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Using temporally explicit habitat suitability models to reduce dynamic threats to mobile species

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Abstract

1. Bycatch constitutes a waste of natural resources and significant economic loss to fisheries. Moreover, bycatch can have an impact on species by reducing population sizes, and an ecosystem-level impact through the significant removal of biomass and subsequent trophic changes. In this regard, it is crucial to refine methods for quantifying interactions between fisheries and bycatch species, and to manage these interactions spatially.

2. A new method is presented for quantifying interactions between fisheries and bycatch species at high spatial and temporal resolutions. Temporally explicit species distribution models are used to examine temporal dynamics of fisheries and bycatch.

3. As a case-study, this method is applied to Australia's Eastern Tuna and Billfish Fishery to estimate interactions with seven principal bycatch species. The application of this method towards evaluating the ability of reserve systems to reduce bycatch is demonstrated, and considerations are outlined for the spatial management of fishery-bycatch species interactions.

4. Australia's Commonwealth Marine Reserve Network had a minimal impact on bycatch reduction, highlighting the need for threats to marine biodiversity to be incorporated directly into reserve design, instead of assuming threats will be incidentally abated after reserves have been proclaimed, or that off-reserve mechanisms will compensate for inadequacies of reserves.

Key words: bycatch, dynamic threat, fisheries, gap analysis, marine protected area (MPA), Maxent, reserve network, species distribution model

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INTRODUCTION

Commercial and recreational fisheries pose a significant direct threat to both target and non-target marine megafauna, leading to population declines and increased extinction risk of some species (Lewison et al. 2004). In some fisheries, the incidental catch of non-target species (hereafter: bycatch) occurs at higher rates than (Uhlmann et al. 2013), and outweighs (Tsagarakis et al. 2013), the catch of target species. This significant removal of biomass can alter trophic webs and have subsequent adverse ecosystem-wide impacts (Dayton et al. 1995). With a large environmental cost, bycatch also provides negligible economic benefit while placing substantial economic burdens on fishers (Dunn et al. 2011). Although there is a recognized need to reduce bycatch and many mitigation measures are employed, bycatch remains a significant, frequently principal, threat to many marine species (Zydelis et al. 2009, Senko et al. 2013).

Proof of concept exists for the application of spatial management to reduce bycatch. Howell et al. (2008) described a Hawaii-based longline fishery that received daily maps of probable habitat for loggerhead turtles (*Caretta caretta*) based on environmental profiles, which the fishery used to avoid areas with high probability of turtle interactions. Australia's Southern and Eastern Scalefish and Shark Fishery uses spatial closures to reduce bycatch of significantly depleted populations of dogfish (*Centrophorus harrissoni*). Fishing closures are in place over dogfish home ranges, with additional closures coming into effect after a threshold of dogfish bycatch has been exceeded (AFMA 2013). Incidental bycatch of southern bluefin tuna (*Thunnus maccoyii*) by Australia's Eastern Tuna and Billfish Fishery is reduced through closures over the predicted location of bluefin habitat, determined dynamically and updated regularly using a three-dimensional temperature habitat model (Hobday et al. 2010). Although some non-spatial approaches to bycatch management are in place, such as move-on rules and bycatch quotas, spatial management is likely to remain important.

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Even with proof-of-concept examples, spatial management to mitigate bycatch threat is challenging because the distributions of bycatch species and fisheries, and therefore the overlap between them, are frequently highly variable in space and time.

Bycatch species can be pelagic, with distributions that fluctuate widely in response to dynamic oceanographic conditions (Weimerskirch 2007, Game et al. 2009, Hill et al. 2015). Fishery distributions can likewise fluctuate as operations shift to target dynamic marine conditions (Zydelis et al. 2011). The high variability of both bycatch species and fisheries makes it difficult to identify when, and where, spatial closures should be used to reduce bycatch. Despite these difficulties, it is increasingly important to refine methods for quantifying relationships between bycatch species and fisheries, and to address these relationships through management (Campbell 2011).

To quantify the relationship between bycatch species and fisheries, two key pieces of information are needed. The first is overlap: locations in time where the distributions of bycatch species and fisheries coincide. While accurate spatial data on fisheries distributions are generally available, the distributions of bycatch species are frequently unknown and must be inferred from fisheries data or tagging studies, for example by using distribution models (see Żydelis et al. 2011) or kernel densities (see Phillips et al. 2006). The second key piece of information needed is bycatch threat, defined for an overlap area as the likelihood of a bycatch event occurring as a function of probability of bycatch species presence and magnitude of fishery effort.

Ideally, to understand bycatch threat, probability of bycatch species presence would consider the environmental and biological drivers of species distributions (e.g. hydrological conditions and life-history requirements) to infer metrics such as species abundance and/or density. Magnitude of fishery effort might be inferred from the amount of gear being used, soak time, and the spatial dimensions of the gear (e.g. net width or number of hooks). In reality, bycatch threat is based on less comprehensive information.

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For example, the bycatch threat in an area of overlap can be calculated as the product of the spatial distribution of foraging effort by bycatch species (expressed as the number of foraging days/year) and mean kilometer gillnet hours (Campbell 2011), or the product of the percentage of distribution of bycatch species and the average number of hooks (Tuck et al. 2011). The term “interaction” is used to capture both overlap and bycatch threat where the distinction is not needed.

The accuracy of estimated interactions between bycatch species and fisheries is limited not only by the type of available data but also by their spatial and temporal resolutions. When interactions are calculated at coarse spatial resolutions, for example within 500 x 500 km pixels, there is low confidence in overlap and bycatch threat at any given point in space. Likewise, when interactions are calculated at coarse temporal resolutions, for example as a single snapshot of average conditions across one or many years of data, there is low confidence in overlap and bycatch threat at any given point in time. Because bycatch can only occur when non-target species and fisheries are present in the same place at the same time, it is crucial to narrow the spatio-temporal window across which interactions are calculated (by increasing resolution) to increase the accuracy of estimates (Dunn et al. 2016). High-resolution interactions can be translated into implications for spatial management to ensure closures are targeted to the right places at the right times to reduce bycatch. While many studies have examined interactions between fisheries and bycatch species, e.g., white sharks (Lyons et al. 2013), sea lions (Campbell 2011, Hamer et al. 2013), dugongs (Grech et al. 2008), and seabirds (Tuck et al. 2011, Sonntag et al. 2012), few studies have evaluated interactions quantitatively for

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spatial management (Dunn et al. 2011; but see examples in Grantham et al. 2008 and Grech et al. 2008).

In this context, a new method is presented for quantifying interactions at high temporal and spatial resolutions. Time-series analysis of historical interactions are used to provide insight into interactions in the near future, allowing for inferences to be drawn about the potential future impacts of spatial management on bycatch reduction. As a case-study, this method is applied to evaluate interactions quantitatively between Australia's Eastern Tuna and Billfish Fishery and its seven most commonly caught bycatch species. The application of this method to evaluate the ability of existing marine protected areas to reduce bycatch is then demonstrated using Australia's Commonwealth Marine Reserve Network. The Network is a system of permanent static reserves established as a conservation tool to protect and maintain biodiversity (CMR 2016), so it is appropriate to test its ability to reduce threats to biodiversity, e.g. bycatch. Interactions can be unpredictable in space and time, and managing these types of interactions through permanent static reserves might be inefficient in terms of opportunity costs to fisheries. Therefore, other spatial management options to accommodate different types of spatio-temporal dynamics are also explored. The ability of the Network to reduce threat to bycatch species remains unexamined, and the analysis is timely given the Australian government's current suspension and review of the Network's management plans.

We proposed our modelling approach as a generic method to understand bycatch threat in relation to options for spatial management, although we are aware of data-related limitations of our case-study. We finish with a discussion of caveats on our results, related primarily to the limitations of data on the distributions of bycatch species.

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These same limitations will constrain policy and operational management of bycatch threat in any marine jurisdiction, calling for approaches to management that account for considerable uncertainties.

METHODS

Case-study

Australia's Eastern Tuna and Billfish Fishery (ETBF) is primarily a longline fishery that operates within the eastern Australian Exclusive Economic Zone from the South Australian/Victorian border in the south to the tip of Cape York in the north, and also within Commonwealth waters around Norfolk Island (Fig. 1a). The selectivity of longline gear is low, resulting in extensive bycatch (Oliver et al. 2015). Globally, longline fisheries have the second highest discard rate of bycatch, following shrimp trawling operations (Keller 2005).

The ETBF has the highest cumulative capture of sharks when compared to eight other Commonwealth fisheries (Phillips et al. 2010), with 85% of the discards of the vulnerable species shortfin mako (*Isurus oxyrinchus*) released dead (Hunt 2013, IUCN 2015). Our study examines ETBF interactions with seven principal shark bycatch species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), tiger shark (*Galeocerdo cuvier*), dusky whaler (*Carcharhinus obscurus*), bronze whaler (*Carcharhinus brachyurus*), silky shark (*Carcharhinus falciformis*), and oceanic whitetip (*Carcharhinus longimanus*). The selected shark species are listed as most commonly caught by the ETBF (AFMA 2011-2013) and are either vulnerable or near threatened (IUCN 2015).

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Australia's Commonwealth Marine Reserve Network (hereafter: reserve network) is comprised of three distinct networks within the ETBF fishing grounds: the Coral Sea Marine Reserve, the Temperate East network, and the South East network (Fig. 1b). The South East network was proclaimed in 2007, followed by the Coral Sea Marine Reserve and the Temperate East network in 2012. The 2012 proclamations, along with others in Australian waters, created the world's largest national network of marine reserves, covering over a third of Australia's marine waters (Devillers et al. 2015). The identification of current and emerging threats was one of the objectives underlying the regional marine planning that gave rise to the reserve network (Commonwealth of Australia 1998). However, the objective carried no requirement for the abatement of threats during reserve design. Subsequent analyses of the reserve network have demonstrated its limited protection of marine biodiversity from threatening processes (Nevill and Ward 2009, Williams et al. 2009, Kearney et al. 2012, Hunt 2013), and criticized the reserve network as residual to extractive uses instead of seeking to regulate extraction (Pressey 2013, Devillers et al. 2015).

Overlap between the ETBF and bycatch species

To determine overlap, or locations and times of coincidence of bycatch species and fisheries, the distributions of each bycatch species and the ETBF were calculated for each month between January 1998 and December 2007 (n=120 months). This time-series begins at the first full year of SeaWiFS' satellite-born mission, and ends at the last full year without major data outages. It was important to match the duration of the SeaWiFS mission because it provides important data on predictors of bycatch species (Table 1) and

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has the highest temporal coincidence with the available species (Table 2). The MODIS Aqua mission provides comparable variables, but did not begin until 2002.

Species distributions

Environmental layers (Table 1) from January 1998 to December 2007 (n=1 layer for static variables; n=120 monthly layers for dynamic variables) were acquired and uploaded into ArcGIS 10.1 (http://www.esri.com/). These types of variables were selected because they are known to influence distributions of pelagic species (Chassot et al. 2011) and, in the case of dynamic variables, because they were available at monthly resolutions over the full time-series. Layers were regridded in ArcGIS from their original resolutions (Table 1) to 9 x 9 km spatial resolution, where necessary, by applying the snap raster and cell size parameters within Environment Settings. Only one variable (mean sea-level anomaly) was upscaled. To upscale, empty 9 x 9 km grids were overlaid on coarser layers, and then populated using values from the coarser layers. Missing pixels were filled using Del2a interpolation within the Marine Geospatial Ecology Tools package (Roberts et al. 2010) with a maximum fill region of 30 pixels (following Welch et al. 2015). The interpolation process reduced the total amount of missing data from 7.2% to 5.5%.

Monthly spatial records for the seven bycatch species were downloaded from the Ocean Biogeographic Information System (http://www.iobis.org/) from January 1998 to December 2007 (Table 2, Figure S1). The Ocean Biogeographic Information System compiles species records from a wide range of sources. Over 98% of shark records came from the Bureau of Rural Sciences National commercial fisheries half-degree data set

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2000-2002, explaining the temporal bias of records to this period. Other records came from the Australian Institute of Marine Science, the Australian Museum, and BOLD Public Fish Data. Records also displayed intra-annual temporal bias to June and July, although the reason for this bias in unknown. Each record was associated with the unique values of environmental variables at the same latitude/longitude during the same month and year as the record sighting in ArcGIS and compiled into a samples-with-data matrix.

The presence-only modeling software Maxent (Philips et al. 2006) was used to produce logistic outputs of monthly habitat suitability for each species, ranging between zero (lowest suitability) and one (highest suitability). The samples-with-data matrix was used to train the distribution models for the seven shark species. All default settings were used with the exception of background point selection. The logistic output requires the assumptions of random sampling across the seascape and across the time-series (Merow et al. 2013), which were not met by our data (Table 1). Following Phillips and Dudik (2008), to remove sampling bias for a given target species, such as blue shark, background points were created from the records of the species not being modelled (the other six shark species). This ensured that the background points for each shark species accounted for both spatial and temporal bias of the sampling effort. Because the presences and the background points shared the same sampling bias, the effect of uneven sampling was effectively removed from the models (Phillips and Dudik 2008).

Ten-fold cross validation was used to test model fit. For each iteration, the area under the receiver operating characteristic curve (AUC) was used to evaluate model fit. AUC values range in principle between 0 and 1; AUCs of 0.5 indicates random discrimination between presences and absences, and AUCs above or below 0.5 indicate

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better or worse than random, respectively (Phillips and Dudik 2008). The seven shark models were projected onto the environmental layers to create ArcGIS rasters of habitat suitability for each species in each month of the time-series (n=840 projections in total).

Fishery distribution

Spatial monthly ETBF effort data from January 1998 to December 2007 were provided by the Australian Fisheries Management Authority. The data included the month, year, longitude, latitude, and number of hooks for each longline set deployed over the time-series. The coordinates referenced the starting location of each set, which is a sufficiently accurate measure for representing fishery effort at this spatial resolution (Dunn et al. 2008). Monthly effort data were converted to rasters in ArcGIS and distribution calculated as the number of hooks in each 9 x 9 km pixel.

Bycatch threat

Bycatch threat within an area of overlap was interpreted as a function of the habitat suitability for bycatch species and the magnitude of fishery effort. An increase in habitat suitability and/or effort will raise the bycatch threat, while a decrease in one or both will reduce the threat. Bycatch threat at a given area of overlap was thus defined as the product of habitat suitability and fishery effort (number of hooks). Monthly bycatch threat was calculated separately for each species across the time-series; e.g. each pixel within a given month had seven associated values for bycatch threat: one for each species.

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Evaluation of the Commonwealth Reserves

Waters within the ETBF fishing grounds were divided into four groups based on exposure to longlining as of the 2012 reserve network proclamation (Fig. 2): exposed (unzoned) waters outside reserves; exposed (zoned) waters within reserves where zones permit longlining; no-take zones within reserves that prohibit longlining; and waters removed from analysis because they are within reserves that prohibit longlining and were proclaimed before or during the analysis time-series (1998-2007). The two exposed groups were differentiated because exposed (zoned) waters can be rezoned to regulate longlining with relative ease compared to establishing new reserves that regulate longlining in exposed (unzoned) waters.

Waters within the removed group were taken out of the analysis to isolate the impact of the new reserves on bycatch threat from the impact of previous reserves. Reserves in this group included the Great Barrier Reef Marine Park adjacent to the Australian coast, and from north to south, the Former Coringa-Herald and Lihou Reef Nature Reserves, the Elizabeth and Middleton Reefs Marine National Nature Reserve, and the Former Lord Howe Island Marine Park (Fig. 2). Reserves within the South-East Network were proclaimed in May 2007, but were not removed because it was assumed that their eight-month impact (May-December 2007) over the ten-year analysis would be negligible. The percentage of bycatch threat within the remaining three exposure groups was calculated for each species in each month across the time-series. Percentages of ETBF effort or bycatch threat in the exposure groups were calculated with respect to totals across waters retained in the analysis.

RESULTS

Species distributions

An overview of the spatial and temporal variability of habitat suitability for any given species can be gained by averaging values across years within each month (Fig. 3). Although variation between years is lost by using a long-term average, this figure provides an understanding of spatial suitability in a given month. For dusky whalers (Fig. 3), high habitat suitability was restricted to northern latitudes during cooler winter months (July-October), with a southward expansion during warmer months. Monthly projections for all species showed inter-annual (Figure S2) and seasonal (Figure S3) variation in habitat suitability between months, although patterns of variation differed between species. Model AUCs (one model for each species, which was projected onto environmental conditions in 120 months) were as follows: blue shark 0.58; silky shark 0.67; bronze whaler 0.61; tiger shark 0.67; dusky whaler 0.73; shortfin mako 0.60; oceanic whitetip 0.63. The reported AUC value for each species is the average of the training AUCs generated during cross validation (Table S1). All AUC values were above 0.5, indicating better than random discrimination between presences and absences; however, values did not approach the maximum potential AUC value of one, which would indicate perfect discrimination.

ETBF effort

The spatial relationship between total fishing effort and spatial protection from longlining can be observed by summing effort across the time series (Fig. 4). Overall,

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8.0% of total longlining effort was within waters that were later protected from longlining by no-take zones (Table 3). The largest spatially consistent area of effort was in the central fishing grounds where there was minimal subsequent protection from no-take zones. Large no-take zones around Tasmania and Norfolk Island were in areas with low fishing intensity. There was a dramatic change in fishing intensity at the boundary of the no-take zone in the Coral Sea, moving from high historical effort outside the zone to low historical effort in waters subsequently protected.

Reserve network evaluation

For all species, the largest percentages (68-74%) of total bycatch threat (i.e. monthly bycatch threat summed across the time-series) were within exposed (unzoned) waters outside of reserves across all months (Table 3). On average, around 21% of bycatch threat was in exposed (zoned) waters now within the marine reserve network. Overall percentages of total bycatch threat within no-take zones now protected from pelagic longlining ranged from 5.9% for shortfin makos to 8.7% for dusky whalers (Table 3). Exposed (unzoned) waters had the largest area extent, covering 54.2% of the analysis area, followed by protected waters now within no-take zones and exposed (zoned) waters (covering 26.4% and 19.4% of the analysis area, respectively) (Table 3). Exposed (unzoned) waters had disproportionately large amounts of longlining effort and bycatch threat, and no-take zones had disproportionately small amounts (Table 3).

The time-series analysis (Fig. 5a) illustrates, for each exposure group, the seasonal and interannual variability in bycatch threat from January 1998 to December 2007, if the marine reserve system had been in place over this period. There was

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generally less than 10% of monthly bycatch threat within protected waters across all months for all species, and at times this dropped to around 1% for most species. For all species, the percentage of monthly bycatch threat within exposed waters in reserves was variable across months, ranging from 5-50%. Generally, the largest percentage of monthly bycatch threat was found within exposed waters outside reserves for all species in all months.

Time-series analysis of monthly bycatch threat in terms of absolute values provides additional information (Fig. 5b). For most species there was no distinct pattern in total bycatch threat across months, with values of monthly bycatch threat comparable between species. However, total monthly bycatch threat for shortfin makos displayed marked seasonality, with lowest bycatch threat in January-March and highest bycatch threat in May-September in all years (Fig. 5b).

DISCUSSION

This study presents a new method of quantifying fishery-bycatch species interactions at high spatial and temporal resolutions. A high level of resolution was achieved through the use of temporally explicit species distribution models, which are infrequently applied in the literature (but see Reside et al. 2010 and Hill et al. 2015). Temporally explicit models are ideal for highly dynamic species such as pelagics because they identify temporal variability in suitability in relation to temporal variability in predictors. These aspects of variability are lost when species records are related to long-term average values of predictors (Reside et al. 2010). Fine spatial and temporal resolutions also allow for increased accuracy of predicted interactions, and preserve

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information on the variability of interactions across seasons and years (Appendices B and C). This type of information can help guide spatial management decisions to reduce fisheries bycatch (Dunn et al. 2016).

Case-study

The 2012 proclamation of the Commonwealth Marine Reserve Network led to a small reduction in bycatch threat from longlining. The design of the reserve network did not explicitly address threats posed by fishing, or guidelines to manage threats from fishing (Kearney et al. 2012). Its zoning reduced the total bycatch threat across seven shark species by a maximum of 8.7% and a minimum of 5.9% (Table 3). This is a disproportionately small reduction, considering that the reserve network covers over 45% of the analysis area, and over half of the reserve network is zoned as no-take (Table 3).

It appears that the network was designed for minimal impact on fisheries, with no-take zones overlapping only 8.0% of total historical effort despite covering 26.4% of the analysis area (Table 3). Exposed (unzoned) waters covered 54.2% of the analysis area but overlapped with about 70% of historical effort (Table 3). Figure 4 indicates that the boundaries of the Coral Sea no-take zone were designed to explicitly avoid areas of intense historical effort, mirroring the findings of Hunt (2013). The marginal impact of the reserve network on fisheries and other extractive activities has been noted by previous studies (Nevill and Ward 2009, Pressey 2013, Devillers et al. 2015). In principle, the primary objective of the reserve network was the conservation of biodiversity, with extractive activities permitted as long as the primary objective was not compromised (NRSMPA 2015). However, the impact of longlining on protected bycatch species

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remains substantial, in fact disproportionately large, after the establishment of the new marine reserves.

Currently, the ETBF employs a number of bycatch-mitigation strategies including gear modifications and restrictions, spatial management, and quota systems (AFMA 2011-2013). As more stock assessments of bycatch species are conducted and continue to reveal population declines – as they have for silky and oceanic whitetip sharks (Rice and Harley 2012a&b) – stricter mitigation strategies will need to be put into effect. For example, output mitigation measures can call for the closure of entire fisheries once bycatch quotas are exceeded (Chilvers 2008, Chassot et al. 2011). Almost every mitigation strategy constitutes an opportunity cost to fisheries (Dunn et al. 2011, O'Keefe and DeCelles 2013). In this context, the ETBF stands to benefit from having static no-take zones - which already represent some opportunity cost - in the right locations to reduce bycatch threat. However, depending on the spatio-temporal dynamics of bycatch threat, other approaches to spatial management (see below) might be more cost-effective and should also be explored.

Towards spatial management of interactions

Estimating interactions

Although there are many examples in the literature of quantified interactions between bycatch species and fisheries, not all exercises explicitly explore data limitations and few translate interactions into management implications. To aid progress in these areas, an analytic approach is outlined to ensure interactions are amenable to spatial management.

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1. State objectives. Objectives should be clearly stated as to whether the purpose of analysis is to manage a particular species, or to manage a particular fishery. This will affect the management area (2), and the types of interactions that need to be estimated (3).

2. Define management area. Ideally, the management area is the full species' or fishery's range, depending on the objective. Management decisions that do not consider the full spatial extent of the bycatch species or fishery risk leaving key areas exposed to threat. In reality, however, full coverage is not always possible due to incomplete data, or species ranging across jurisdictions. In these cases, investigators should seek to increase the spatial extent of analysis to jurisdictional boundaries, e.g. exclusive economic zones; or ecoregions (Spalding et al. 2007). Investigators should also, as far as possible, account for management decisions outside the area being analyzed. For example, Hunt's (2013) analysis examined fishery-bycatch interactions in Australia's portion of the Coral Sea in the context of the greater Western and Central Pacific.

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3. Determine principal overlapping fisheries or bycatch species. Estimated interactions should include the full suite of principal fishery-bycatch interactions within the management area, depending on the objective. For exercises aiming to manage a particular bycatch species, interactions should be estimated with all of the main overlapping fisheries, to avoid leaving the species vulnerable to uninvestigated fisheries (e.g. Fossette et al. 2014). If the objective is to manage a particular fishery, interactions

should be estimated for all principal bycatch species (e.g. Tuck et al. 2011). Management decisions based on these interactions will be best able to maximize the amount of bycatch avoided while minimizing opportunity cost through holistic fishery management, as opposed to applying different mitigation measures for different bycatch species.

4. Evaluate comprehensiveness of raw data (Fig. 6). The comprehensiveness of raw data sets for fisheries and bycatch species should be evaluated to understand and reduce limitations. Four broad measures of comprehensiveness are outlined as starting points for consideration, although this list is not intended to be comprehensive. Accuracy (Fig. 6a) determines confidence in records' positions in time and space, and confidence that species were correctly identified. Spatial accuracy can range from meters (e.g. limited by the GPS capabilities) to tens of kilometers (e.g. the shark data set analyzed here). Time-series length (Fig. 6b) determines the ability of data sets to portray inter-annual and seasonal variability, and long-term trends. The 10-year data set used in this study captures inter-annual and seasonal variability, but is too short to reveal the long-term trends interpretable with the 50-year Northeast Fisheries Science Center Bottom Trawl Survey (Polities et al. 2014). Coverage of the ranges of bycatch species and fisheries operations within the management area (Fig. 6c) and the dimensions of records (Fig. 6d) determine the ability of records to represent of the underlying population structure (in the case of bycatch species), or to represent the full fishery operation (in the case of fisheries records).

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5. Explore options to increase comprehensiveness. Attempts to increase comprehensiveness inevitably involve trade-offs. Moving from records to distribution models reduces false negatives in the data set, but at the risk of introducing false positives (Rondinini et al. 2006). In this present study, models were used to improve the spatial resolution of species data from 50 km (Fig. 6a) to 9 km, at the risk of propagating errors and sampling biases in the original data set. Investigators might be able to supplement their data with other regional data sets, potentially increasing comprehensiveness in terms of time-series length, coverage of species' ranges within management areas, and dimensions of records, but depending on data sources, at the risk of reduced accuracy. Independent data sets could also be used to validate models, thereby increasing accuracy. Data sets for bycatch species and fisheries, and therefore the estimated interactions between them, will never be fully comprehensive, and it will be necessary to make spatial management decisions in the face of uncertainty. Data sets that rate poorly on criteria for comprehensiveness (Table 4) pose risks to bycatch species, and it will be important for management decisions to accommodate these risks. More comprehensive data sets are unlikely to be available in the near future in most regions unless much larger investments in data collection are made, but management must proceed despite data limitations, acknowledging that an incomplete picture is better than no picture at all.

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Implications of spatio-temporal dynamics

Most reserve systems are designed to protect static features, e.g. patterns of biodiversity (Ban et al. 2013), but do not necessarily protect features that are dynamic in space and time (Ban et al. 2012). Nevertheless, dynamic features such as fishery-bycatch interactions can be characterized to guide approaches to static and dynamic spatial management. As a starting point, pixels containing interactions could be categorized on a species-specific basis, for each month of the year, using two long-term metrics calculated between years of the time-series: 1) magnitude of bycatch threat; and 2) variability of bycatch threat, i.e. the total sum and variance of bycatch threat between years of the time-series, respectively. These two monthly metrics indicate the likelihood and constancy of bycatch events across years, respectively, and can help planners prioritize pixels for protection within each month and identify the appropriate form of management (Fig. 7).

Examining these two metrics across months indicates what types of management are needed for different times of the year. Pixels in the lower right quadrant are top priorities for protection: high magnitudes of threat indicate high likelihood of bycatch events occurring, and low variability indicates persistence between years, giving planners confidence that management decisions will remain relevant in the near future. These top-priority pixels could be managed with static no-take zones if they remain in that category across months, or with seasonal no-take zones during the months they occur reliably in this quadrant. Seasonal patterns are likely because the distributions of bycatch species can be dictated by variables that display predictable seasonal variability, including temperature and chlorophyll a (Weeks et al. 2006).

When pixels fall into the second or third priority categories, real-time spatial management might be appropriate. These two categories have high variabilities of bycatch threat, indicating unpredictable conditions between years. Permanent no-take zones for pixels in these categories might have limited impacts in many years, so effective management will require flexible designs that can be updated to reflect real-time

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conditions. Real-time management strategies have been effectively applied to minimize bycatch. Examples include regular production of bycatch maps (Holmes et al. 2011, Bethoney et al. 2013, O'Keefe and DeCelles 2013) and maps of habitat preferences for bycatch species (Howell et al. 2008, Hobday et al. 2010), with fishing activities adjusted accordingly.

Pixels should be monitored during portions of the year when they fall into the fourth priority category. Because these pixels have predictable conditions between years (as indicated by low variability of bycatch threat), an increase in either fisheries effort or habitat suitability for bycatch species (such as warming temperatures causing shifts in species' ranges) could move these pixels into the top priority category. It would be advantageous to anticipate such changes so that management can respond appropriately before significant bycatch occurs.

Identifying objectives for bycatch reduction

The spatial management of interactions should be guided by specific quantitative objectives for how much species-specific bycatch threat to avoid. For example, oceanic whitetip sharks, which are highly vulnerable due to low fecundity and high fishing mortality (Rice and Harley 2012a), might need a higher percentage objective than blue sharks or shortfin makos, which are less vulnerable due to high growth rates and fecundity (Phillips et al. 2010; see Pressey and Taffs 2001 for incorporating vulnerability into percentage objectives). In a similar vein, insurance multipliers (Allison et al. 2003) might be employed to set species-specific objectives that reflect the likelihood of

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interactions and the recovery rate (determined using life history traits such as fecundity, spawning biomass, and recruitment).

While scaling objectives to perceived conservation needs has advantages, the objectives remain somewhat arbitrary unless linked to models of population persistence. Stock assessment models that derive past and future population trends from life-history traits and data on fisheries impact (e.g. bycatch per unit effort, fishing mortality, discard rate) can provide insights into the effect of different fisheries on population trends and future population trajectories under current management. For example, stock assessment models for silky sharks and oceanic white tip sharks in the Western Pacific indicate levels of fishing mortality far in excess of the maximum sustainable yield, with the greatest impact attributed to longlining (Rice and Harley 2012a&b). These models could be used to examine effects of the approximately 8% reduction in total longline bycatch threat achieved by the Commonwealth Marine Reserve Network, and to identify levels of bycatch reduction needed to achieve persistence of the stocks.

Critiques and caveats

Model AUCs in this study were generally low, with the highest value of 0.73 for the dusky whaler. Low AUCs are not necessarily to be expected for pelagic species (Zydelis et al. 2011, Martin et al. 2012, Pennino et al. 2013). However, low AUCs do not necessarily indicate poor models; AUCs are highly sensitive to the geographic spread of species occurrences and absences (Reside et al. 2011). Consequently, an AUC value is indicative not only of model fit, but also of the structure of the data set used to build it.

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Due to the strong bias of recent protection in avoiding areas with highest fishery effort (Fig. 4, Table 3), it is unlikely that poorly-fitted models would have greatly affected the distribution of bycatch threat within the three exposure groups. Bycatch threat can only occur in areas that contained fishery effort, and 92% of total historical effort was outside waters recently placed in no-take zones. Therefore, we consider that our analysis accurately highlights the limited impact of the Commonwealth Marine Reserve Network on reducing bycatch, and that these results merit discussion during the reserve review process. Ideally, the identification of candidate areas for management would be informed by models with better data, and better model fit. However, this would require more comprehensive bycatch species data sets (preferably containing absence records), that are unlikely to be available in the near future, although the utility of fisheries data sets for modeling distributions of bycatch species should be explored. In the interim, managers must proceed with the best available data, which might include our models, and manage for uncertainties in ways that reduce risk to bycatch species.

Conclusion

It is well understood that there are incentives related to economics and political expediency to place reserves in locations that minimize inconvenience to extractive activities (Devillers et al. 2015). It is less widely understood that this bias in locating reserves reduces their potential value in avoiding biodiversity loss (Pressey et al. 2015). This study presents a new method for estimating high-resolution interactions between fisheries and bycatch species, and demonstrates that reserve systems do not necessarily mitigate bycatch threat unless specifically designed to do so. Moving forward, it will be

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important to explicitly address threat abatement during the design process. One approach is to design reserves to mitigate stated amounts of species-specific threat. Another is to quantify the impact of threat on species abundance, and to set species-specific objectives for how much loss in abundance should be avoided. Both approaches place reserves in locations where they can provide the most potential benefit to biodiversity despite competing ocean uses, and thereby maximize the biodiversity bang for each conservation buck.

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Supplementary Information (short legends)

Figure S1. Presence records for the seven bycatch species

Figure S2. Inter-annual variation in habitat suitability for bycatch species

Figure S3. Seasonal variation in habitat suitability for bycatch species

Table S1. Ten-fold cross validation results

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Table 1. Environmental datasets used in species distribution models. GEBCO: General Bathymetric Chart of the Oceans. NASA: National Aeronautics and Space Administration. AVISO+: archiving, validation, and interpretation of satellite oceanographic data. NOAA: National Oceanic and Atmospheric Administration. MODIS: Moderate Resolution Imaging Spectrometer. SeaWiFS: Sea-viewing Wide Field-of-view Sensor. MGET: Marine Geospatial Ecology Tools (Roberts et al 2010). *http://www.gebco.net/; ** http://www.aviso.altimetry.fr/en/home.html

		Parameter	Provider	Sensor	Unit	Source	Original resolution	# of layers
Static								
	1	Bathymetry	GEBCO	N/A	meters	*	2 x 2 km	1
	2	Slope	GEBCO (derived)	N/A	degree	*	2 x 2 km	1
Dynamic								
	3	Distance from night-time Cayula-Cornillon fronts	NASA (derived)	MODIS Aqua, Terra	decimal degree	MGET	4 x 4 km	120
	4	Particulate organic carbon	NASA	SeaWiFS	mol/m3	MGET	9 x 9 km	120
	5	Mean sea-level anomalies	AVISO+	Many	meters	**	28 x 28 km	120
	6	Night-time sea-surface temperature	NOAA	Pathfinder V5	°C	MGET	4 x 4 km	120
	7	Chlorophyll a	NASA	SeaWiFS	mg/m-3	MGET	9 x 9 km	120
	8	Diffuse attenuation coefficient at 490 nm	NASA	SeaWiFS	m-1	MGET	9 x 9 km	120

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Table 2. The temporal distribution of records across the time-series (January 1998 to December 2007) for the seven shark species. a. distribution of records across years; b. distribution of records across months.

a	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**
Blue shark	0	4	295	298	328	1	0	0	0	0
Silky shark	12	2	4	3	6	0	0	0	0	0
Bronze whaler	3	11	166	198	211	0	0	0	0	0
Tiger shark	28	31	118	155	136	3	16	13	6	1
Dusky whaler	5	5	31	63	65	0	0	0	1	0
Shortfin mako	11	48	305	288	336	1	0	0	0	0
Oceanic whitetip	0	0	113	182	223	0	0	0	0	0

b	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Blue shark	0	0	0	0	0	3	928	0	0	0	0	0
Silky shark	0	0	0	0	0	3	24	0	0	0	0	0
Bronze whaler	0	0	0	0	0	11	578	0	0	0	0	0
Tiger shark	2	2	1	0	6	29	446	0	13	8	6	2
Dusky whaler	0	0	1	0	0	5	164	0	0	0	0	0
Shortfin mako	0	0	0	0	0	58	913	0	0	0	0	0
Oceanic whitetip	0	0	0	0	0	0	523	0	0	0	0	0

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Table 3. Percentages of total bycatch threat for each species, total longlining effort, and analysis area in the three longline exposure groups as of the 2012 reserve network proclamation: exposed waters – both unzoned and zoned – and protected waters within no-take zones. Percentages are totaled across the three longline exposure groups; i.e. waters that were removed from the analysis are not considered in the calculation.

		Exposed (unzoned)	Exposed (zoned)	Protected
Total bycatch threat	Blue shark	71.4%	21.3%	7.3%
	Silky shark	70.2%	21.9%	7.9%
	Bronze whaler	69.8%	22.1%	8.1%
	Tiger shark	70.3%	21.8%	8.0%
	Dusky whaler	68.5%	22.8%	8.7%
	Shortfin mako	74.1%	20.1%	5.9%
	Oceanic whitetip	69.9%	22.0%	8.0%
Total effort		70.1%	21.9%	8.0%
Analysis area		54.2%	19.4%	26.4%

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Figure 1. The study area. a. Australia's Eastern Tuna and Billfish Fishery grounds (grey); b. the Commonwealth reserve networks within the Eastern Tuna and Billfish Fishery grounds: the Coral Sea Marine Reserve (red), the Temperate East network (green), and the South East network (blue).

Figure 2. Exposure of waters within the study area to longlining. Waters in which longlining was prohibited before or during the analysis time-series (January 1998 – December 2007, shown in red) were removed from the analysis to isolate the impact of the new no-take zones that prohibit longlining ("protected", green). Reserves in the South East network were established in May 2007, and were assumed to have negligible influence on reducing bycatch threat over the ten-year time-series. Exposed (zoned) indicates areas within reserves zoned to allow longlining.

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Figure 3. Monthly models showing long-term averages of habitat suitability for dusky whalers calculated across years of the time-series. Average habitat suitability for any given month is highest in dark brown areas, and lowest in dark blue areas.

Figure 4. The overlap between total Eastern Tuna and Billfish Fishery effort across the time-series and waters protected from longlining by no-take zones as of the 2012 reserve network proclamation (green). Waters that were removed from the analysis are show in black cross hatch.

Figure 5. Time-series of spatial overlap between bycatch threat and the Commonwealth Marine Reserve Network. Plots show the percentage (a) and absolute value (b) of monthly bycatch threat (calculated as the product of habitat suitability and number of hooks) for each species within the three longline exposure groups as of the 2012 reserve network proclamation: exposed to longlining, both zoned and unzoned, and waters protected from longlining by no-take zones.

Figure 6. Evaluation of comprehensiveness of raw data. This table uses language to guide the evaluation of data sets for bycatch species. However, the same measures can and should be applied to fisheries data sets. Measures should be evaluated for each species and fishery independently. Four measures of comprehensiveness (a-d) are applied to three different data sets for bycatch species. 1. The National Oceanic and Atmospheric Administration's North East Fisheries Science Center (NEFSC) Bottom Trawl Survey (Politis et al. 2014) is the world's longest running fishery-independent sampling program. 2. The shark data set used in this study, which was comprised of public records from the Ocean Biogeographic Information System. 3. A notional short-term satellite-tagging data set, such as those used by Bugoni et al. (2009) and Campbell (2011). For (a), we show one of several possible measures of accuracy, in this case spatial resolution of records. Coverage of species range within management area (c) is applicable only to our shark data set because this measure can be evaluated only when management areas are defined. For (d), number of individuals and number of records can be considered equivalent for large data sets. However, the distinction becomes important when evaluating small data sets. For example, one record for each of 100 individuals can be considered more

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comprehensive than 100 records for one individual. Gradients for each measure increase in comprehensiveness from left to right.

Figure 7. Protection priority (1, highest; 4, lowest) and management implications for pixels containing different categories of interactions. For each month, pixels containing interactions are located on the plot using two values calculated across years of the time-series for a given species: magnitude of bycatch threat (the total sum of threat between years) and variability of bycatch threat (the variance of threat between years). Management implications for each priority category are relevant to portions of the year when pixels fall into that category, e.g. pixels that move between top and second priority across months might be managed with seasonal no-take zones during months when they are top priority, and real-time management during the remainder of the year.

Supplementary Information (full legends)

Figure S1. The distribution of presence records for the seven bycatch species (black dots) within the study area (grey polygons).

Figure S2. Examples of inter-annual variation in monthly habitat suitability for bycatch species. Plots show the January distributions of oceanic whitetip, shortfin, silky and tiger sharks from 1998-2007. Habitat suitability for any given month is highest in dark brown areas, and lowest in dark blue areas.

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Figure S3. Examples of seasonal variation in monthly habitat suitability for bycatch species. Plots show the distributions of blue, bronze whaler and dusky whaler sharks for each month in 2007. Habitat suitability for any given month is highest in dark brown areas, and lowest in dark blue areas.

Table S1. Maxent 10-fold cross validation results for the seven bycatch species. Area under the receiver operating characteristic curve (AUC) and regularized training gain are both measures of goodness of fit.

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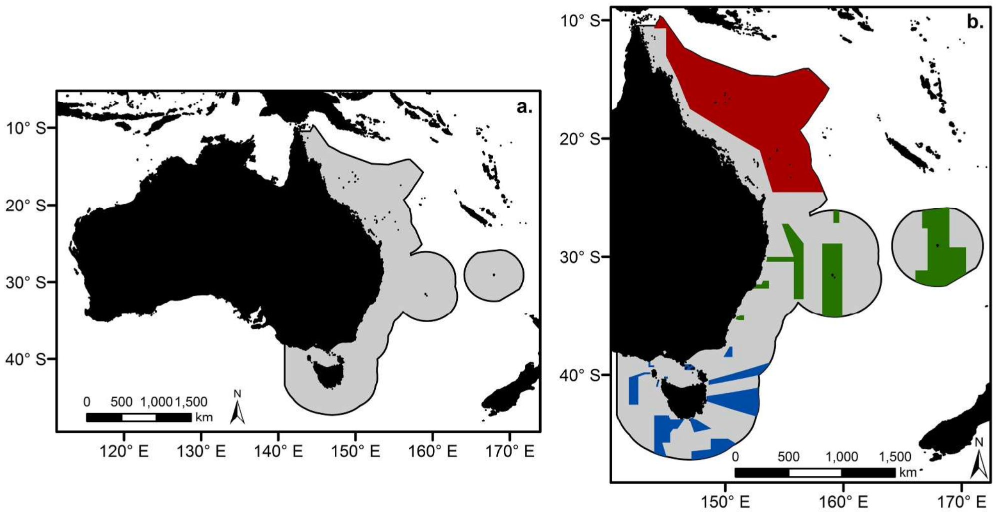

Figure 1. The study area. a. Australia's Eastern Tuna and Billfish Fishery grounds (grey); b. the Commonwealth reserve networks within the Eastern Tuna and Billfish Fishery grounds: the Coral Sea Marine Reserve (red), the Temperate East network (green), and the South East network (blue).
Fig. 1
110x58mm (600 x 600 DPI)

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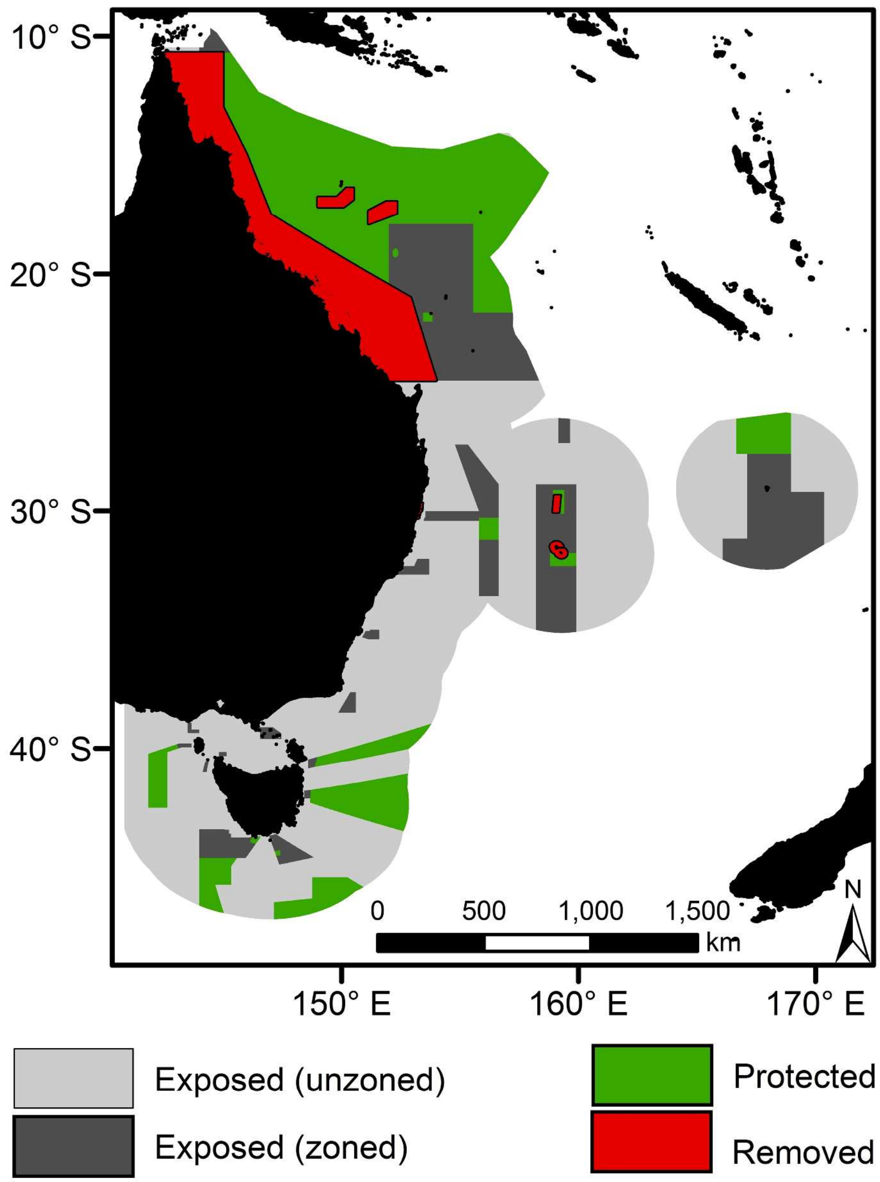

Figure 2. Exposure of waters within the study area to longlining. Waters in which longlining was prohibited before or during the analysis time-series (January 1998 – December 2007, shown in red) were removed from the analysis to isolate the impact of the new no-take zones that prohibit longlining ("protected", green). Reserves in the South East network were established in May 2007, and were assumed to have negligible influence on reducing bycatch threat over the ten-year time-series. Exposed (zoned) indicates areas within reserves zoned to allow longlining.
Fig. 2
125x166mm (600 x 600 DPI)

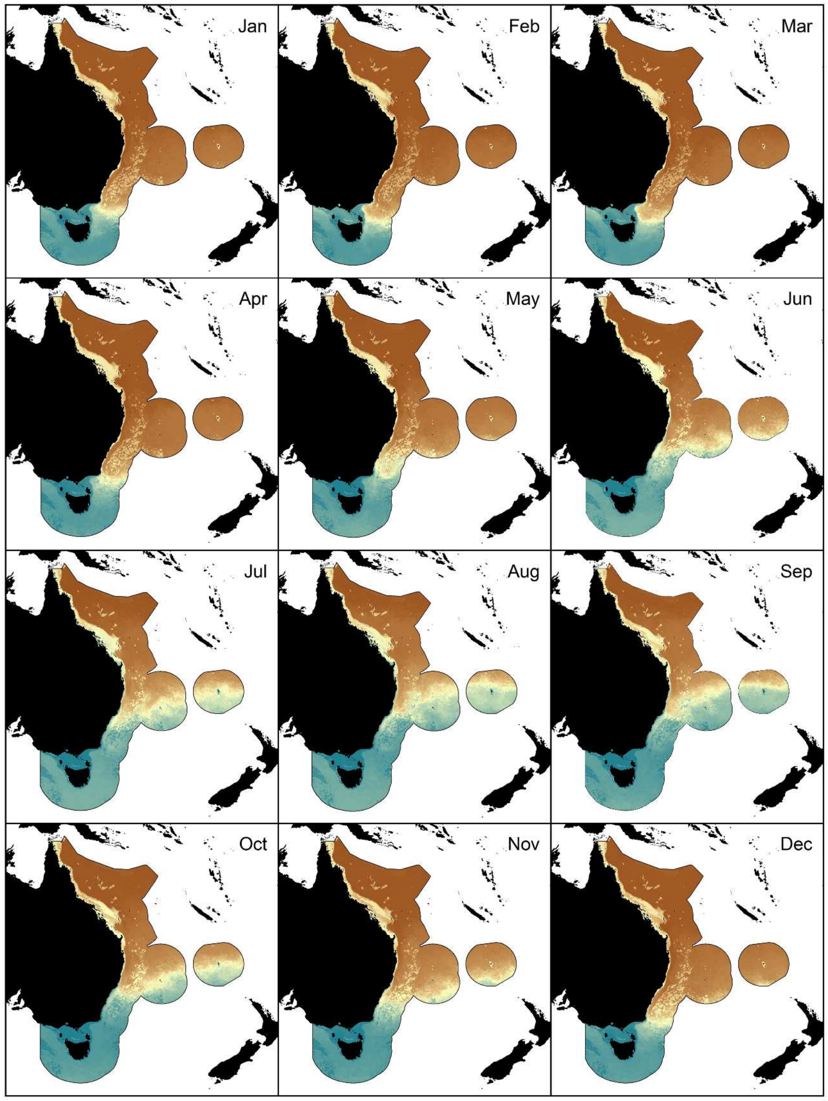

Figure 3. Monthly models showing long-term averages of habitat suitability for dusky whalers calculated across years of the time-series. Average habitat suitability for any given month is highest in dark brown areas, and lowest in dark blue areas.
Fig. 3
279x361mm (300 x 300 DPI)

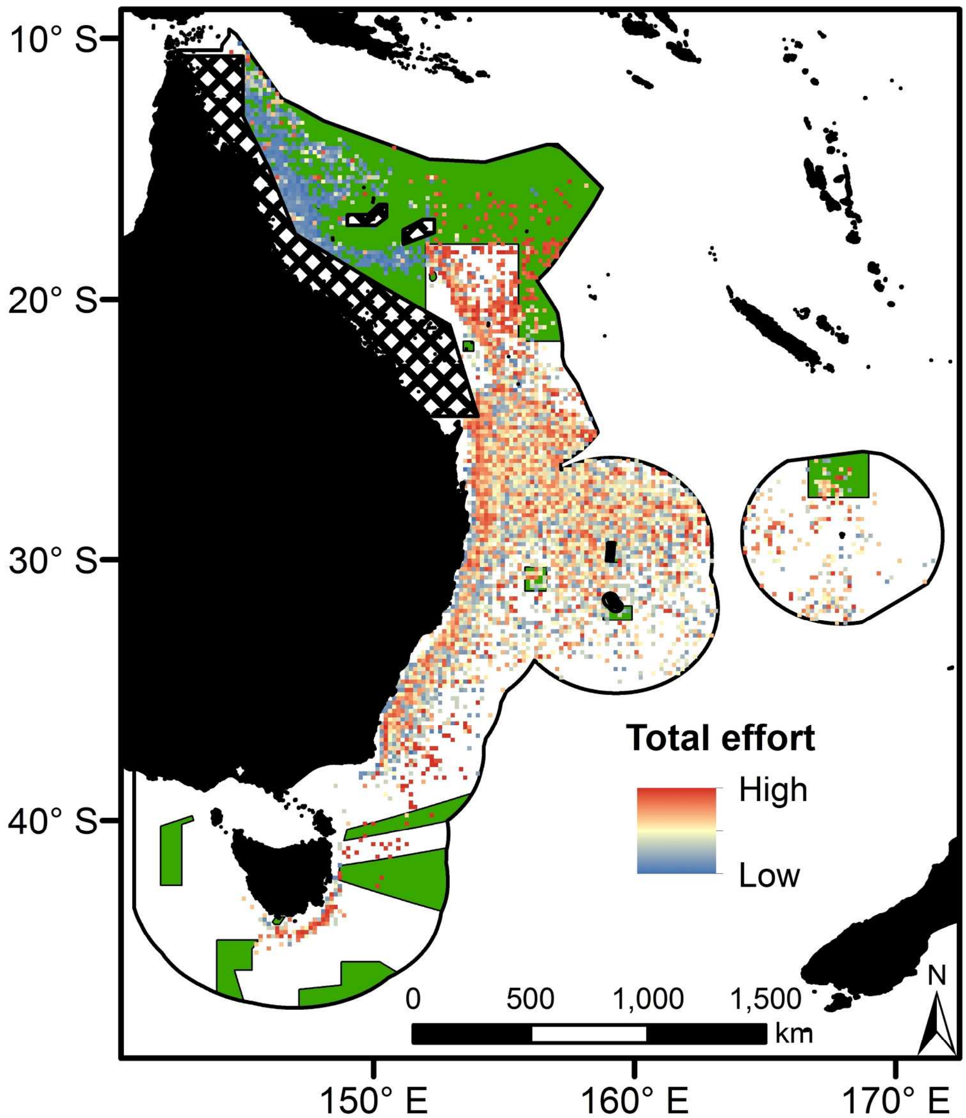

Figure 4. The overlap between total Eastern Tuna and Billfish Fishery effort across the time-series and waters protected from longlining by no-take zones as of the 2012 reserve network proclamation (green). Waters that were removed from the analysis are show in black cross hatch.
Fig. 4
109x126mm (600 x 600 DPI)

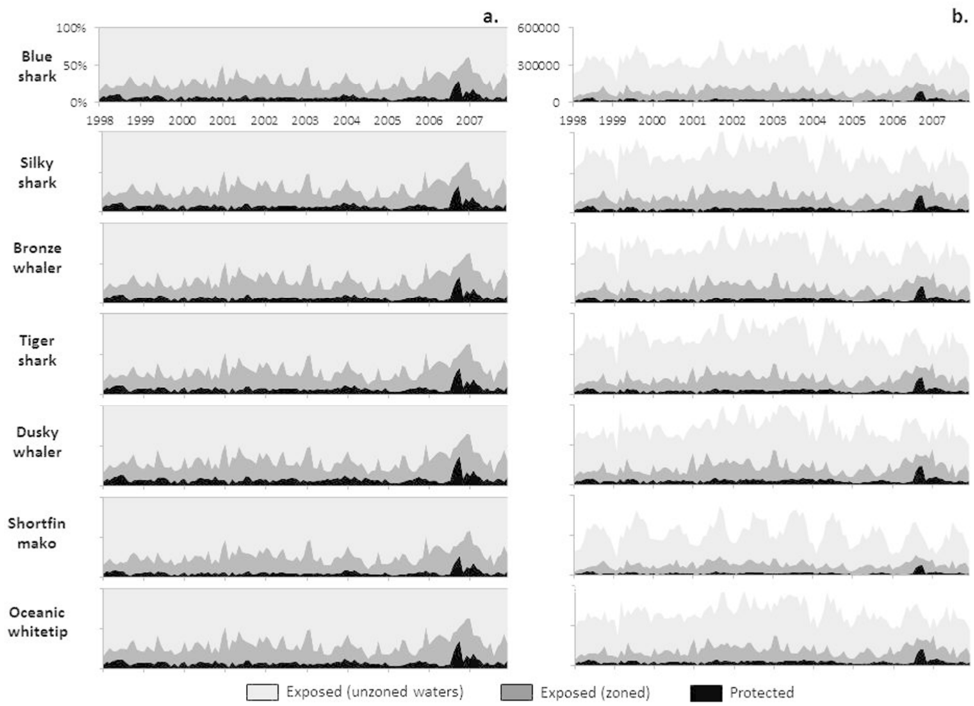

Figure 5. Time-series of spatial overlap between bycatch threat and the Commonwealth Marine Reserve Network. Plots show the percentage (a) and absolute value (b) of monthly bycatch threat (calculated as the product of habitat suitability and number of hooks) for each species within the three longline exposure groups as of the 2012 reserve network proclamation: exposed to longlining, both zoned and unzoned, and waters protected from longlining by no-take zones.
Fig. 5
254x190mm (96 x 96 DPI)

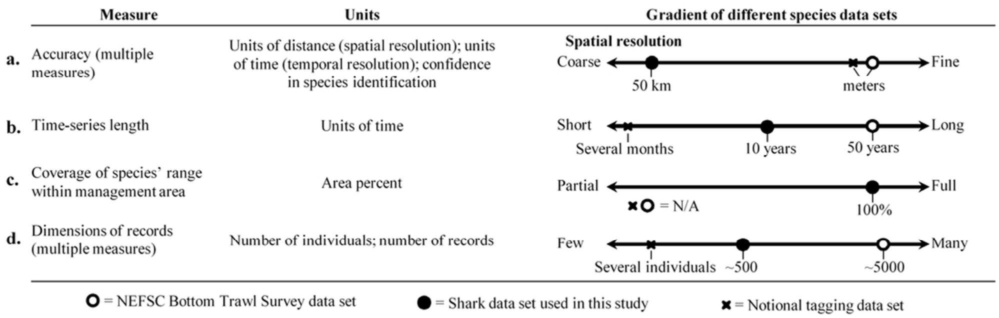

Figure 6. Evaluation of comprehensiveness of raw data. This table uses language to guide the evaluation of data sets for bycatch species. However, the same measures can and should be applied to fisheries data sets. Measures should be evaluated for each species and fishery independently. Four measures of comprehensiveness (a-d) are applied to three different data sets for bycatch species. 1. The National Oceanic and Atmospheric Administration's North East Fisheries Science Center (NEFSC) Bottom Trawl Survey (Politis et al. 2014) is the world's longest running fishery-independent sampling program. 2. The shark data set used in this study, which was comprised of public records from the Ocean Biogeographic Information System. 3. A notional short-term satellite-tagging data set, such as those used by Bugoni et al. (2009) and Campbell (2011). For (a), we show one of several possible measures of accuracy, in this case spatial resolution of records. Coverage of species range within management area (c) is applicable only to our shark data set because this measure can be evaluated only when management areas are defined. For (d), number of individuals and number of records can be considered equivalent for large data sets. However, the distinction becomes important when evaluating small data sets. For example, one record for each of 100 individuals can be considered more comprehensive than 100 records for one individual. Gradients for each measure increase in comprehensiveness from left to right.

Fig. 6

46x15mm (600 x 600 DPI)

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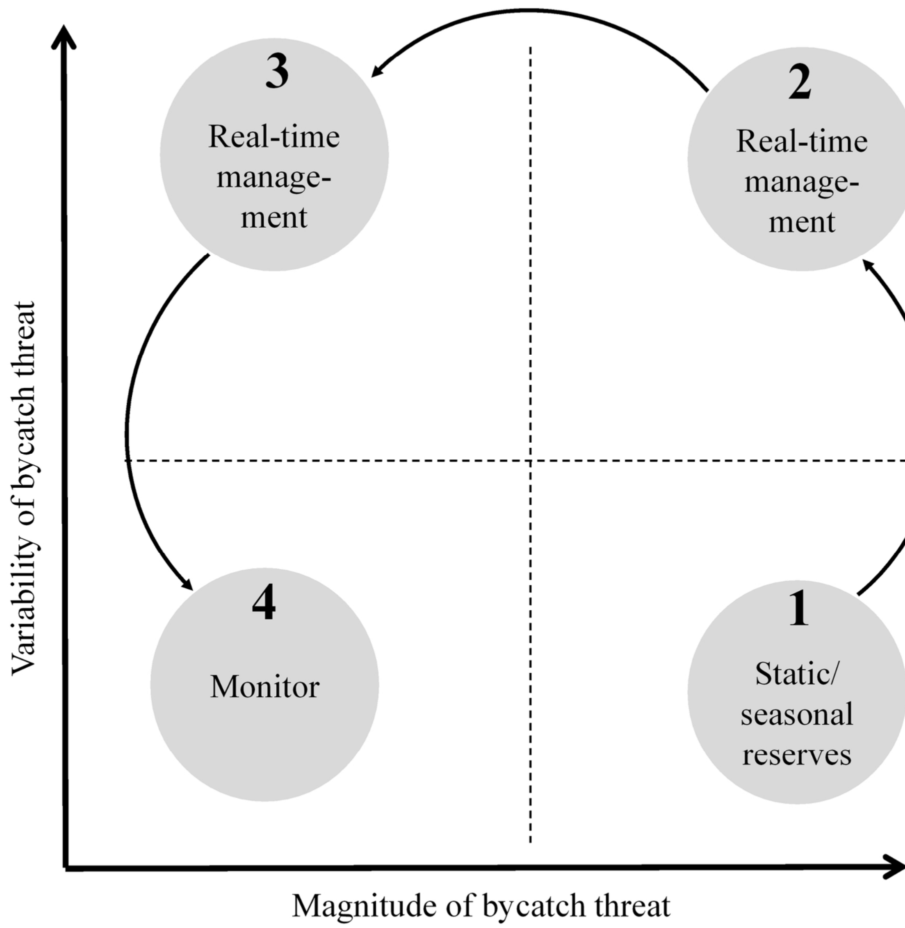

Figure 7. Protection priority (1, highest; 4, lowest) and management implications for pixels containing different categories of interactions. For each month, pixels containing interactions are located on the plot using two values calculated across years of the time-series for a given species: magnitude of bycatch threat (the total sum of threat between years) and variability of bycatch threat (the variance of threat between years). Management implications for each priority category are relevant to portions of the year when pixels fall into that category, e.g. pixels that move between top and second priority across months might be managed with seasonal no-take zones during months when they are top priority, and real-time management during the remainder of the year.
Fig. 7
81x80mm (600 x 600 DPI)