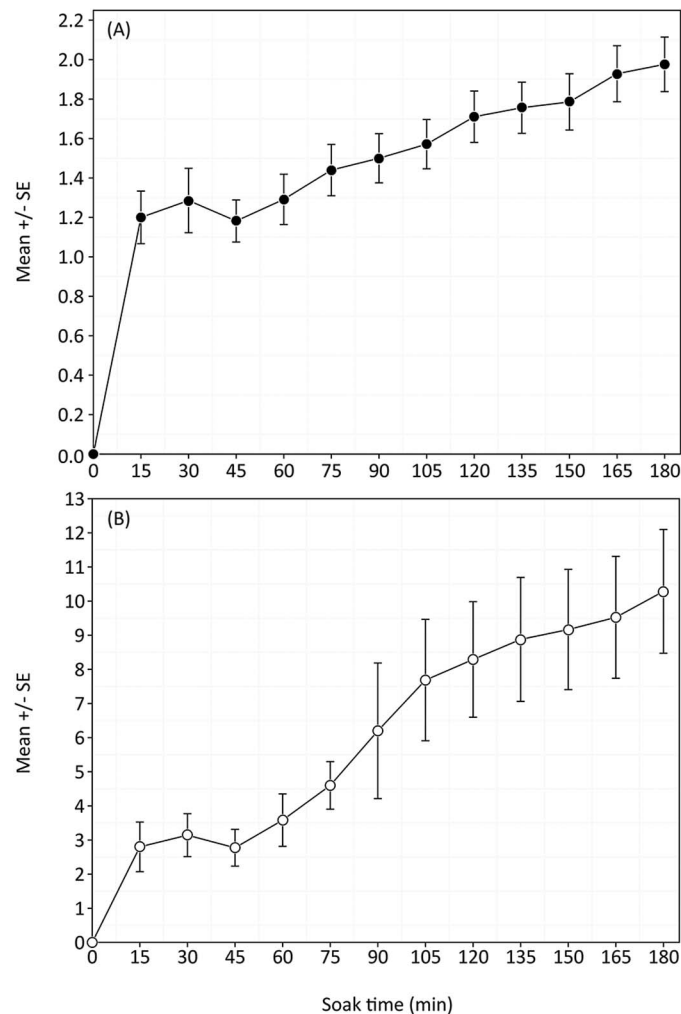
Fig. 3. Temporal accumulation of new species (A) and individuals (B, as measured by MaxN per species) in drifting baited stereo-video samples. Values represent means over all deployments.

lation, even after 180-minute soaks (Fig. 3). Our results mimic those of Santana-Garcon et al. (2014b), with an initially sharp increase in species count immediately after deployment followed by a lesser but sustained sloped after ca. 15–30 minutes, and an approximately constant rate of increase for the number of individuals.

Habitat suitability models

Pelagic fishes and sharks were detected in 55 of 307 sampled grid cells. The average ± 1 SD cumulative length of transects surveyed per cell was 738.95 ± 526.71 m. All input variables but depth were selected in the best MaxEnt models, and a tuning with a regularization parameter of β

= 7 received the greatest statistical support based on the AICc. Easting and SST variance were identified as the two most influential parameters both individually and within larger model sets. Slope variance, rugosity and northing made smaller contributions in this order. Covariate response curves indicated that suitability increased as both easting and northing did, but exhibited a negative response to higher rugosity, slope and sea surface temperature variability (Appendix E). This suggests that pelagic animals may prefer more thermally stable habitats over seafloors of northerly and northeasterly aspect. The highest ranked single-visit occupancy models (i.e., of lowest AICc) included both depth and

Table 2. Model-averaged parameter estimates from occupancy models of pelagic wildlife in the Perth Canyon. SD is the square root of the unconditional variance estimator. Importance is calculated for β coefficients as the sum of the model weights for models containing that parameter.

Parameter	Mean	SD	2.5%†	97.5%‡	Importance
β [Depth]	0.119	0.130	−0.135	0.373	0.29
β [Cross-sectional curvature]	−0.066	0.102	−0.266	0.135	0.21
β [Longitudinal curvature]	−0.104	0.139	−0.375	0.168	0.23
β [Easting]	0.620	0.467	−0.295	1.534	0.50
β [Fractal dimension]	0.057	0.103	−0.145	0.260	0.06
β [Northing]	−0.030	0.057	−0.141	0.081	0.11
β [Rugosity]	−0.053	0.091	−0.231	0.126	0.12
β [Slope variability]	−0.008	0.020	−0.048	0.031	0.06
β [SST variability]	−0.069	0.091	−0.247	0.108	0.21
P [log(Effort)]	0.784	0.444	−0.086	1.654	...

† Lower and ‡ upper limits of the 95% confidence interval, approximated as 1.96 ± SD.

easting. These two variables were identified as the most important (Table 2), and respectively emerged in 55% and 100% of the reduced set of 51 models used for ensemble building (which had a cumulative selection weight of 0.502). Curvatures and SST variance were equally influential, and exerted a negative effect on occupancy. There was a strong positive effect of sampling effort on detectability (Table 2).

The average ± 1 SD estimated probabilities of detection and occupancy were 0.33 ± 0.21 and 0.51 ± 0.26, respectively (Fig. 4). There was a positive correlation between MaxEnt and occupancy outputs ($R^2 = 0.22$, $F_{2430} = 687.7$, $p < 0.001$; Fig. 5), however discrimination power of model types was similarly moderate (TSS = 0.25), meaning that each model class had an approximately equal weight in the final ensemble predictions (Fig. 6).

Final ensemble forecasts showed that much of the Perth Canyon head appears to provide suitable habitat for pelagic wildlife, irrespective of marine reserve boundaries. A distinctive area of low suitability was identified along the main canyon axis. The northeastern walls and upper reaches of the canyon favored higher suitability, with areas of greater probability concentrating on, and intersecting, the southeastern border of the national park (Fig. 7).
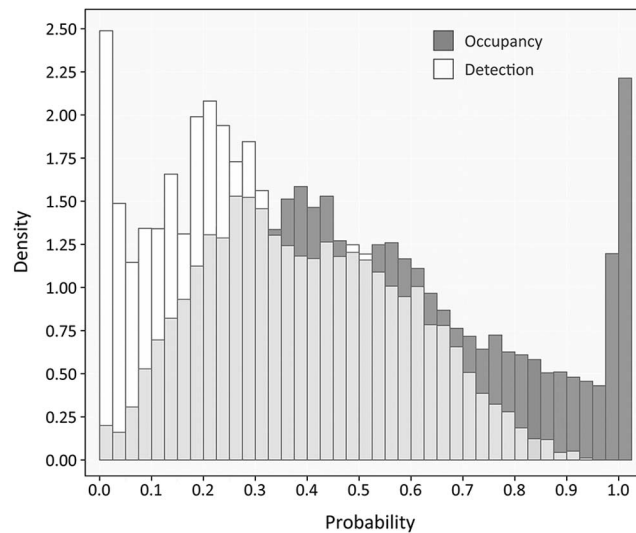

Fig. 4. Density distribution of predicted probability values from the single-visit occupancy model fit to detections of fishes and sharks.
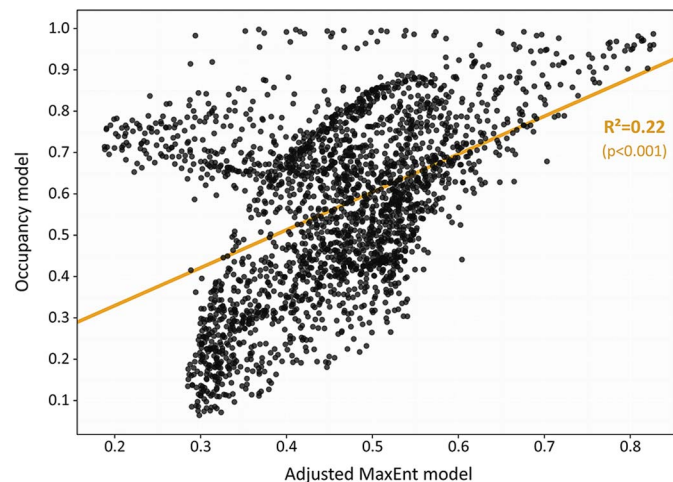
Fig. 5. Relationship between the probability predictions derived from MaxEnt and occupancy models.

Discussion

The advent of giant reserves (Singleton and Roberts 2014) has brought about opportunities for widespread conservation across the world's oceans, allowing signatories of the Convention on Biological Diversity (CBD) to move towards their 2020 targets (Toonen et al. 2013). With the expansion of marine reserves into pelagic environments have also come challenges, as the successful management of these areas within human-dominated seascapes inevitably calls for an appropriate knowledge of species assemblages and their dynamics through both space and time (McClellan et al. 2014) that current marine sampling techniques may struggle to elucidate. Indeed, biodiversity is seldom observed and visually monitored over such broad scales (Mallet and Pelletier 2014), and Kaplan et al. (2014) argue that, in their current implementation, camera surveys are inadequate for assessing reserve effects, a pursuit further obstructed by the practical difficulties associated with accessing and exploring remote sites with intricate submarine topography.

We contend that the novel drifting stereo-videography technique described herein may afford solutions to these issues and represent a satisfactory pathway to fulfill the geographical coverage requirements that "fixed" designs do not necessarily meet. Importantly, free-moving cameras retain all the qualities that have made

BRUVS flexible and effective tools for monitoring generalist carnivores. They are inexpensive, non-destructive, straightforward to deploy, retrieve and operate, and they yield a permanent archive of high-definition footage that not only offers a remarkably valuable format for educational purposes (Cutler and Swann 1999) but also generates quantitative data on species composition, relative abundance and size structure while documenting the natural behavior, sex, and body
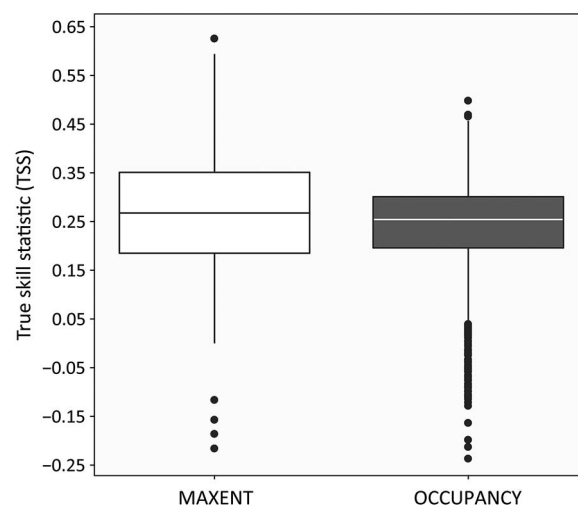

Fig. 6. Comparison of the discriminatory power of MaxEnt and occupancy techniques, as measured by the true skill statistic (TSS). TSS values were derived from $n = 50$ bootstrap replicates of the original data.
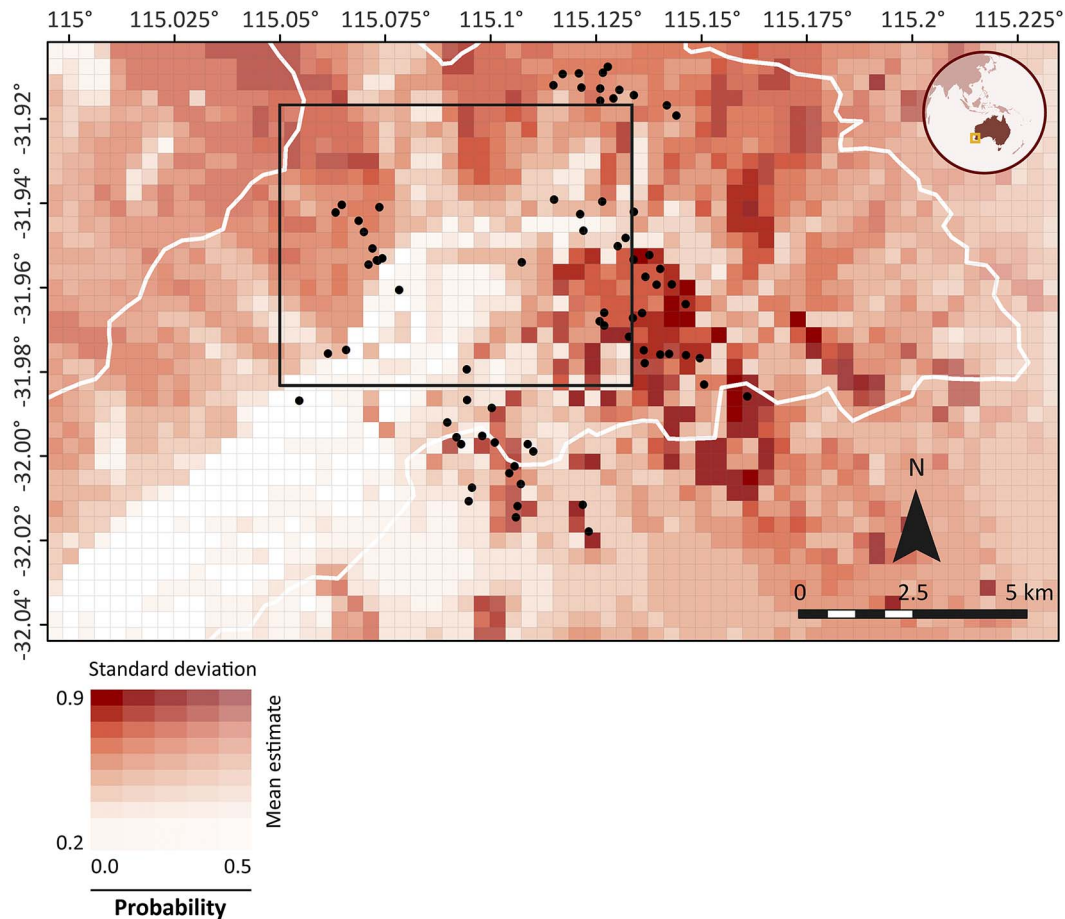
Fig. 7. Predicted habitat suitability for pelagic fishes and sharks derived from the final model ensemble. The standard deviation of probability estimates is coded with fading colors as per figure key. Wildlife detections appear as black circles and the outline of the canyon (as per Huang et al. 2014) is shown in white.

condition of pelagic biota in ways that other methods cannot. Combined with bait attraction, their capacity for high replication can additionally be harnessed to collect geographically resolved occurrence data on an array of endangered, often cryptic and sparsely distributed upper-trophic level fauna across administrative boundaries (Mallet and Pelletier 2014), thereby permitting responses to human activities and zoning schemes to be investigated, as illustrated here.

Despite its heavy human usage and proximity to one of Australia's biggest population centers (Rennie 2005), the Perth Canyon has been the focus of surprisingly little midwater research (with the exception of marine mammal surveys, e.g., McCauley et al. 2000) and remains a globally

data-deficient region for migratory fishes and sharks (but we note that a deep-water expedition to the area took place in March 2015; http://www.schmidtocean.org/story/show/3036). Species distribution models (SDMs) have proven helpful tools to guide conservation efforts for large carnivores in the face of sparse information (Corkeron et al. 2011). Our aim, therefore, was to apply SDM techniques to establish the first baseline picture of oceanic wildlife habitat preferences in relation to the placement of the formerly eastern-most marine national park within the wider Perth Canyon CMR.

Model projections outlined the tip of the canyon head and its eastern and northern slopes as regions of elevated suitability for a diversity of pelagic organisms, a finding consistent with both

expectations from simulations of flow dynamics and existing knowledge of topography-controlled primary productivity patterns in the area (Rennie et al. 2009*b*), and which also mirrors the documented behavior of other predator species such as pygmy blue whales (McCauley et al. 2004, Rennie et al. 2009*a*). Because various competing hypotheses regarding the underlying ecology of a focal species may be equally suitable in explaining the patterns observed in the data, building ensemble predictions is a useful endeavor that can help overcome the uncertainties of model selection (Latif et al. 2013). The congruence between our two approaches evinced a seemingly trivial effect of visual biases on predicted distributions under the conditions of the present pilot study (as was the case for Gormley et al. 2011). We thus agree with the conclusions of Sequeira et al. (2012) that "MaxEnt [...] can produce similar prediction maps to those generated by [other techniques]. Being an easier tool to employ, MaxEnt is useful to develop species distribution models quickly that give results analogous to more robust regression models", although we caution that this might simply be an artifact of our decision to only allow search effort to influence detectability, which was clearly incomplete. Indeed, the moderate discriminatory power of our models stands as evidence that occupancy models may still outperform MaxEnt should other sources of detection heterogeneity be accounted for, a question that ought to be clarified with further testing of data derived from baited videography surveys. This need not be a daunting task, as while we concede that the point-and-click interface of MaxEnt must be appealing to the non-initiated public, object-oriented scripting offers identical (if not superior) degrees of flexibility, and developers have gone a long way in enhancing the usability and accessibility of their packages.

We sympathize with the view of Yackulic et al. (2013) that "all maps are partial truths" and acknowledge that the caveats and shortcomings ensuing from the use of bait in remote camera systems should be considered. These are relatively well-known and broadly relate to (1) the trophic/functional groups being attracted; (2) the type, freshness, amount, moisture content or consistency of the bait mixture itself; (3) the size and dispersal of the feeding plume it generates;

and (4) the array of behaviors that animals may exhibit in response to bait availability (Harvey et al. 2007). We discuss each of them below.

Trophic group

Several empirical studies have demonstrated that baited setups are little affected by differential species attraction, as all wildlife that enter or pass through their field of view are recorded on video, irrespective of whether the animals are indifferent to the instruments, seen to actively interact with the bait, or are merely drawn in by the commotion created by other conspecifics/species feeding (Cappo 2010). To quote Cappo et al. (2003), "[studies] in both low and high latitudes have shown that, although only a small percentage of visitors actually feed at the bait, the effect of the bait plume is to bring in more species not just from a few carnivorous or scavenging functional groups, but also from herbivores, corallivores and most other mobile functional groups". Likewise, Harvey et al. (2007) showed that bait usage promoted higher numbers of predator and scavenger species, but without any impact on the abundances of herbivorous or omnivorous fishes. There have been suggestions, nonetheless, that baited setups may lead to sampling biases towards "larger, mobile, demersal and pelagic species" (Cappo et al. 2004). We argue that such bias, if it did indeed apply, is a strength as it would make possible the monitoring of apex predator guilds (such as pelagic sharks or large scombrids like tunas, bonitos, or mackerels) that are typically cryptic, increasingly exposed to anthropogenic mortality (Dulvy et al. 2008, Collette et al. 2011) and of high monetary and conservation value. We note that Cappo et al. (2004), despite their statement above, (1) seem to support this idea and emphasize that "[baited remote videos] may have a particular role in studies of larger, rarer elasmobranchs and teleosts of special conservation interest"; and (2) also conclude that both the field methods they trialed (i.e., prawn trawls vs. baited cameras) discriminated the same spatial and temporal patterns in fish assemblage structure. We therefore treated potential species-specific biases as negligible.

Bait type

Bait selection constitutes another possible

source of errors. An attracting odor can theoretically form from any water-soluble compound in a fish tissue (Westerberg and Westerberg 2011), but oily mixtures have long proven far superior to white-fleshed alternatives (e.g., urchins or squid) in terms of their capacity to lure animals (Whitelaw et al. 1991, Wraith et al. 2013). In recognition of persistent inconsistencies in bait choice/manipulation across studies as well as the urgent need to standardize research protocols, a panel of experts in marine videography was held at the University of Western Australia in July 2011 to produce a nationally approved set of operating guidelines for the deployment of baited cameras (Harvey et al. 2012b). Among these was the use of a standard weight of pilchards in all deployments lasting up to one hour in duration. We closely followed these recommendations and we are thus confident that our setup should in all aspects be comparable to previous research run around the Australian continent.

Bait release

The dynamics of bait delivery into the water column are very complex and likely to fluctuate both spatially and temporally. Løkkeborg (1990) and Westerberg and Westerberg (2011) demonstrated that the release of odor is a declining function proportional to the inverse square root of time [... for] "all *solid* natural baits over a wide range of bait sizes and soak durations". They propose that dicing solid baits into smaller pieces may optimize the concentration of odorants in the plume and the advection of soluble organic compounds. By crushing heads/guts into a slurry (following the methods described in Letessier et al. 2013), we believe that we maximized the solubility of our bait and its potential to create as continual an olfactory stimulus as possible throughout the deployments. This theory is valid where camera rigs are anchored in a fixed location and bait chambers act as obstacles to the current flow (Westerberg and Westerberg 2011), since turbulent eddies and moving water effectively "flush" the bait to create a meandering and gradually expanding plume (similar to the smoke plume emanating from a chimney) with decreasing downstream odor strength (Heagney et al. 2007). Our drifting systems depart from this scenario as they are displaced together with the

water mass they sit in (i.e., they represent *Lagrangian* drifters), meaning that bait release rates might be diminished. Our observations in the field (i.e., hundreds of deployments of video cameras throughout the Indian and Pacific Oceans, as of the date of writing of this paper) seem to corroborate this and indicate that varying quantities of flesh particles may remain in the bait canisters upon recovery. We however make two observations: (1) Although they somewhat undermine the "aesthetics" of the video footage, the heaving movements of the instruments in response to surface swell may offset Lagrangian drifting and help foster bait dispersion into the water column; and (2) on occasion, camera rigs travel in different directions to the apparent water flow, implying that surface circulation patterns may diverge from those at play at depth. When this happens, the metallic frame of the instruments could easily increase drag and act as a "sea anchor", allowing some degree of bait release to occur. The lack of clear species accumulation through time coupled with the high proportion of carnivores captured on camera both appear to confirm this, although it is noteworthy that sharks are also sensitive, and possibly attracted, to low-frequency acoustic cues (Myrberg 2001), and that thigmotactic tendencies (i.e., associations with floating objects) have been reported in numerous fishes (e.g., Capello et al. 2013). Both processes may contribute to the observed sighting rates and partly compensate for a reduced odor plume (to an unknown level). Of course, fewer fish detections in the midwater could also ensue from the naturally sparser distributions and typically lower abundances of animals found in these environments, rather than from a pure bait effect. Disentangling the two should be an important focus of future research.

Bait plume dispersal

Empirical evidence suggests that both temporal (McLean et al. 2010, McLean et al. 2011) and spatial (Langlois et al. 2012) signals in community structure can be discerned with baited cameras, at least where strong and reasonably stable current-induced bait plumes can form. Heagney et al. (2007) nevertheless warned that fluid density, current speed, shear, or direction could greatly influence the size of the effective

"zone of attraction" (what Letessier et al. [2013] refer to as the "catchment area" and Farnsworth et al. [2007] term "bait zone"), and the rates of bait release. This hurdle is exacerbated by the fact that interactions between oceanographic (e.g., tidal currents) and atmospheric (e.g., wind speed and wind-driven mixing) conditions that govern bait dispersal are challenging to predict consistently (and in three dimensions, integrated over depth) and may change dramatically within very short periods of time. Some attempts have been made to develop a range of plausible plume diffusion models to capture this process, derive appropriate measures of effective sampling effort and in conjunction with knowledge of fish swimming speeds, make predictions of bait attendance rates that could help correct estimates of occupancy and abundance (e.g., Sainte-Marie and Hargrave 1987, Heagney et al. 2007). These models, however, often rely on unverified assumptions about fish behavior to and in the vicinity of the bait source as well as physiological (e.g., average and maximum swimming speed) information that is rarely obtainable. It is also generally accepted that bait plume forecasting may only yield accurate results under constraints of unidirectional current flow over the bait and minimal fish-bait interactions (Harvey et al. 2012b)—conditions which, in practice, are seldom met. In this study, we consequently assumed that the plume from each unit diffused over an equivalent distance (Heagney et al. 2007). Dye-release simulation experiments similar to those undertaken by Mathew et al. (2010) could be contemplated to bypass this issue and help mimic the dispersion of bait particles at larger ranges, but these would likely lack the resolution needed to account for discrepancies in bait plume advection at the scale of individual camera rigs. A more pragmatic approach would be to attach small current sensors to the instruments' frames to obtain in situ measurements of flow speeds. This is also a significant avenue future research should explore.

Behavioral responses to bait availability

Bait elicits complex behavioral responses in fishes. The nature, strength, timing and duration of these responses will be a function of the animals' olfactory performance (Bailey and Priede 2002), prey search strategies (Vabø et al. 2004), population density, home range size, locomotory abilities, activity rhythms (diel, seasonal, reproductive and lunar), appetite and satiation levels (Stoner 2004), curiosity, as well as intra- and inter-specific interactions (e.g., schooling behavior, predator avoidance). The acoustic tracking of fish around bait dispensers could afford promising solutions, but this approach hasn't been tested to date. Here, we made no assumptions in terms of reaction to the bait, simply counting the animals present within the field of view.

Detectability

Detectability is contingent upon a myriad of parameters that are often challenging if not impossible to appraise. These include characteristics of the chosen sampling strategy (e.g., soak time, deployment depth, bait preparation; Monk et al. 2012), features of the environment (e.g., weather, water turbidity, light levels; Coggins et al. 2014), but also traits of the animals under investigation (e.g., camouflage strategies, body size, shyness, distance of approach, agonistic interactions with conspecifics, circling behavior; Bozec et al. 2011). Recent studies have demonstrated that fish density around the bait and agonistic behaviors from conspecifics or other species may discourage some animals from approaching BRUVS and negatively bias detection rates if these maintain their distance outside the field of view of the cameras (Dunlop et al., in press). Several authors have also produced estimates of detection rates in an array of riverine, estuarine, and coastal (benthic) fish species (e.g., MacNeil et al. 2008, Melnychuk and Walters 2010). To our knowledge, we are however the first to make one available for pelagics (oceanic sharks in particular).

Notwithstanding the aforementioned biases, it is critical to emphasize that the use of bait as an attractant in remote camera systems is advantageous (Dorman et al. 2012) and underpins their success as sampling instruments that can (1) alleviate some of the issues associated with gear or diver avoidance (particularly in areas beyond diveable depths and for the shy and more behaviorally adaptable large-bodied species; Watson et al. 2010), (2) maximize individual and species encounter rates (Stewart and Beukers 2000), and (3) therefore yield higher statistical

power to detect trends in assemblage dynamics and structure (Watson et al. 2005). This is crucial for pelagic studies as numerous open ocean predators are elusive, sparsely distributed, and occur in low densities.

Concluding statement

As vast portions of shelf and oceanic ecosystems (including seamounts) remain unexplored, our knowledge of biodiversity patterns across the deeper Indian Ocean is still patchy, with important information gaps for long-lived, migratory megafauna (Wafar et al. 2011). Since the implementation of ecological monitoring techniques in these remote habitats has historically been a slow process, data availability is still one of the biggest barriers to modern conservation planning. Drifting cameras provide an opportunity to fill these knowledge gaps by offering a simple but powerful framework for the visual exploration of deep-water areas, regardless of geographic location. It should be emphasized that our forecasts of species distributions are not meant to represent absolute depictions of the realized niches of predatory fishes and sharks in the Perth Canyon. Indeed, wildlife occurrence likely follows strong seasonal cycles that the current study could not encapsulate, and it is plausible that animals aggregate in the area in greater numbers at a different time of the year (e.g., Walli et al. 2009). Rather, this work should be taken as a preliminary yet essential snapshot "current-state-of-knowledge" within a data-deficient region that can serve as a null hypothesis about the habitats that organisms may occupy—to be refined, re-parameterized and validated against future studies. It is a compelling example, however, of the versatility of drifting baited videography as a tool that can aid in determining where conservation efforts are most pressingly needed, and when teamed with explicit SDMs, act as a catalyst for effective policy development in the pelagic ocean. This is crucial given the 2013 suspension of all CMR management plans—we indeed showed that a proportion of encounters took place in the multiple-use waters surrounding the former protected no-take zone, indicating that the recreational and commercial fishing, industrial vessel traffic, and military training operations to which the canyon is presently exposed may require additional consideration.

We have described the cameras' design, deployment and limitations to encourage their objective uptake within a larger mosaic of available sampling tools. Although a significant step forward, we do not believe their introduction is an end point to the development of marine videography; the emergence of solar-powered battery technologies and internet-operated satellite-linked video relays (Raif et al. 2005) will undoubtedly soon facilitate their evolution into a new breed of fully autonomous instruments.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Summary of input environmental predictors (listed in alphabetical order).

Variable†	Unit‡	Data provider§	Source¶	Software#	Comment
Curvature (CS)	rad/m	GA	B2	DEM Surface tools	3 × 3 cell neighborhood
Curvature (L)	rad/m	GA	B2	DEM Surface tools	3 × 3 cell neighborhood
Depth	m	GA	B1		
Eastness	rad	GA	A	ArcGIS 10.2 Raster calculator	
Fractal dimension	d.u.	GA	B2	FocalD script in Landserf 2.2	9 × 9 cell neighborhood
Northness	rad	GA	A	ArcGIS 10.2 Raster calculator	
Rugosity	d.u.	GA	B2	DEM Surface tools	
Slope	deg	GA	S1	DEM Surface tools	
Slope variance	d.u.	GA	S2	ArcGIS 10.2 Spatial analyst	
SST	deg	NASA	T	ArcGIS 10.2 Spatial analyst	Based on values retrieved for each survey day ($n = 5$)
SST variance	d.u.	NASA	T	ArcGIS 10.2 Spatial analyst	Based on values retrieved for each survey day ($n = 5$)
Topographic position index	m	GA	B2	Land Facet Corridor Tools	8 × 8 cell neighborhood

Notes: The pruned variables are shown in boldface. Slope and SST variances are calculated as coefficients of variation (in %).
† Variables: CS (Cross-sectional curvature); L (Longitudinal curvature).
‡ Units: deg (degrees); d.u. (dimensionless unit); m (meters); rad (radians); rad/m (radians per meter).
§ Data providers: GA (Geoscience Australia); NASA (National Aeronautics and Space Administration).
¶ Data sources: A: Topographic aspect grid, http://www.ga.gov.au/metadata-gateway/metadata/record/76991/; B1: Australian Bathymetry and Topography Grid (June 2009), http://www.ga.gov.au/metadata-gateway/metadata/record/gcat_67703; B2: Derivative of B1; S1: Topographic slope grid, http://www.ga.gov.au/metadata-gateway/metadata/record/gcat_76992; S2: Derivative of S1; T: Multi-scale Ultra-high Resolution Sea Surface Temperature, http://mur.jpl.nasa.gov/.
# Software: DEM Surface Tools http://www.jennessent.com/arcgis/surface_area.htm; FocalD http://www.soi.city.ac.uk/~jwo/landserf/landserf220/doc/addons/focalD.html; Land Facet Corridor Tools http://www.jennessent.com/arcgis/land_facets.htm.
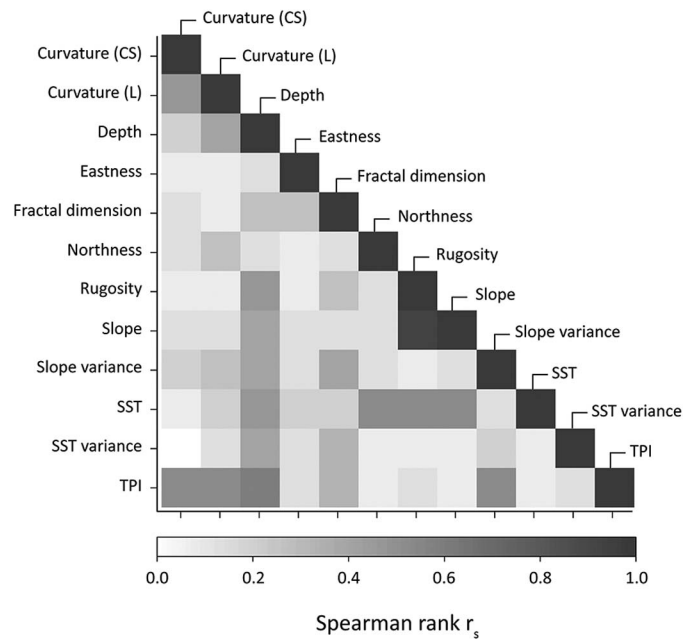
APPENDIX B

Fig. B1. Spearman rank correlation (r_s) matrix between all environmental variables. CS: Cross-sectional curvature; L: Longitudinal curvature; SST: Sea surface temperature; TPI: Topographic position index.

APPENDIX C

Video sequence showing some of the pelagic fish and sharks observed in the Perth Canyon Commonwealth Marine Reserve between March 30, 2013 and May 17, 2013. The footage was generated using a novel system of drifting baited cameras that sampled at depths of 10, 30, and 50 m below the ocean surface. [http://dx.doi.org/10.1890/ES14-00380.2]
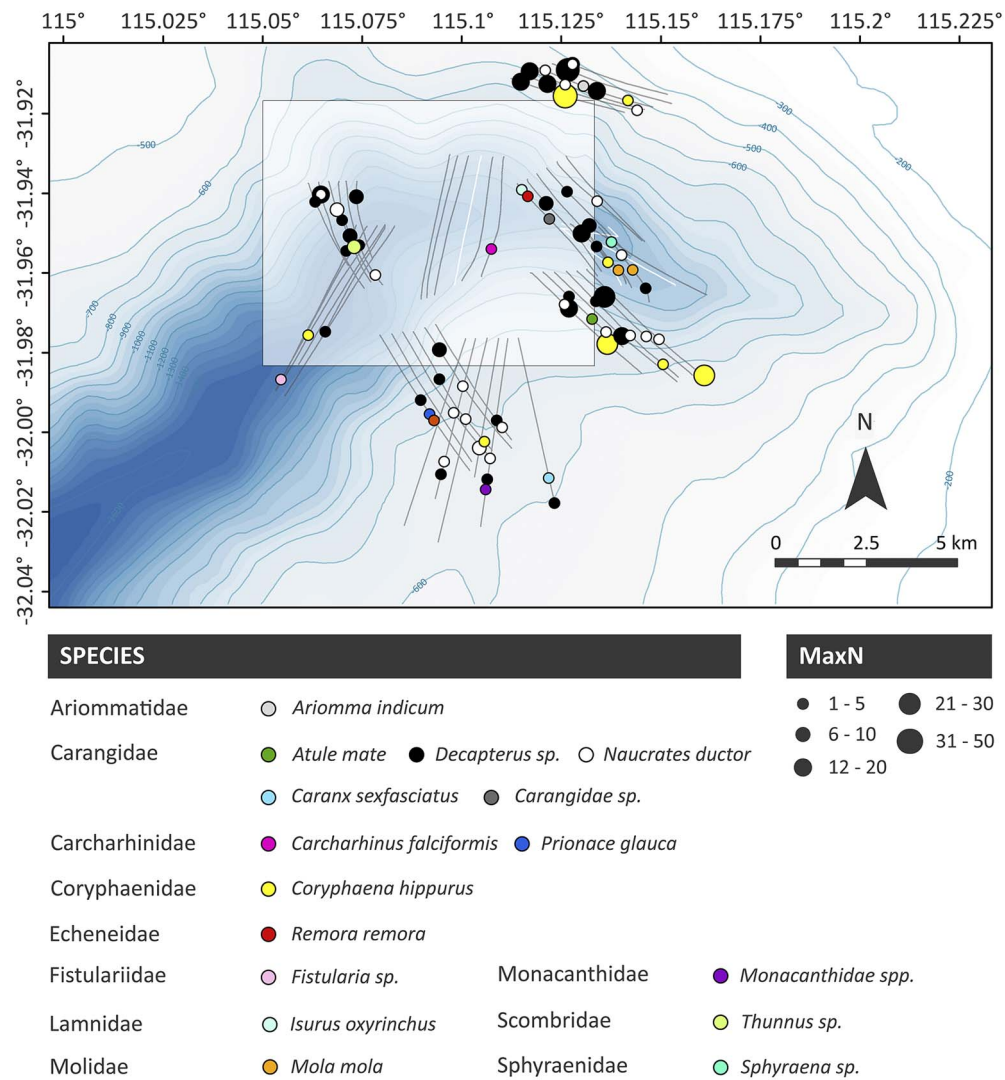
APPENDIX D

Fig. D1. Location of wildlife sightings, color-coded by species. Circle size reflects relative abundance, as measured by MaxN. Bathymetry and park boundaries are shown as per Fig. 2.
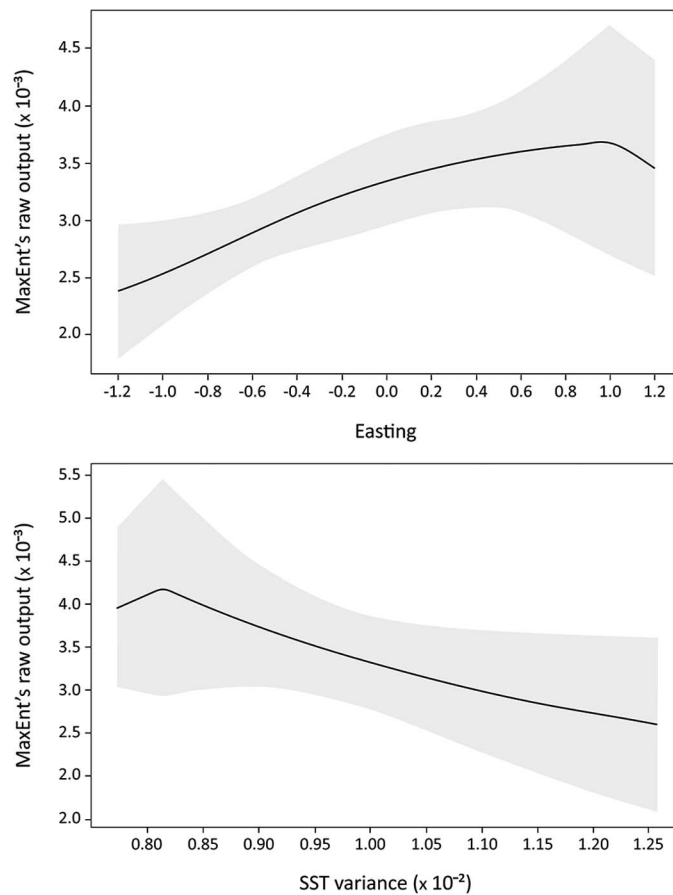
APPENDIX E

Fig. E1. Example MaxEnt response curves for easting and sea surface temperature variance from one of the models used in ensemble building. The curves show how predictions change as each variable is varied, keeping all other predictors at their average sample value.

SUPPLEMENT

Raw species data (sightings) collected by drifting baited stereo-videography in the Perth Canyon CMR (*Ecological Archives*, http://dx.doi.org/10.1890/ES14-00380.1.sm).