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ABSTRACT

Aim: Trawling leads to widespread direct human disturbance on the seabed. Knowledge of the extent and consequences of this disturbance is limited because large-scale distributions of seabed fauna are not well-known. We map faunal distributions in the Australian Exclusive Economic Zone (EEZ) and quantify the proportion of their abundance that occurs in areas 1) that are directly trawled, and 2) where legislation permanently prohibits trawling — defined as percentage *exposure* or *protection* respectively. Our approach includes developing a method that integrates data from disparate seabed surveys to spatially expand predicted benthos distributions.

Location: Australia

Methods: We collate data from 18 seabed surveys to map the distribution of seabed invertebrates (benthos) in nine regions. Our approach combines data from multiple surveys, groups taxa within taxonomic classes, and uses Random Forests to predict spatial abundance distributions of benthos groups from environmental variables. Exposure and protection of benthos groups were quantified by mapping their predicted abundance distributions against the footprint of trawling and legislated boundaries of marine reserves and fishery closures.

Results: Trawling is currently prohibited from more area of Australia's EEZ (58%) than is trawled (<5%). Across 134 benthos-groups, 96% had greater protection of abundance than exposure. The mean trawl exposure of benthos-group abundance was 7%, compared to mean protection of 38%; whereas the mean abundance neither trawled nor protected was 55%. Fishery closures covered 19% less study area than marine reserves, but overlapped with a higher proportion (5% more) of benthos-group abundance.

Main Conclusions: This study provides the most extensive quantitative assessment of the current exposure of Australia's benthos to trawling. Further, it highlights the contribution of

fishery closures to marine conservation. These results help identify regions and taxa that are at greatest potential risk from trawling, and supports managers to achieve balance between conservation and sustainable industries in marine ecosystems.

INTRODUCTION

Seabed fauna are critical for the functioning of marine ecosystems. Seabed invertebrates (benthos) help oxygenate the sea floor, break down organic material, provide habitat structure and food sources for other organisms (Tagliapietra & Sigovini, 2010). Accordingly, benthos are often used as indicators for assessing the status and health of marine ecosystems (Rosenberg *et al.*, 2004). From a human perspective, benthos support a range of commercial industries (Hiddink *et al.*, 2011; Choi & Joon Choi, 2012). However, many benthic species are sensitive to disturbance; thus, the extent and intensity of human activity in marine ecosystems can ultimately disrupt the services that benthos provide (Thrush & Dayton, 2002). While the importance of benthos in marine ecosystems is recognized, their distributions and extent of threats on them are largely unknown, particularly across large spatial scales.

Seabed trawling and dredging (hereafter "trawling") yield ~25% of global seafood catches (FAO, 2009), yet are considered the most widespread human source of direct physical disturbance to benthos (Hinz *et al.*, 2009). Much research has focused on investigating the impacts of trawling on benthic species and communities (Kaiser *et al.*, 2006). Experimental and comparative studies indicate that trawling reduces species abundance and biomass (Burridge *et al.*, 2003; Kaiser *et al.*, 2006), and can lead to longer-term restructuring of benthic communities (Hiddink *et al.*, 2006a; Hinz *et al.*, 2009). While there is much debate about the severity and extent of trawl impacts (Hilborn, 2007), rather few studies have measured these on large scales (>50 km^2) where spatial variation in trawling intensity will influence the aggregate impact (Jennings *et al.*, 2001; Hiddink *et al.*, 2006a; Pitcher *et al.*, 2016a).

Marine reserves and fishery closures are two management tools that are used to protect species and habitats from human disturbance (Rice, 2005). Previously, marine reserve designation was largely opportunistic (Roberts *et al.*, 2003), but now systematic approaches that take account of biota distributions may be used for planning spatial closures (Schmiing *et al.*, 2014). Even though closures and reserves may not be specifically established for protection and conservation of benthos, they may provide fortuitous benefits (Pitcher *et al.*, 2007a). Protected areas that are not located in areas of high benthos abundance or diversity may have little benefit for the state of benthic ecosystems, and can have negative effects if fishing is displaced to benthos rich areas (Pitcher *et al.*, 2015). Thus, benefits for benthos cannot be assumed, and distributions of benthic habitats and fauna should be assessed and incorporated when planning spatial closures (Hiddink *et al.*, 2006b).

Knowledge of the large-scale distribution of benthos is essential for impact assessments, conservation and management. Given incomplete knowledge of benthic distributions and the challenge of large-scale and high-resolution sampling (Fisher *et al.*, 2011), models are often developed and used to predict species distributions beyond sampled sites (Elith & Leathwick, 2009). Attempts to apply these models are often constrained by sparse and patchy survey data, often only available as presence/absence or even presence-only records and at coarse taxonomic resolution (Compton *et al.*, 2013). Despite investment in some large-scale benthic surveys in Australia (Pitcher *et al.*, 2007b; Pitcher *et al.*, 2016b), it is not feasible to address all constraints. Hence, alternative methods need to be adopted for predicting distributions and trawling impacts in data-limited situations, and to expand the extent of assessed regions. Advances in the use of data-limited approaches for making large-scale predictions of benthos distributions would enable management decisions on the mitigation of seabed impacts in more areas of the world.

We aim to quantify, across large spatial scales, the proportion of benthos abundance currently distributed in areas that are trawled — defined as *exposure* — and in marine reserves or fishery closure areas where legislation permanently prohibits trawling — defined as *protection*. Our analysis is based on benthos distributions predicted from seabed survey data. We also develop approaches to utilize sparse and disparate datasets with the intention of expanding the spatial extent of distribution mapping — an approach that can be widely applicable elsewhere. Here we focus on the Australian Exclusive Economic Zone (EEZ), where the diversity of environments and seabed fauna is high (Ponder *et al.*, 2002), and management measures are already influencing the distribution of trawling activity; including large MPAs (e.g. The Great Barrier Reef Marine Park: Day & Dobbs, 2013; Commonwealth Marine Reserves: Department of the Environment, 2016) and ecosystem-based fisheries management (McLoughlin *et al.*, 2008).

METHODS

Large-scale distributions of benthos were modelled and predicted from available surveys and environmental variables across Australia's EEZ. We sought to maximise the extent of predictions by utilising data from disparate surveys (e.g. different sampling devices, abundance metrics, locations and levels of taxonomic resolution). Benthos taxa were aggregated to the rank of class — the taxonomic resolution consistently recorded among datasets and with reported trawl-sensitivities (Collie *et al.*, 2000). Within classes, taxa were grouped according to their correspondence with assemblages of sites and their abundance data were aggregated and modelled. Finally, benthos group distributions were mapped and used to quantify the proportion of their abundance that overlaps with the trawl footprint (exposure) and trawl closed areas (protection).

Collating large-scale datasets across Australia

We collated available data across Australia's continental EEZ (9.14 million km^2, Fig. 1) for large-scale benthic surveys, trawl footprint, trawl closed areas and environmental variables (predictors).

Benthic surveys

Invertebrate data were obtained from 18 benthic surveys in nine Australian regions (Fig. 1; Table S1 in Supporting Information). These data were collected from 3200 sites by four gear types: beam trawl (119 sites), grab (462 sites), epibenthic sled (2438), and prawn trawl (1028 sites). The taxonomic classes that comprised the largest number of sampled taxa were used in analyses: Bivalvia, Demospongiae, Echinoidea, Gastropoda, Gymnolaemata, Holothuroidea, Malacostraca, Ophiuroidea and Polychaeta. The number of taxa identified in each survey ranged from 277 to 4067, and their abundances were recorded as counts or weight, usually standardised by sampled area.

Trawl footprint

Trawl effort data for 3–5 years in 2007–2012 were acquired from the relevant authorities responsible for management of each fishery (Table S2). Average annual trawl effort in hours per 0.01° grid cell (~1.1 km) was re-scaled to total swept area, based on the gear swept-width and towing speeds for each fishery. Total annual swept area was divided by grid area to give the swept-area ratio *F* of each cell. Trawl footprints were estimated in two ways: (1) by assuming trawling was randomly distributed within cells, thus the trawled proportion of each cell is $1-e^{-F}$ and is representative of the annual trawl footprint, and (2) by assuming trawling is uniformly distributed within cells, thus the trawled proportion of each cell is F if $F<1$, otherwise 1, and is representative of a multi-year trawl footprint (for details see Pitcher *et al.*, 2016c; Pitcher *et al.*, 2016d).

Trawl closed areas

All available data on the location of marine reserves/parks and fishery closures were collated for the Australian EEZ (Table S3; Table S4). We examined each management and zoning plan to include only spatial areas that permanently prohibit trawl fishing. All areas that prohibit trawling were combined and mapped using ArcGIS (ESRI, 2014). We note that for many Commonwealth Marine Reserves protection is planned but not yet in effect.

Environmental data

Environmental data for modelling and predicting the distribution of benthos comprised 37 environmental variables mapped to the Australian EEZ on a 0.01° grid (Table S5). Predictors that did not vary among surveyed sites (SD=0) or were missing for parts of a region were excluded from individual analyses.

Statistical methods

Benthos distributions were modelled and predicted using Random Forests (RF), an ensemble of decision trees with binary splits (Breiman, 2001). Analyses were implemented in the R computing environment (R Core Team, 2015) using package ‘randomForest’ (Liaw & Wiener, 2002). Importance of each predictor was calculated as the increase in Out-of-Bag (OOB) mean squared error (MSE) when the values of the predictor were randomly permuted. We used conditional importance as implemented in ‘extendedForest’ to take into account correlations between predictors (Ellis *et al.* 2012). Model performance (measured by OOB R^2) was improved in all analyses by iteratively excluding predictors with low importance until OOB R^2 stopped improving. We optimized the number of terminal nodes of trees (‘maxnodes’) by iteratively fitting RFs with maxnodes increasing from 1, in blocks of 10, until OOB R^2 decreased for two consecutive blocks. The number of terminal nodes associated with the highest OOB R^2 was selected for the final model.

Predicting benthos distributions

Nine regions on the continental shelf of Australia (area = 1.44 million km^2; ~16% of EEZ; Fig. 1) were assessed based on the availability of large-scale benthic survey datasets (Table S1). Each study region was bounded by the latitude, longitude and depth-range of surveyed sites. Analyses for each region followed a three-step process: arranging data-matrices, grouping taxa and predicting current benthos distributions using RF (Fig. 2; Appendix S1 – R code example).

Step 1. Arranging data into a matrix

The RF analyses required a site-by-taxon matrix (biomass or count data) for each of the nine regions. Three approaches based on the complexity of regional survey datasets were used to produce the matrix (Appendix S1).

i) *Single gear approach*

For regions where benthos were sampled with one gear type (e.g. sled, prawn trawl or grab), abundance data were arranged into a conventional site-by-taxon matrix.

ii) *Multiple gears approach*

In some regions, multiple gears were used to sample benthos at the same sites. Where surveys used two devices that had substantive overlap in species composition, taxa data were combined by accounting for catchability differences between gears (note: epifauna and infauna, e.g. trawls vs grabs were not combined). A multiplicative scaling-factor was estimated for each taxon sampled by both gears, using an iterative process, similar to Chen *et al.* (2007): (i) an initial scaling-factor, equivalent to the back-transformed difference between gear means of the log-transformed data, was used to rescale abundance (on the natural scale) for the gear with lower catchability, (ii) a random forest (RF) was fitted to the log-transformed re-scaled data-matrix, with all environmental variables as predictors to account for environmental influences on abundance; (iii) an incremental scaling-factor was estimated by minimising least squares on the residuals of the RF fit, then back-transformed and used to re-scale the rescaled data-matrix again. Steps two and three were repeated until the incremental scaling-factor converged. The final scaling-factor for each taxon was estimated as the cumulative-product of the initial and incremental scaling-factors. Both gear-types were considered to sample the taxon with adequate reliability for scaling-factors in the range 0.2 – 5, and data from both gears were used by scaling-up abundances for the gear with lower catchability. If scaling factors were outside this range, data from the lower catchability gear was considered too unreliable and we used data only from the gear having the higher catchability. Where the same sites were sampled with two gears, we calculated the mean site abundances of each taxon after scaling-up the data from the gear with lower catchability. If sites were not all sampled by both gears a ‘hybrid’ site-by-taxon matrix was created, where for taxa requiring a scaling-factor, data were the mean of the observed and rescaled abundances at all sites (averaged at sites with both gears), and for taxa sampled with only one gear, data were the observed abundances, and at sites sampled by the other gear abundances were estimated with RF modelling.

Subsequent calculations on the hybrid matrix required abundance data on the natural scale. However, where predicted abundances were used, the back-transformation introduces a bias and a correction factor is required to adjust predicted values (Cowpertwait & Metcalfe, 2009). Hence, we applied an empirical adjustment factor on the natural scale, estimated from the ratio of the mean of the observed values and the mean of their corresponding back-transformed predicted values.

iii) Disparate datasets approach

In some regions benthos were sampled by multiple surveys that, although spatially interspersed, were disparate in: spatial extent, time, taxonomic resolution and identification, sampling device and abundance metrics. These datasets could not be cross-standardised nor could taxa be merged. To integrate these disparate datasets, we fitted RF models (log response) for each taxon within each survey dataset separately, with environmental variables as predictors. These RF models were used to predict each taxon's abundance at sites sampled by all other surveys. Predictions were then back-transformed to the natural scale, applying an adjustment factor as described in the previous section. Thus a 'hybrid' site-by-taxon matrix was created with observed abundances where available, otherwise predicted abundances.

Because the disparate surveys could not be standardised, we normalised the hybrid matrices via a series of scalings: 1) the abundance of each taxon (including rare taxa) was divided by its total abundance so that across surveyed sites each taxon's abundance summed to one. Next, 2) each taxon was scaled by the proportion of abundance it comprised of its own survey dataset, so that each dataset summed to one. Finally, 3) these values were multiplied by the total number of taxa in the dataset, so that each dataset summed to the total number of taxa comprising that dataset. The normalised hybrid matrices, now with the same number of sites, were joined together to provide a single hybrid matrix.

<u>*Step 2: Determining benthos groups*</u>

We aggregated taxa at taxonomic class level because of: taxonomic inconsistencies among datasets, reported sensitives of benthos to trawling, and to provide concise presentation of results. However, different species within classes can have very different distributions. Thus, within classes, we grouped taxa with similar distributions so that resulting distributions more usefully reflect distributions of constituent species. Various methods exist that can group taxa based on the correlation of their abundances at sites, but most do not objectively define the number of groups. Multivariate Regression Trees (MRT; De'ath, 2012) provide an objective method for grouping sites based on the sampled abundances of taxa and their relationships with environmental variables. Hence, first we grouped sites using MRT, then assigned taxa to site-group assemblages using the Dufrêne & Legendre (1997) indicator-species metric (DLI).

(i) Group sites by multivariate regression trees

MRTs (R package 'mvpart'; De'ath, 2012), group sites by minimizing heterogeneity in multi-taxon composition data through repeated splitting on environmental values. The response variables were the site-by-taxon matrix (or hybrid matrix), log-transformed, excluding rare taxa (presence at <5 sites). Tree size (number of terminal nodes = groups) was selected by cross-validation, using the "1SE" criterion, which indicates the smallest tree having prediction error within one standard error of the minimum cross-validated error. The terminal nodes of the tree represent site-group assemblages of taxa, with homogeneity of composition defined by this criterion.

ii) Assign taxa to groups and aggregate abundance

We calculated the DLI metric of the relative frequency and abundance of each taxon for each site group (function ‘indval’ in R package ‘labdsv’; Roberts, 2010), based on the site-by-taxon matrix on the natural scale (created in Step 1). We assigned each taxon to the group in which it attained its highest DLI score. This also enabled inclusion of rare taxa and assignment of them to the appropriate group. Group abundance was calculated by summing taxon abundances (on the natural scale) at sites from the site-by-taxon matrix.

Step 3: Predicting benthos distributions

The abundance distributions of benthos groups were modelled with RF. Where model performance indicated a meaningful level of prediction success (cross-validated OOB R^2 $\geq$5%), we used the model to predict and map the current distribution of benthos groups to a regional-scale grid of environmental variables. The influence of variables in each benthos-group model was obtained from the RF predictor importance measure (%IncMSE). We summarized predictor importance across models by scaling importance by its proportionate contribution to model performance (OOB R^2) for each benthos group. These proportions were then averaged across all models, per region and per class to estimate overall predictor importance.

Calculating benthos trawl exposure and protection

Benthos group abundance distributions were mapped (on a 0.01° grid) against trawl footprints and boundaries of areas closed to trawling to quantify their trawl *exposure* and *protection*. Specifically, we quantified *exposure* by summing the predicted group abundance in trawled grid cells, calculating the trawled proportion of each cell (calculated using both the random and uniform methods, to represent the annual and multi-year exposure respectively), and dividing by total group abundance. *Protection* was quantified by summing group abundance in cells identified to permanently prohibit trawling via legislated fishery closures, marine reserves or both, and dividing by total group abundance. We also quantified the proportion of group abundance in cells neither trawled nor protected.

RESULTS

Prediction performance and important predictors

The performance of RF prediction models (Fig. S1; Fig. S2) varied widely among benthos groups within all regions. The OOB R^2 values tended to be highest for Exmouth Gulf & Shark Bay and lowest for Pilbara Coast (Fig. S1). The most important predictor across all benthos models was sediment sand fraction (Fig. S3; Fig. S4). Other important variables were bottom-water temperature and oxygen concentration, surface photosynthetically active radiation, sediment gravel and mud fractions. Predictor importance varied widely across the nine regions, such that the most important predictor for each region was different, but sediment properties (sand, mud, gravel) were always among the most important predictors (Fig. S3). Across taxonomic classes, predictor importance was less variable (Fig. S4). Sand was the most important predictor for class Bivalvia, Ophiuroidea, Malacostraca and Polychaeta; gravel was the most important variable for Demospongiae and Gymnolaemata; and the annual average bottom-water temperature (°C) was most important for Echinoidea, Gastropoda and Holothuroidea.

Trawl exposure and protection across Australia's EEZ

Trawl fishing is prohibited from 57.9% of Australia's EEZ; marine reserves cover 37.2% of the EEZ and fishery closures cover 30.3%, with a 9.5% overlap of both (Fig. 3). The recent national annual and multi-year trawl footprints are 0.9% and 1.1% of Australia's entire EEZ, and the area of grid-cells in which any trawl effort is recorded is 4.4% of the EEZ. Thus, ~37.7% of the EEZ is neither trawled nor protected.

Trawl exposure and protection across study regions

The proportion of trawled and protected areas varied substantially among the nine case-study regions (Fig. 4; Table S6). Regions having the highest proportion of protection were the Great Barrier Reef followed by Exmouth Gulf & Shark Bay. The areas with least protection were the Pilbara Coast and Gulf of Carpentaria. The highest proportion of trawl footprints were in Exmouth Gulf & Shark Bay and the lowest were in the Great Australian Bight and West Coast — other regions were intermediate. The predicted distributions of benthos groups differed within regions, thus their protection and trawl exposure varied, including between groups within taxonomic classes. For example, the variation between three different distribution groups of sea urchin (Echinoidea) taxa in the Gulf of Carpentaria (Fig. 5).

Protection and exposure also ranged widely across all 134 benthos groups for which distributions were predicted and mapped by this study (Table S7; Table S8). As a proportion of their abundance, almost all benthos groups (129/134; 96%) had higher protection from trawling (mean=38%; median=40%) than exposure to trawling (mean=6.5%; median=3.2%; Fig. 6). Only five benthos groups, in four regions, had higher exposure than protection. In all five cases, a greater proportion of their abundance was neither trawled nor protected. Indeed, overall, the greatest proportion of group abundances occurred in areas that were neither protected nor trawled (mean for all 134 groups =55.5%). Among regions, there tended to be a consistency of protection and exposure related to the extent of trawling and reserved/closed areas within the study region. However, across all regions, there was no apparent pattern of protection or exposure related to taxonomic classes (Fig. 6b).

Comparing across regions, benthos in Exmouth Gulf & Shark Bay had the highest exposure to trawling (mean=26.7%; Fig. 6a); yet, this region had comparably high protection (mean=43.1%), primarily due to extensive fishery closures. In contrast, benthos in Pilbara Coast had the least protection, but also low exposure to trawling. Benthos groups in the Great Barrier Reef had the highest protection by marine reserves compared to other regions, but its trawl fishery closures have been fully incorporated into its protected areas, so combined protection of its benthos groups (mean=52%) was similar to that of several other study regions (Fig. 6a).

Regions having the most variation in protection among benthos groups included the Great Barrier Reef (min =13%, max=80%) and Spencer Gulf (min=4%, max=79%) (Fig. 6a), reflecting widely differing benthos group distributions in relation to reserves and closures. The least variation occurred in the South East (min=33%, max=56%), and Pilbara Coast regions (min=3%, max=26%). In all regions, variation in benthos trawl exposure was considerably less than variation in benthos protection. The largest trawl variation was in the Great Barrier Reef and Exmouth Gulf & Shark Bay, and the smallest variation in the Great Australian Bight and West Coast.

Over all benthos groups, greater protection of their abundance was provided by fishery closures (mean=23%; median=20%) than by marine reserves (mean=22%; median=14%; Fig. 6a). This was despite fishery closures covering 19% less area than marine reserves (17.7% vs 21.9%; Table S6). However, slightly more individual benthos groups, by number, had greater protection of abundance in marine reserves (77/134; 57%) than in fishery closures (57/134; 43%). Exposure to scallop dredging occurred only in the Southeast region and was minimal (max exposure <0.1%; Table S8); hence this gear-type was excluded from presentation of results.

DISCUSSION

This study provides the most extensive quantitative assessment of the current trawl exposure and protection of Australia's benthic invertebrates. The exposure of most Australian benthos to trawling was relatively low, whereas benthos protection was typically about 6-fold higher. However, for most benthos groups more than half of their benthos abundance was neither protected nor trawled, highlighting the importance of untrawled open areas when considering trawl-impact risks. Our results imply that overall, Australia's benthos may be at low risk from trawling. Although, we caution that the results indicate potential rather than realised risks to sustainability and, while the potential risks appeared low overall, there were some cases of higher exposure and lower protection. Further, exposure and protection alone do not account for the sensitivity of benthos to trawl impacts or their capacity to recover. The typically low exposures observed do, nevertheless, suggest that even if impacts in trawled areas were high and recovery was slow, large proportions of abundance outside trawled areas may sustain most benthos at regional scales.

While trawling is prohibited over a large proportion (58%) of Australia's EEZ, most of these areas are located in waters deeper than 1,000 m where no bottom trawling occurs (Pitcher, 2016). The proportion of area closed to trawling was substantially lower in our shallower study regions (33%, Table S6). Similarly, the national footprint of all Australian trawling as a proportion of the entire EEZ (at ~1% trawled, or 4.7% area of grid-cells with effort) is smaller than the trawl footprints in our study regions (at ~3% trawled, or 14% area of grid-cells with effort; Table S6). Thus, the high proportion of area protected at the EEZ scale cannot be assumed at regional scales, where local protection and risks must be quantified to guide appropriate management actions. Other pressures besides trawling that may affect benthic fauna should also be considered, such as coastal pollution, acidification and climate change (Hiddink *et al.*, 2015).

Fishery legislated closures are often overlooked as a marine conservation tool (Ward & Hegerl, 2003). The contribution of fishery closures to management of commercial stocks is generally well accepted (Stefansson & Rosenberg, 2005), but they can also provide habitat protection (Asch & Collie, 2008). Our study highlights their contribution to protection of Australia's benthos. Interestingly, we found that fishery closures provide higher protection of benthos abundance than marine reserves, despite their smaller coverage of the study regions. This may be due to the strategic placement of fishery closures targeting fisheries stock management or productive nursery habitats. While our results indicate that fishery closures contribute to benthos protection, the best sustainability outcomes are achieved when a variety of management tools are applied (e.g. effort reductions, catch limits and permanent/temporal spatial closures (Hiddink *et al.*, 2006b; Dichmont *et al.*, 2013; Pitcher *et al.*, 2015).

The synthesis presented here enables broad-scale comparisons across regions. The region with the greatest protection of benthos abundance was the Great Barrier Reef. Interestingly, one form of protection (either reserves or closure) dominated benthos protection in each region with the exception of the West Coast, the only region with relatively equal protection of benthos by reserves and closures. Exmouth Gulf & Shark Bay had the most extensive relative trawl footprint and its benthos had the highest exposure to trawling. However, protection provided by closures in this region was relatively high, offsetting the high exposure. In contrast, benthos in the adjacent Pilbara Coast had the lowest trawl exposure, even though this region did not have the smallest trawl footprint. Thus, while the regional extent of reserves/closures and trawl footprints did influence overall benthos protection and exposure, the distributions of individual benthos groups differed substantially within regions and directly affected individual group protection and exposure (e.g. Fig. 5; Fig. 6). Hence, understanding the potential risk of trawling requires information on distributions, since benthos exposure cannot be assumed from trawl footprint alone.

Patterns of exposure and protection appeared unrelated to taxonomic class. However, distribution relationships with environmental variables did tend to show patterns related to class. Moreover, sediment (sand and gravel) were particularly important for six of nine taxa groups. In comparison, the most import predictors varied widely by region, but sediment and bottom-water properties were prevalent. These findings are consistent with other observations of strong associations between sediment properties and benthos composition, richness and diversity (Collie *et al.*, 2000; Sutcliffe *et al.*, 2014). Thus, we recommend studies aiming to predict benthos distributions prioritise the collection of sediment and bottom water properties.

Defining the extent of study area boundaries is a vexed issue for many spatial studies (Piet & Quirijns, 2009). Our choice of study areas was limited to the extent of existing benthic surveys to avoid extrapolating beyond the data range. However, our results would differ if we used different boundaries such as large marine ecosystems (LMEs; http://www.lme.noaa.gov/), marine ecoregions (Spalding *et al.*, 2007), or fisheries management regions (Pitcher *et al.*, 2016d). For example, in the Great Australian Bight there are trawl fishery closures at depths less than 10 m, yet our study region did not encompass such shallow depths due to the distribution of surveyed sites. If it did, perhaps our results would have indicated higher protection for benthic taxa, although it is also likely that taxonomic composition would differ at shallower depths. Therefore, study area boundaries need to be carefully considered in the context of relevant management questions.

There are inherent limitations when conducting large-scale spatial studies that integrate scarce available survey data and rely on modelling to predict distributions. First, available data may be biased towards the objectives of the initial survey. For example, fishery-dependent data are often relied upon and, in the case of Exmouth Gulf & Shark Bay, the surveys were largely confined to the active trawl grounds, resulting in the higher relative trawl footprints for that region in our study. Second, it is implicit that some details observed by finer-scale studies will not be picked up by a large, cross-regional study. Moreover, we aggregated benthos into groups, which would inherently introduce additional uncertainty compared with species-level analyses (Pearman *et al.*, 2010). Nevertheless, our broad cross-regional finding that trawl exposure was low and protection was high, is consistent with species-level regional analyses (Pitcher *et al.*, 2007b; Pitcher *et al.*, 2015; Pitcher *et al.*, 2016b). Third, modelling and predicting regional benthos distributions will always introduce uncertainty due to sampling variability/error in source data, imperfect relationships between benthos and environment and biological/ecological processes among others. For these reasons, we report the OOB prediction performance of benthos models (Fig. S1; Fig. S2), and acknowledge uncertainty in the estimates of protection and exposure. If such limitations can be minimised, the greatest impediment limiting large-scale assessments is actually the availability of suitable survey data. We anticipate that as more data are deposited in the evolving database repositories, more large-scale assessments of trawling may be feasible.

In conclusion, we discovered greater proportions of benthos abundance in our study regions were distributed in protected and/or closed areas rather than in trawled areas. Our study also highlights the importance of fishery closures in providing protection for benthic invertebrates. These results are a first step in quantifying large-scale risks and impacts of trawling on benthos and can help managers identify priorities for focusing future status assessments. Future work should expand our analysis to quantify risk from trawling and determine whether benthos are sustainable under the current regimes of exposure and protection. Such future quantitative sustainability assessments can help managers identify if any taxa and regions may be at higher risk from trawling, determine the effectiveness of current management, and guide decisions about the need for future management measures. Our approach for combining scarce and disparate benthic invertebrate data into distribution models can be widely applied to other marine taxa and regions where data are sparse and trade-offs with anthropogenic pressures need to be assessed. Such analysis can help managers achieve balance between conservation and sustainable industries in marine ecosystems.

ACKNOWLEDGEMENTS

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DATA ACCESSIBILITY

Benthic survey data sources are provided in Table S1. Trawl effort data are confidential and source information is in Table S2. Marine reserve and Fishery closure data are available from sources provided in Table S3 and Table S4. Environmental predictor data are available from sources provided in Table S5.

AUTHOR CONTRIBUTIONS

TM, CRP, NE and WR conceived the ideas; TM and CRP collated the data, TM analysed the data. All authors contributed to the writing, led by TM.

BIOSKETCH

Tessa Mazor is a postdoctoral fellow at the Commonwealth Scientific and Industrial Research Organisation (CSIRO). The fellowship project aims to conduct both national and global quantitative ecological risk assessments of trawling, working with the Ocean and Atmosphere research team and linking to a multi-national project “Trawling: finding common ground on the scientific knowledge regarding best practices” (http://trawlingpractices.wordpress.com).

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FIGURES

Fig. 1 Map of nine study regions around Australia showing locations of sites sampled by one or more of four gear-types.

Fig. 2 Flowchart of the steps used to predict and map benthos-group distributions from raw survey data (left). The box (right) details the three approaches (Single Gear Approach, Multiple Gears Approach and Disparate Datasets Approach) and the process used to create the site-by-taxon matrix from collated benthic survey datasets. Note that survey gears with non-overlapping benthos composition (e.g. epifauna in trawls vs. infauna in grabs), were not combined, but treated separately as single gears.

Fig. 3 Map of areas where trawling is prohibited within Australia's Exclusive Economic Zone EEZ (see Table S3; Table S4).

Fig. 4 Area statistics of the study regions: a) relative total areas of the study regions (for absolute area, see Table S6); b) percentage area within regions comprising fishery closures, reserves and overlap of both; and c) percentage area within regions comprising grid cells with trawl effort recorded, and the trawl footprint area for multi-year exposure and single-year exposure.

Fig. 5 Predicted distributions of three groupings of sea-urchin taxa (class: Echinoidea) in the Gulf of Carpentaria (Figure 1 – study region 1). Areas that exclude trawling are represented by black polygons with parallel hatching. Each group has different trawl exposure (Group

1=1.6%; Group 2=6.4%; Group 3=4.7%) and protection (Group 1=6.4%; Group 2=17.5%; Group 3=5.8%) as proportions of their abundance. See Tables S7 and S8 for group and model details.

Fig. 6 Box plots summarizing protection and trawl exposure of 134 benthos groups, as proportions of their abundance in each a) region, and b) taxa group — calculated by mapping their distributions against marine reserves and fishery closure boundaries — and their combination, and against the multi-year footprint of trawling. Horizontal lines denote the medians and box plot error bars represents the variation of different benthos groups.

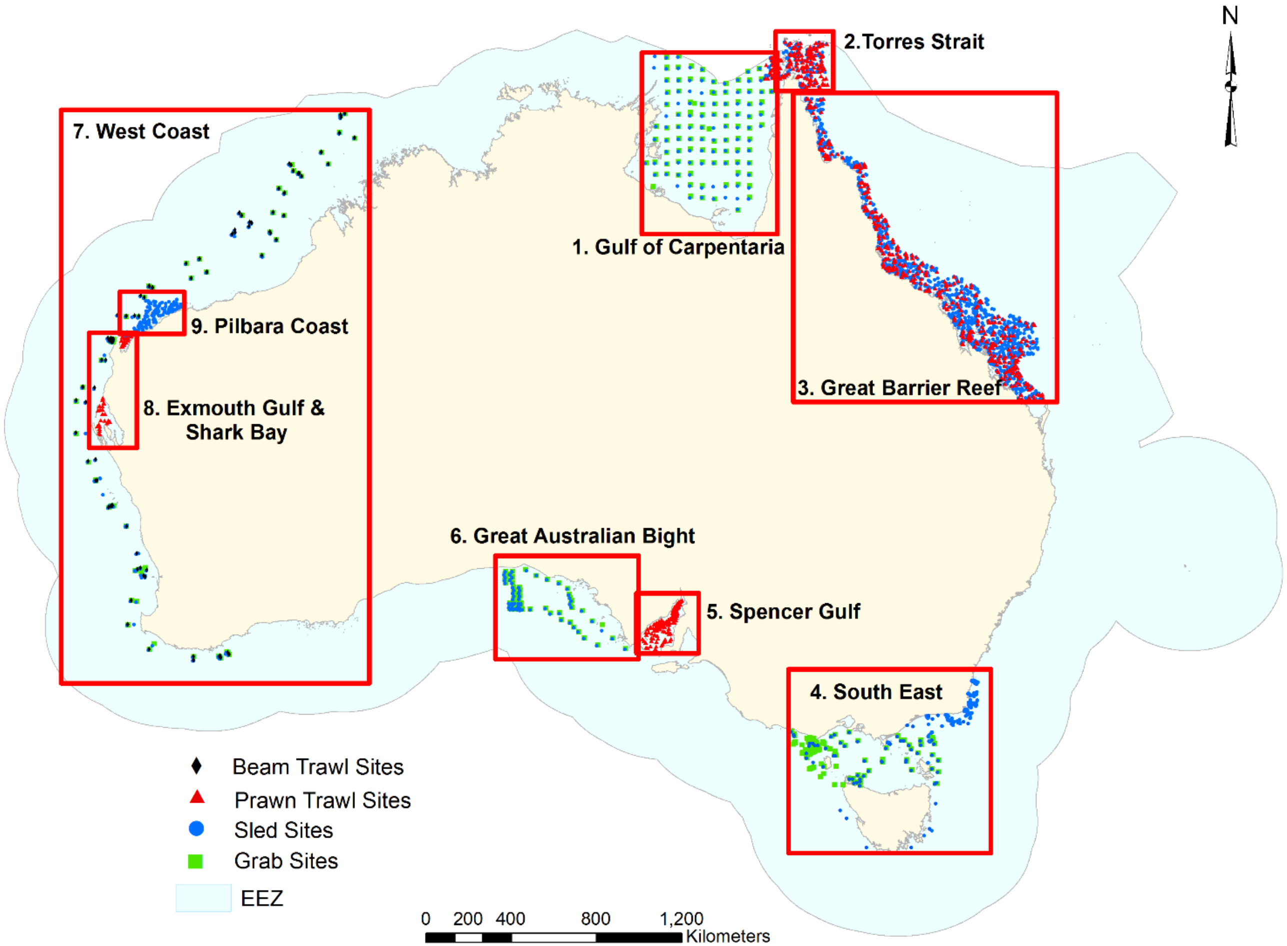
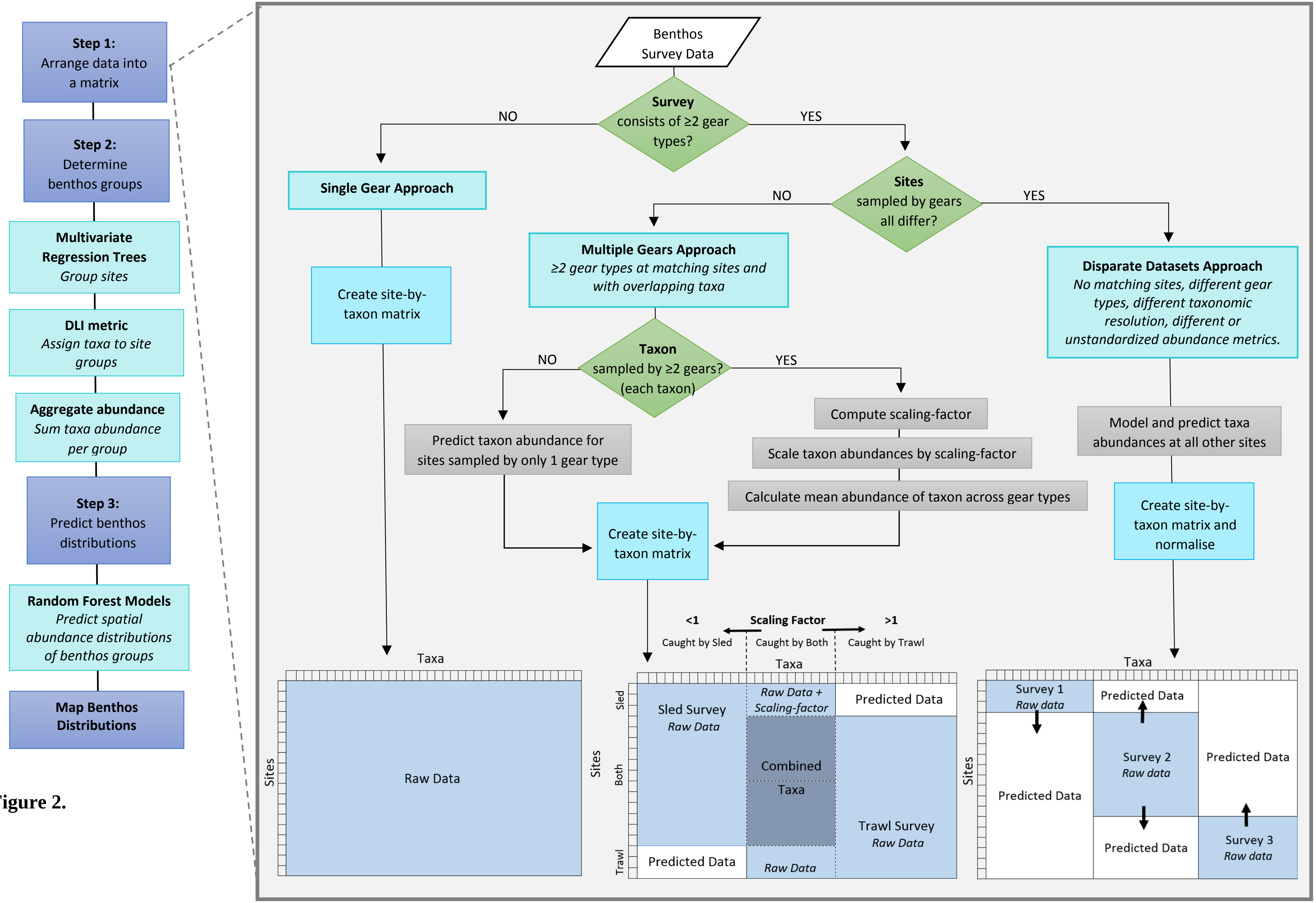

N
2.Torres Strait
7. West Coast
1. Gulf of Carpentaria
9. Pilbara Coast
8. Exmouth Gulf & Shark Bay
3. Great Barrier Reef
6. Great Australian Bight
5. Spencer Gulf
4. South East
Beam Trawl Sites
Prawn Trawl Sites
Sled Sites
Grab Sites
EEZ
0 200 400 800 1,200
Kilometers

Figure 1.



Step 1:
Arrange data into a matrix
Step 2:
Determine benthos groups
Multivariate Regression Trees
Group sites
DLI metric
Assign taxa to site groups
Aggregate abundance
Sum taxa abundance per group
Step 3:
Predict benthos distributions
Random Forest Models
Predict spatial abundance distributions of benthos groups
Map Benthos Distributions
Benthos Survey Data
Survey consists of ≥2 gear types?
NO
YES
Single Gear Approach
Sites sampled by gears all differ?
NO
YES
Multiple Gears Approach
≥2 gear types at matching sites and with overlapping taxa
Disparate Datasets Approach
No matching sites, different gear types, different taxonomic resolution, different or unstandardized abundance metrics.
Create site-by-taxon matrix
Taxon sampled by ≥2 gears? (each taxon)
NO
YES
Compute scaling-factor
Predict taxon abundance for sites sampled by only 1 gear type
Scale taxon abundances by scaling-factor
Model and predict taxa abundances at all other sites
Calculate mean abundance of taxon across gear types
Create site-by-taxon matrix
Create site-by-taxon matrix and normalise
<1
Scaling Factor
>1
Caught by Sled
Caught by Both
Caught by Trawl
Taxa
Sites
Raw Data
Taxa
Sites
Sled
Both
Trawl
Sled Survey
Raw Data
Raw Data + Scaling-factor
Predicted Data
Combined Taxa
Trawl Survey
Raw Data
Predicted Data
Raw Data
Taxa
Sites
Survey 1
Raw data
Predicted Data
Predicted Data
Survey 2
Raw data
Predicted Data
Predicted Data
Survey 3
Raw data

Figure 2.

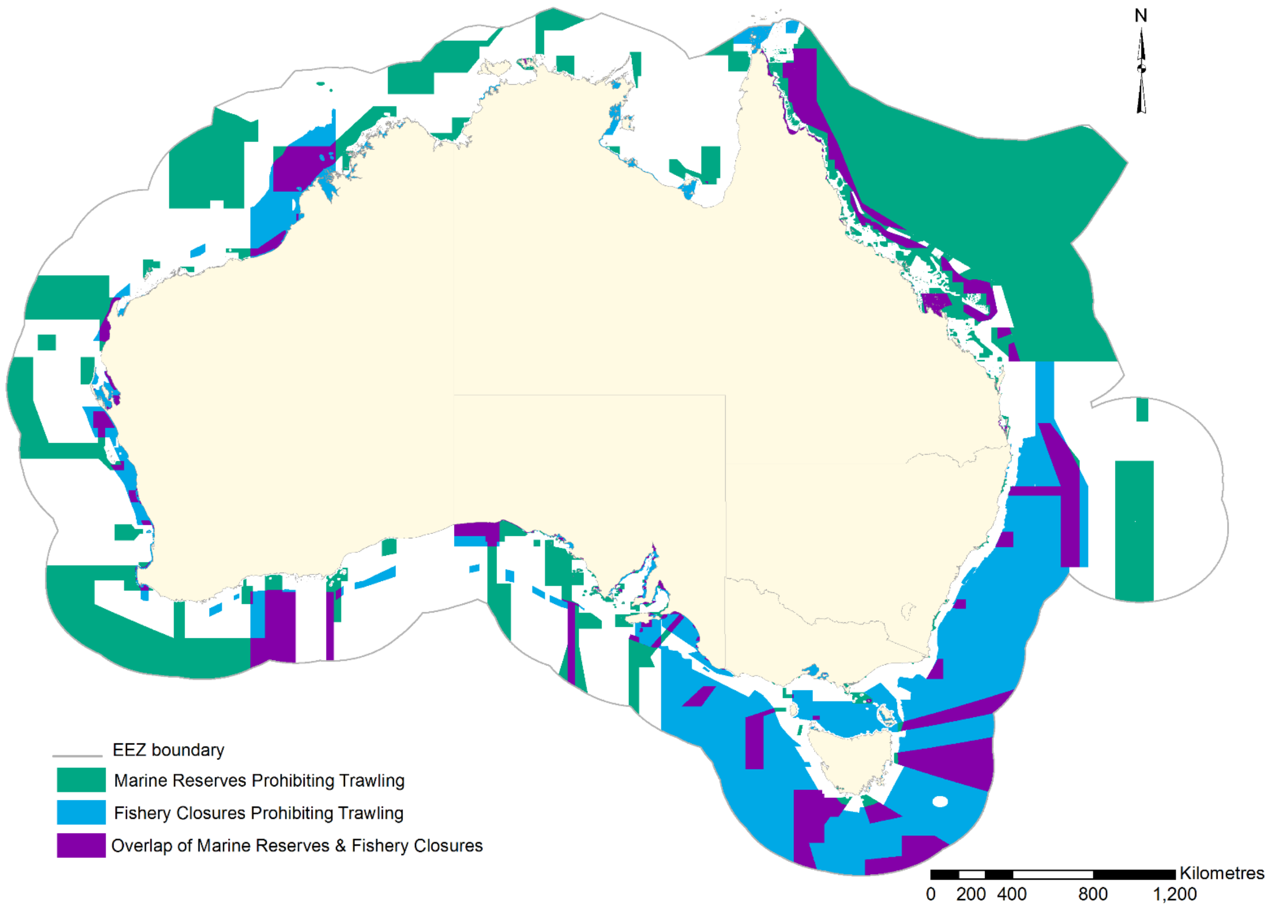
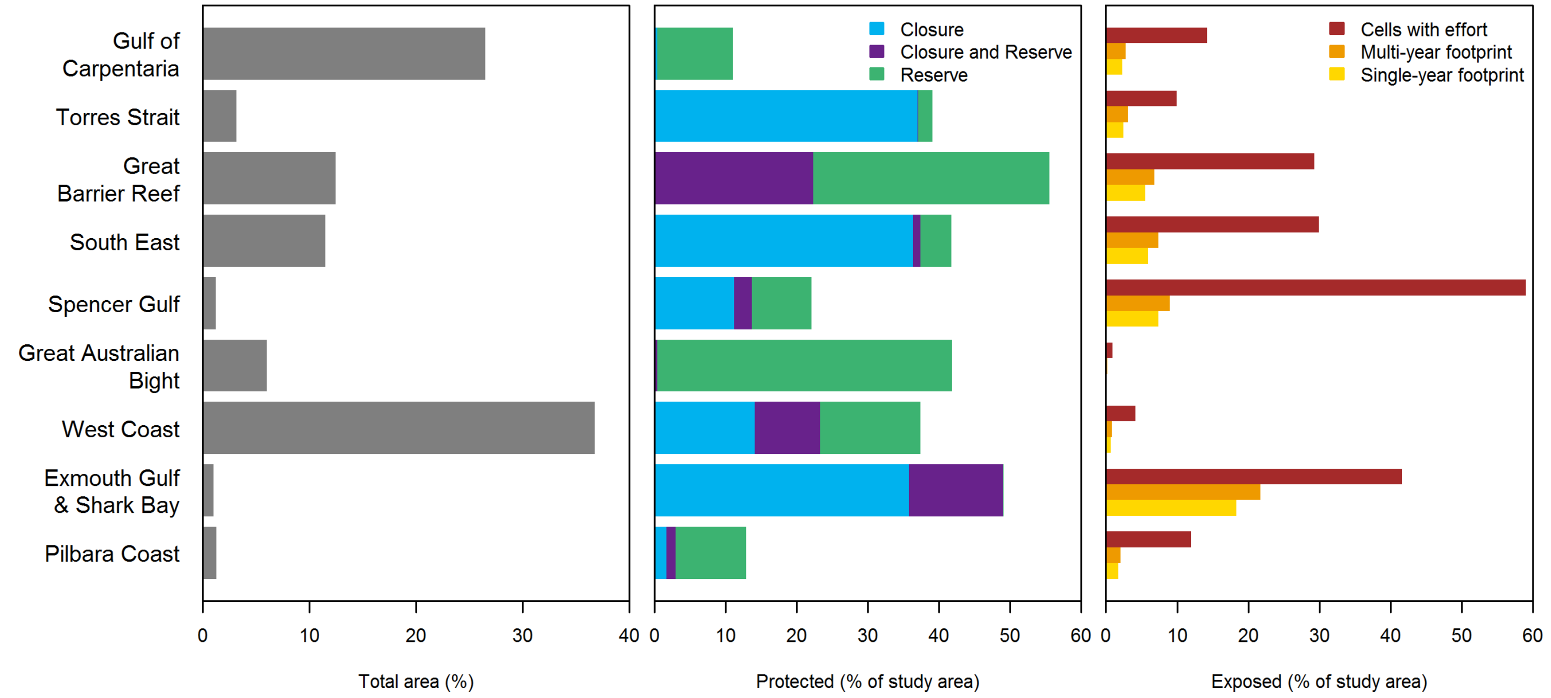

N
EEZ boundary
Marine Reserves Prohibiting Trawling
Fishery Closures Prohibiting Trawling
Overlap of Marine Reserves & Fishery Closures
Kilometres
0 200 400 800 1,200

Figure 3.



Gulf of Carpentaria
Torres Strait
Great Barrier Reef
South East
Spencer Gulf
Great Australian Bight
West Coast
Exmouth Gulf & Shark Bay
Pilbara Coast
0
10
20
30
40
Total area (%)
Closure
Closure and Reserve
Reserve
0
10
20
30
40
50
60
Protected (% of study area)
Cells with effort
Multi-year footprint
Single-year footprint
0
10
20
30
40
50
60
Exposed (% of study area)

Figure 4.

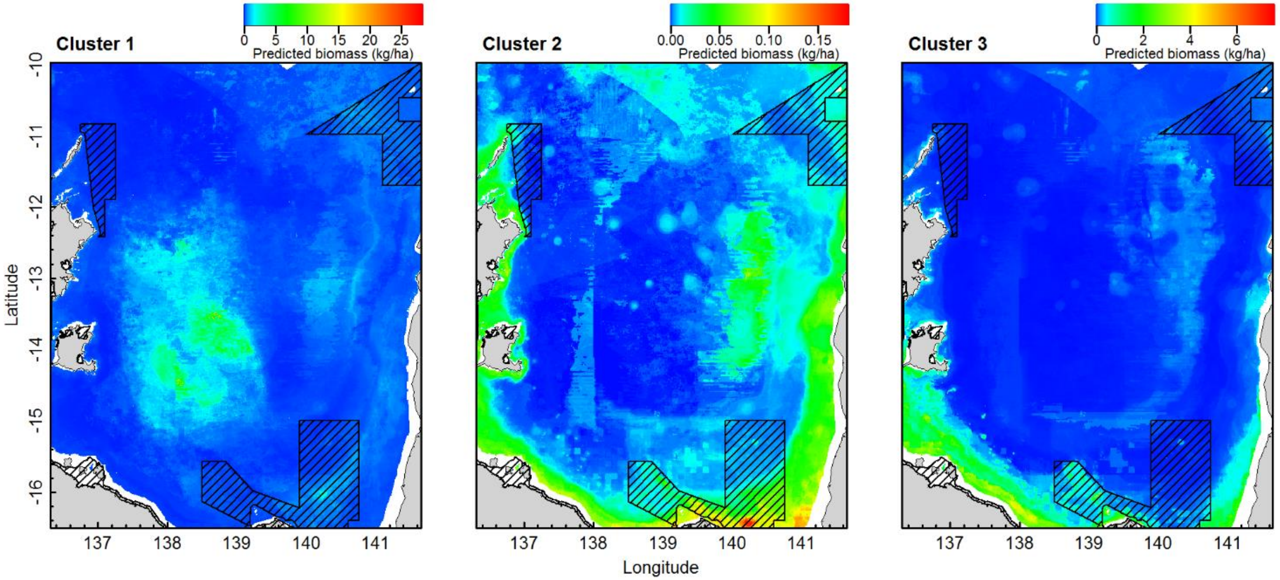
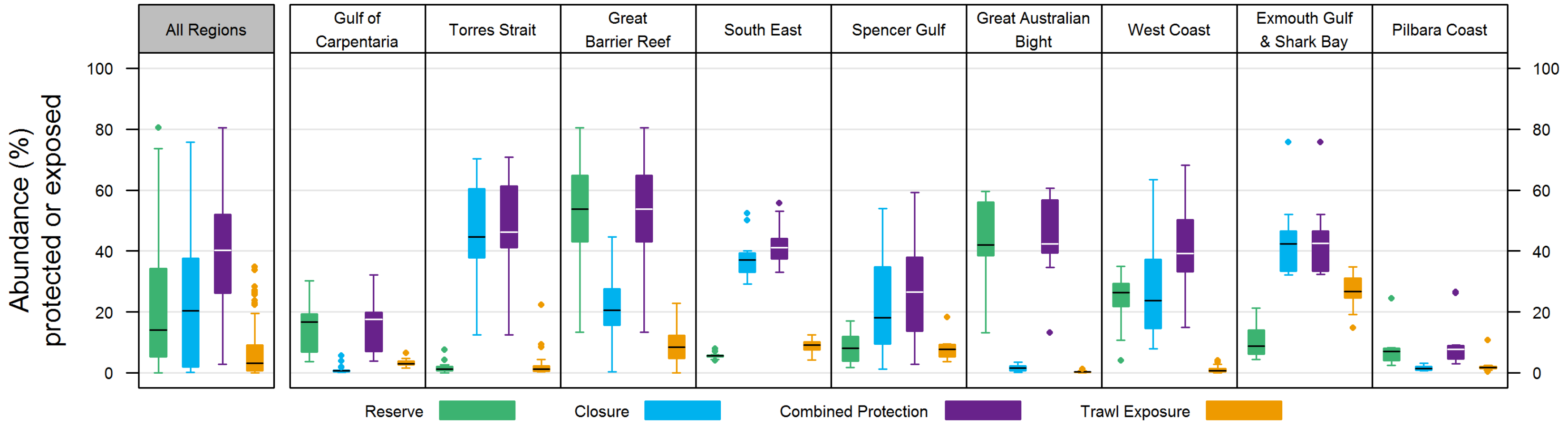

Cluster 1
0 5 10 15 20 25
Predicted biomass (kg/ha)
Cluster 2
0.00 0.05 0.10 0.15
Predicted biomass (kg/ha)
Cluster 3
0 2 4 6
Predicted biomass (kg/ha)
Latitude
-10
-11
-12
-13
-14
-15
-16
137
138
139
140
141
Longitude

Figure 5.

a)


All Regions
Gulf of Carpentaria
Torres Strait
Great Barrier Reef
South East
Spencer Gulf
Great Australian Bight
West Coast
Exmouth Gulf & Shark Bay
Pilbara Coast
Abundance (%) protected or exposed
0
20
40
60
80
100
Reserve
Closure
Combined Protection
Trawl Exposure

b)

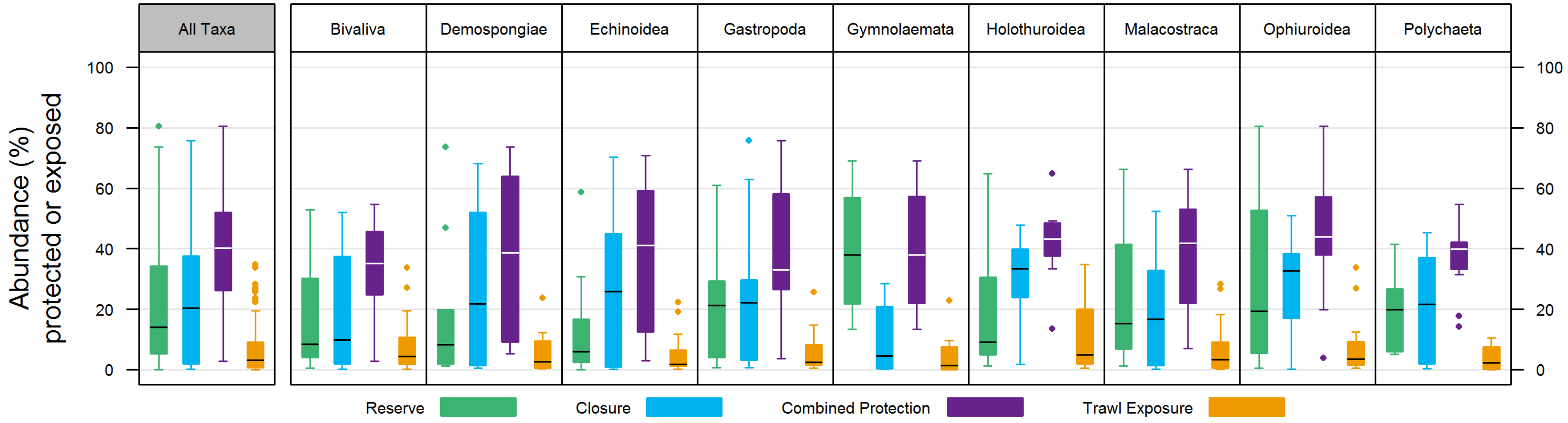

All Taxa
Bivaliva
Demospongiae
Echinoidea
Gastropoda
Gymnolaemata
Holothuroidea
Malacostraca
Ophiuroidea
Polychaeta
Abundance (%) protected or exposed
0
20
40
60
80
100
Reserve
Closure
Combined Protection
Trawl Exposure

Figure 6.