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Using temporally explicit habitat suitability models to assess threats to mobile species and evaluate the effectiveness of marine protected areas

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Abstract

A principal role of marine protected areas (MPAs) is to mitigate the decline of biodiversity. A key part of this role is to reduce the effects of fisheries on bycatch of vulnerable species. 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. 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. This method is applied to Australia's Eastern Tuna and Billfish Fishery to estimate interactions with seven principal bycatch species. The ability of MPAs to reduce bycatch is evaluated, and considerations are outlined for the spatial management of fishery-bycatch species interactions. Australia's Commonwealth Marine Reserve Network had a minimal impact on bycatch reduction under both the 2012 proclaimed and the 2015 panel-recommended zonings. These results highlight the need for threats to marine biodiversity to be incorporated directly into design of MPAs, and for close scrutiny of assumptions that threats will be incidentally abated after MPAs have been proclaimed, or that off-reserve mechanisms will compensate for inadequacies of MPAs.

Key words: bycatch, fisheries, gap analysis, Maxent, reserve network, species distribution model

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, either released alive or discarded dead (hereafter: bycatch), occurs at higher rates than, and outweighs the catch of target species (Tsagarakis et al. 2013, Uhlmann et al. 2013). 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, with many mitigation measures employed, bycatch remains a significant, frequently principal, threat to many marine species (Zydelis et al. 2009, Senko et al. 2013).

Spatial management schemes have been successfully implemented 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 non-spatial approaches are also employed to reduce bycatch, such as move-on rules and bycatch quotas, these approaches are frequently applied within a spatial framework and implemented in the places and times in which bycatch is most likely to occur (e.g. Hobday and Hartmann, 2006). Therefore, spatial management of bycatch is likely to remain an important component of the bycatch mitigation toolkit.

Although examples exist, 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 ephemeral and seasonal oceanographic conditions (Weimerskirch 2007, Game et al. 2009, Hill et al. 2015). Fishery distributions can likewise fluctuate as operations shift to exploit migratory target species and in reaction to time-area management regulations (Dunn et al. 2011, 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 spatiotemporal 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 (Phillips et al. 2006, Žydelis et al. 2011). 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 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. 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 (the probability of bycatch species presence) and mean kilometer gillnet hours (magnitude of fishery effort) (Campbell 2011), or the product of the percentage of distribution of bycatch species (the probability of bycatch species presence) and the average number of hooks (magnitude of fishery effort) (Tuck et al. 2011). The term "interaction" is used here 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 occur only 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 used to design closures that are targeted to the right places at the right times to reduce bycatch. While many studies have estimated 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), most interactions were estimated at course spatial and/or temporal resolutions (Online Resource A).

In this context, a new method is presented for quantifying interactions at high temporal and spatial resolutions using temporally explicit habitat suitability models. Time-series analysis of historical interactions are used to provide foresight into potential interactions in the near future, allowing for an estimate of the ability of planned spatial management to reduce bycatch in the near future. As a case-study, this method is applied to quantitatively evaluate interactions 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 and proposed marine protected areas to reduce bycatch is then demonstrated using Australia's Commonwealth Marine Reserve Network (hereafter: reserve network). The reserve network is a system of permanent static reserves established as a conservation tool to protect and maintain biodiversity (CMR 2016), so it is crucial to test its ability to reduce threats to biodiversity, including bycatch. The ability of the reserve 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 reserve network's management plans.

We propose our method as a generic approach to investigate bycatch threat in relation to options for spatial management in any marine jurisdiction, although we are aware of data-related limitations of our case-study. Model performance was restricted by the spatial and temporal resolution of the best available species data at the time of analysis. However, these limitations are likely to apply to many species dataset for analysis of bycatch interactions, given the monetary and operational challenges of collecting species records. We therefore use our case-study as a platform to discuss how data comprehensiveness constrains policy and operational management of bycatch threat, and explore approaches to management that account for data 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 shortfin mako (*Isurus oxyrinchus*), listed as vulnerable by the IUCN Redlist, released dead (Hunt 2013, IUCN 2015). Sharks have limited biological productivity and therefore are particularly vulnerable to longline fisheries that selectively remove the oldest and largest individuals (Sibert et al. 2006, Cortés et al. 2010). Our study examines ETBF interactions with seven principal shark bycatch species: blue shark (*Prionace glauca*), shortfin mako, 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).

Australia's Commonwealth Marine 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). Following strong resistance from commercial and recreational fisheries over the loss of fishing grounds (Voyer and Kenchington 2016), the 2012 proclaimed zoning was suspended and an independent review was launched in 2014 by the Australian government. The outer boundaries of the reserves were not subject to change, so the focus of the review was on the internal zonings that prescribe allowed uses (Buxton and Cochrane 2015). The review was completed in 2015, and the adjusted panel-recommended zoning was released in September 2016, which will inform the final management plan (CMR 2017).

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 through reserve design. Analyses of the 2012 proclaimed zoning 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 2012 zoning as being residual by avoiding extractive uses rather than mitigating their impacts (Pressey 2013, Devillers et al. 2015). The 2015 panel-recommended zoning further reduced constraints on commercial and recreational fisheries, exacerbating the residual nature of the reserve network (Buxton and Cochrane 2015, Pressey et al. 2016). Here, we hindcast bycatch threat and quantify the abilities of the 2012 and 2015 zonings to abate historical bycatch threat in order to understand the networks' potential for biodiversity protection in the future.

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).

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 selected because they are known to influence distributions of pelagic species (Chassot et al. 2011). Layers were regridded in ArcGIS 10.1 from their original resolutions 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 occurrence records for the seven bycatch species were downloaded from the Ocean Biogeographic Information System (http://www.iobis.org/) from January 1998 to December 2007 (Fig. 1a and Table 2). 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 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 occurrence record was associated with the unique values of environmental variables at the same latitude/longitude during the same month and year and compiled into a samples-with-data matrix.

The presence-only modeling software Maxent (Phillips 2004, Phillips et al. 2006, Elith et al. 2010) 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. In a samples-with-data matrix, environmental conditions at the times and locations of the species occurrences and background points (i.e. locations where a species hasn't necessarily been detected, similar to pseudo-absences) are extracted before the Maxent run. The resultant models preserve the relationships between short-term environmental predictors and species presence. All default settings were used with the exception of background point selection. The default settings have been validated over a wide range of species, sampling biases and numbers of occurrences (see Phillips and Dudik (2008) and the help tab within the Maxent application for comprehensive parameter descriptions). Background point selection was done using a targeted background, because the logistic output requires the assumptions of random sampling across the seascape and across the time-series (Merow et al. 2013), which are rarely met by species datasets (Araújo and Guisan 2006). Following Phillips and Dudik (2008). To remove sampling bias for a given target shark, the records of all the other six shark species were used as background points. In other words, background points are the locations where the other six shark species occurred but the target shark was not found. This methodology ensured that the background points for each shark species accounted for both spatial and temporal bias of the sampling effort (Reside et al. 2010). 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). The seven shark models were predicted over the environmental layers to create rasters of habitat suitability for each species in each month of the time-series (n=840 projections in total).

Ten-fold cross validation was used to test model fit. For each iteration, the area under the receiver operating characteristic curve (AUC) was calculated. AUC values range in principle between 0 and 1; AUCs of 0.5 indicate random discrimination between presences and absences, and AUCs above 0.5 indicate better than random (Phillips and Dudik 2008).

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 sufficiently accurate for representing fishery effort at the spatial resolution of our analyses (Dunn et al. 2008). To calculate fishery distribution, a raster file was created for each month within the time series (1998-2007) in which each 9x9 km pixel was valued with the total number of hooks deployed in that month.

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. Each pixel within a given month therefore had seven associated values for bycatch threat.

Evaluation of the Commonwealth Reserves

Waters within the ETBF fishing grounds were divided into four categories based on exposure to longlining under two reserve network zonings: 2012 proclaimed zoning and the 2015 panel-recommended zoning (Fig. 2a,b). Overlap with historical bycatch threat was calculated individually for the 2012 proclaimed and the 2015 panel-recommended zonings. The purpose of this analysis was to evaluate the potential of each zoning to mitigate bycatch. The four exposure categories were: 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 were within reserves that prohibited longlining and were proclaimed before or during the time-series analysis (1998-2007). Zoned and unzoned areas that permit longlining 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 category 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 the removed category 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. This decision was based on two assumptions: first, that the eight-month effect of these reserves on bycatch threat (May-December 2007) over the ten-year analysis would be negligible; and, second, that the establishment of these reserves would have been informed by almost all the information on effort and bycatch threat available to us.

The percentage of fishery effort and bycatch threat within the remaining three exposure categories was calculated for each species in each month across the time-series, for both the 2012 proclaimed and the 2015 panel-recommended zonings. Percentages of fishery effort or bycatch threat in the exposure categories were calculated with respect to totals across waters retained in the analysis. Although fishery effort was integrated into the bycatch threat metric (i.e. the product of habitat suitability and fishery effort), effort was also evaluated independently to isolate its impact.

Results

Monthly habitat suitability layers and total bycatch threat for each species can be interactively explored in a reactive R Shiny web application: https://heatherwelch.shinyapps.io/etbf_bycatch_app/ ; hereafter referred to as the Bycatch App.

Species distributions

Monthly projections for all species showed inter-annual (Online Resource B, Bycatch App) and seasonal (Online Resource C, Bycatch App) variation in habitat suitability between months, although patterns of variation differed between species. Model AUCs (one model for each species, which was predicted over 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 (Online Resource D). 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 overall spatial relationship between total fishing effort and spatial protection from longlining in the 2012 and 2015 zonings can be observed by summing effort across the time series (Fig. 3a,b). In the 2012 proclaimed zoning, 8.0% of total longlining effort was within waters that were later protected from longlining by no-take zones (Table 3). This value was reduced to 3% under the 2015 panel-recommended zoning. The largest spatially consistent area of effort was in the central fishing grounds where there was minimal subsequent protection from no-take zones in either the 2012 or 2015 zonings. The large no-take zones in the 2012 and 2015 zonings 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 in the 2012 proclaimed zoning, moving from high historical effort outside the zone to low historical effort in waters subsequently protected. In the 2015 panel-recommended zoning, protection of this area of low historical effort was removed, allowing fisheries to regain nearly complete access to waters adjacent to the Great Barrier Reef.

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 areas that remained exposed in unzoned waters outside of reserves across all months (Table 3, Bycatch App).

This was consistent between the 2012 proclaimed and the 2015 panel-recommended zonings, because the outer boundaries of the reserves remained unchanged. On average, around 22% of bycatch threat was in waters that remained exposed but zoned in 2012, increasing to around 27% in 2015. Overall percentages of total bycatch threat within no-take zones protected from pelagic longlining by the 2012 zoning ranged from 5.9% for shortfin makos to 8.7% for dusky whalers (Table 3). For each species, these values decreased on average by 5% in the 2015 zoning.

In both 2012 and 2015, exposed (unzoned) waters had the largest areal extent, covering 54.2% of the analysis area, followed by protected waters within no-take zones and exposed (zoned) waters (Table 3). Between 2012 and 2015, 7.5% of the total analysis area was rezoned as exposed (zoned) in 2015, after being protected from longlining in 2012. This rezoning reduced protected areal extent by 28%. In both the 2012 and 2015 zonings, exposed (unzoned) waters had disproportionately large amounts of longlining effort and bycatch threat, and no-take zones had disproportionately small amounts (Table 3).

A time-series analysis of the overlap between exposure categories and both monthly effort and monthly bycatch threat, if the zonings had been in place from January 1998 to December 2007, illustrates the temporal consistency of the patterns observed above. In all months except three, there was more overlap with effort in exposed (zoned) waters in the 2015 zoning compared to the 2012 zoning (Fig. 4a). Similarly, in all months except three, there was less overlap with effort in protected waters in the 2015 zoning compared to the 2012 zoning. These same patterns were present in the time-series analysis of exposure category overlap with monthly bycatch threat between the 2015 and 2012 zonings (Fig. 4b).

Discussion

This study presents a new method of quantifying fishery-bycatch species interactions at high spatial and temporal resolutions. High resolutions were achieved through the use of temporally explicit species distribution models, which are infrequently applied in the literature (but see Reside et al. 2010, Hazen et al. 2016, Hill et al. 2016, Scales et al. 2016). Temporally explicit models are important for highly dynamic species such as pelagics because they identify changes in suitability in relation to temporal variability in predictors. These aspects of variability are lost when species occurrence 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 information on the variability of interactions across seasons and years (Online Resources B,C, Bycatch App). This type of information can help guide decisions about spatial management to reduce fisheries bycatch, even when underlying data are patchy (Dunn et al. 2016). 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. Given the data limitations in this present study, which apply to many such exercises, and to aid progress in these areas, an analytic approach is outlined to ensure interactions are amenable to spatial management (Online Resource E).

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 2012 proclaimed zoning did not explicitly address threats posed by fishing, or provide guidelines to manage threats from fishing (Kearney et al. 2012). The 2012 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 2012 proclaimed zoning is zoned as no-take (Table 3).

It appears that the ability of the reserve network to mitigate bycatch threat will be further compromised if the 2015 panel-recommended zoning is implemented. Compared to having no protection from longlining, the 2015 zoning will reduce the total bycatch threat for each shark species by a minimum of 2.3% and a maximum of 3.0% (Table 3). On average across species, the 2015 zoning increases the bycatch threat by 5.0% compared to the 2012 proclaimed zoning.

Both 2012 proclaimed and 2015 panel-recommended zonings provide little protection against bycatch, and minimally limit fishing efforts in the area; exposed (unzoned), i.e., unprotected, waters cover 54.2% of the analysis area and contain about 70 % of historical fishing effort. (Table 3). Under the 2012 zoning, no-take zones overlapped only 8.0% of total historical effort despite covering 26.4% of the analysis area (Table 3). Figure 3a indicates that the 2012 boundaries of the Coral Sea no-take zone were designed to explicitly avoid areas of intense historical effort, mirroring the findings of Hunt

(2013). Despite minimal fishery impact in the 2012 proclaimed zoning, the 2015 panel-recommended zoning was designed to further avoid areas that were historically fished, with no-take zones overlapping only 3.0% of total historical effort (Table 3). This reduction in fishery displacement was achieved by downgrading no-take zones to zones with partial protection that allow some forms of fishing. It has been well established that partially protected zones are not able to confer the same advantages to biodiversity as no-take zones (Lester and Halpern 2008, Edgar et al. 2014).

Concern over the marginal impact of the reserve network on fisheries and other extractive activities has been previously expressed (for the 2012 proclaimed zoning: Nevill and Ward 2009, Pressey 2013, Devillers et al. 2015; for the 2015 panel-recommended zoning: EDO 2016, OSCA 2016, Pressey et al. 2016). 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, longlining bycatch threat for protected shark species remained substantial, in fact disproportionately large, after the proclamation of the 2012 zones, and stands to increase if the 2015 panel-recommended zones are adopted into the final management plan.

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, non-static approaches to spatial management (see below) might be more cost-effective and should also be explored.

Towards spatial management of interactions

Implications of spatio-temporal dynamics

Fishery-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. Dynamic features such as interactions can be characterized to guide approaches to both 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. Respectively, these metrics could refer to the total and inter-annual variance of bycatch threat across the years of the time-series. These two monthly metrics indicate the likelihood and constancy, respectively, of bycatch events across years, and can help planners prioritize pixels for protection within each month and identify the appropriate approach to management (Fig. 5).

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, 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. 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, and therefore effective management will require flexible designs that can be updated to reflect real-time conditions (see examples of real-time management in Howell et al. 2008, Hobday et al. 2010, Holmes et al. 2011, Bethoney et al. 2013, O'Keefe and DeCelles 2013). For example, when this analysis is applied to January interactions in the ETBF, most pixels fall into the second and third priority categories, indicating that real-time management could be used as an off-reserve mechanism to mitigate bycatch.

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, e.g. Hill et al. 2015) 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, with the ultimate goal of population persistence. 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 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 could be used provide insights into the effect of different objectives and management scenarios within the ETBF.

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.

Due to the strong bias of 2012 and 2015 protection in avoiding areas with highest fishery effort (Fig. 3a&b, Fig. 4, Table 3), it is unlikely that poorly fitted models would have greatly affected the distribution of bycatch threat within the three exposure categories. Bycatch threat could occur only in areas that contained fishery effort, and over 92% of total historical effort was outside waters placed in no-take zones in both the 2012 and 2015 zonings. Therefore, we consider that our analysis accurately highlights the limited impact of the Commonwealth Marine Reserve Network on reducing bycatch threat, 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 (Online Resources B,C), and better model fit. The importance of different types of predictor variables will change depending on study species and location, and should be also selected on a case-by-case basis. Most crucially, better models will require more comprehensive data on bycatch species, which 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 demonstrates that reserve systems do not necessarily mitigate bycatch threat unless specifically designed to do so. From hereon, it will be important to explicitly address threat abatement during the process of designing marine reserves. 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, preferably linked to persistence, 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. The method proposed here allows interactions between fisheries and bycatch species to be estimated at high resolutions, thereby providing planners with the necessary information to mitigate an important biodiversity threat during the reserve design process.

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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

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

(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

Table 3. Percentages of total bycatch threat for each species, total longlining effort, and analysis area in the three longline exposure categories as of the 2012 proclaimed and 2015 panel-recommended zonings: exposed waters – both unzoned and zoned – and protected waters within no-take zones. Percentages are totaled across the three longline exposure groups within each zoning scheme. Waters that were removed from the analysis are not considered in the calculation.

		Exposed (unzoned)			**Exposed (zoned)**			**Protected**		
		2012	2015	Difference	2012	2015	Difference	2012	2015	Difference
Total bycatch threat	Blue shark	71.4%	71.4%	0.0%	21.3%	25.9%	**4.6%**	7.3%	2.7%	**-4.6%**
	Silky shark	70.2%	70.2%	0.0%	21.9%	26.9%	**5.0%**	7.9%	2.9%	**-5.0%**
	Bronze whaler	69.8%	69.8%	0.0%	22.1%	27.3%	**5.2%**	8.1%	2.9%	**-5.2%**
	Tiger shark	70.3%	70.3%	0.0%	21.8%	26.9%	**5.1%**	8.0%	2.8%	**-5.2%**
	Dusky whaler	68.5%	68.5%	0.0%	22.8%	28.5%	**5.7%**	8.7%	3.0%	**-5.7%**
	Shortfin mako	74.1%	74.1%	0.0%	20.1%	23.6%	**3.5%**	5.9%	2.3%	**-3.6%**
	Oceanic whitetip	69.9%	69.9%	0.0%	22.0%	27.2%	**5.2%**	8.0%	2.8%	**-5.2%**
Total effort		70.1%	70.1%	0.0%	21.9%	26.9%	**5.0%**	8.0%	3.0%	**-5.0%**
Analysis area		54.2%	54.2%	0.0%	19.4%	26.9%	**7.5%**	26.4%	18.9%	**-7.5%**

Figure Legends

Figure 1. The study area. Australia's Eastern Tuna and Billfish Fishery grounds - grey, (a); the Commonwealth reserve networks within the Eastern Tuna and Billfish Fishery grounds (b): the Coral Sea Marine Reserve (red), the Temperate East network (green), and the South East network (blue). The spatial distribution of shark species occurrence records are shown in (a) as black dots.

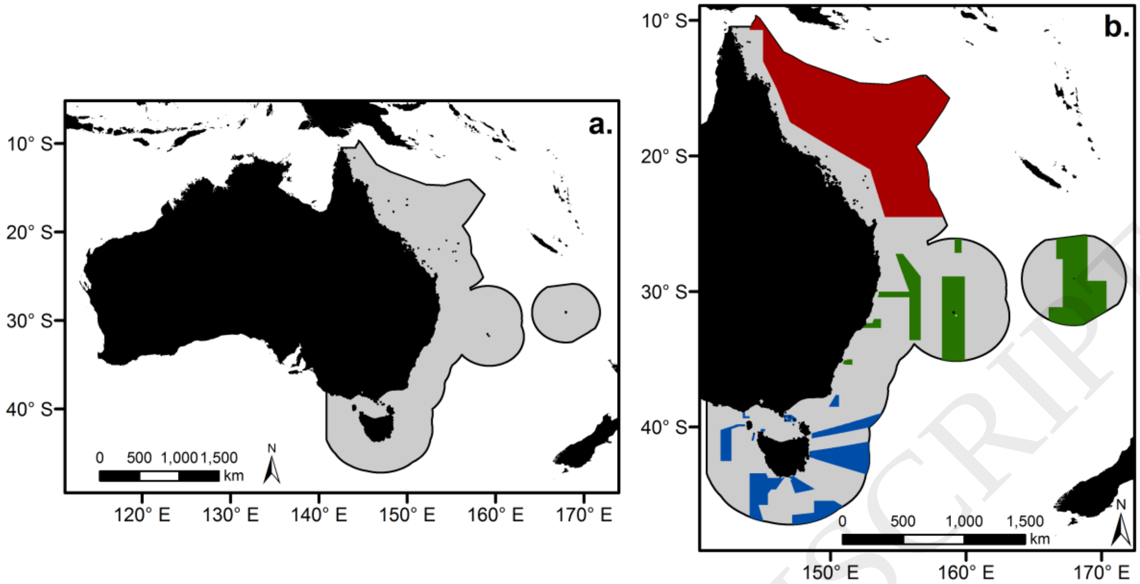
Figure 2. Categories of exposure to longlining in the waters of the study area: under the 2012 proclaimed zoning (a), and with the 2015 panel-recommended zoning (b). Four exposure categories were used: exposed (unzoned) waters outside reserves that allow longlining (light grey), exposed (zoned) waters within reserves that allow longlining (dark grey), protected zones that prohibit longlining (green), and removed waters in which longlining was prohibited before or during the analysis time-series (red).

Figure 3. The overlap between total Eastern Tuna and Billfish Fishery effort across the time-series and waters protected from longlining subsequent to the time-series. Protected waters (green) are shown for the 2012 proclaimed zoning (a) and the 2015 panel-recommended zoning (b). Waters that were removed from the analysis are show in black cross hatch.

Figure 4. Time-series of overlap between the Commonwealth Marine Reserve Network and both effort and bycatch threat. Plots show monthly effort (a) and bycatch threat

summed across all species (b) within two exposure categories for both the 2012 proclaimed and the 2015 panel-recommended zonings. Exposure categories within the Network are zoned waters exposed to longlining and waters protected from longlining by no-take zones. Exposed (unzoned) waters (not shown in figure) were beyond the scope of the 2015 review. For these waters, there was no change in overlap with bycatch threat or effort between 2012 and 2015.

Figure 5. Protection priority and possible management approaches for combinations of magnitude and variability of bycatch threat. 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 sum of threat across years) and variability of bycatch threat (the variance of threat across years). Priority 1 is highest, and 4 is lowest. Management implications for each priority category are relevant to portions of the year when pixels fall into that category. For example, 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.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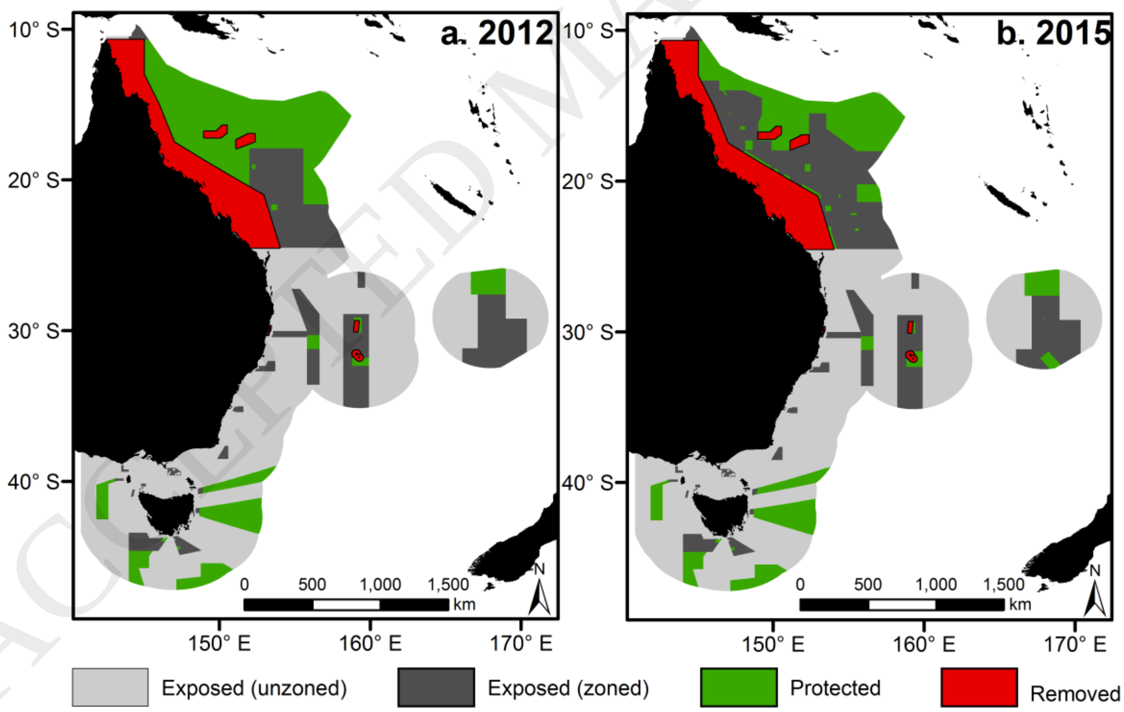
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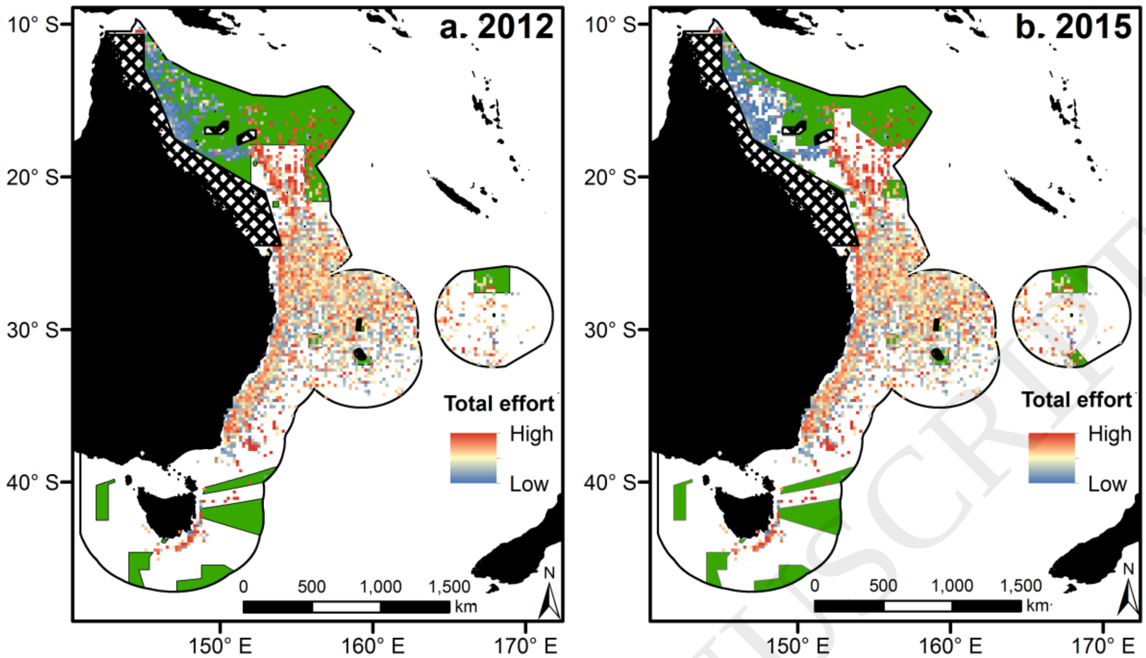
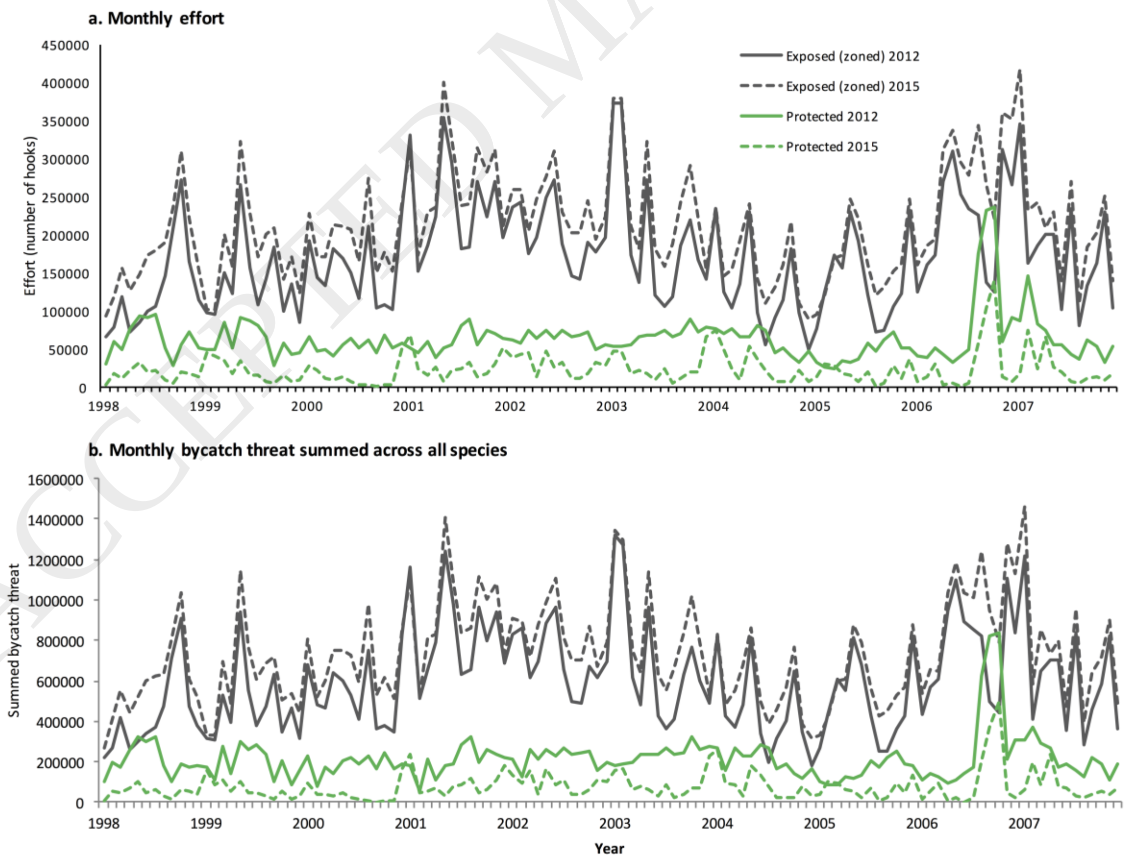
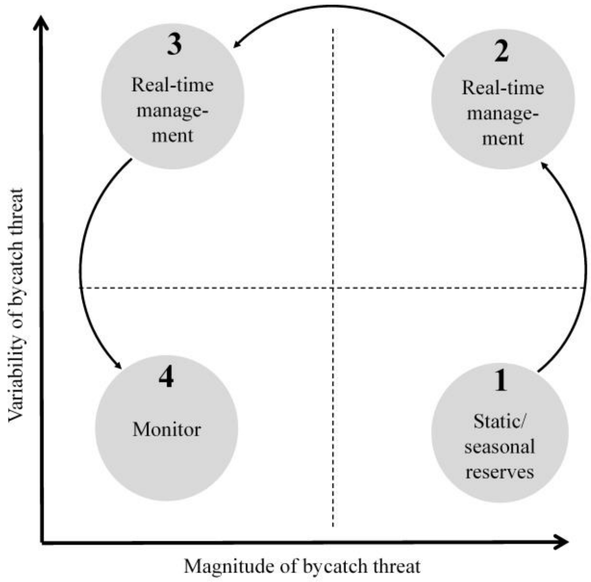
0 500 1,000 1,500
km
N
Exposed (unzoned)
Exposed (zoned)
Protected
Removed



a. 2012
b. 2015
10° S
20° S
30° S
40° S
150° E
160° E
170° E
Total effort
High
Low
0
500
1,000
1,500
km
N



a. Monthly effort
Effort (number of hooks)
Exposed (zoned) 2012
Exposed (zoned) 2015
Protected 2012
Protected 2015
b. Monthly bycatch threat summed across all species
Summed bycatch threat
Year


3
Real-time
manage-
ment
2
Real-time
manage-
ment
4
Monitor
1
Static/
seasonal
reserves
Variability of bycatch threat
Magnitude of bycatch threat