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Research article

Implications for the conservation of deep-water corals in the face of multiple stressors: A case study from the New Zealand region

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ABSTRACT

The waters around New Zealand are a global hotspot of biodiversity for deep-water corals; approximately one sixth of the known deep-water coral species of the world have been recorded in the region. Deep-water corals are vulnerable to climate-related stressors and from the damaging effects of commercial fisheries. Current protection measures do not account for the vulnerability of deep-water corals to future climatic conditions, which are predicted to alter the distribution of suitable habitat for them. Using recently developed habitat suitability models for 12 taxa of deep-water corals fitted to current and future seafloor environmental conditions (under different future climatic conditions: SSP2 - 4.5 and SSP3 - 7.0) we explore possible levels of spatial protection using the decision-support tool Zonation. Specifically, we assess the impact of bottom trawling on predictions of current distributions of deep-water corals, and then assess the effectiveness of possible protection for deep-water corals, while accounting for habitat refugia under future climatic conditions. The cumulative impact of bottom trawling was predicted to impact all taxa, but particularly the reef-forming corals. Core areas of suitable habitat were predicted to decrease under future climatic conditions for many taxa. We found that designing protection using current day predictions alone, having accounted for the impacts of historic fishing impacts, was unlikely to provide adequate conservation for deep water-corals under future climate change. Accounting for future distributions in spatial planning identified areas which may provide climate refugia whilst still providing efficient protection for current distributions. These gains in conservation value may be particularly important given the predicted reduction in suitable habitat for deep-water corals due to bottom fishing and climate change. Finally, the possible impact that protection measures may have on deep-water fisheries was assessed using a measure of current fishing value (kg km⁻² fish) and future fishing value (predicted under future climate change scenarios).

1. Introduction

Corals without symbiotic zooxanthellae, typically occurring in water below the photic zone, are known as cold-water or deep-water corals. Deep-water corals occur throughout the world's oceans, with most species occurring at locations with temperatures of 4–12 °C and depths of 200–2000 m (Roberts et al., 2009). Many taxa of deep-water corals are considered providers of important ecosystem functions and services. For example, some species of the Order Scleractinia (stony corals) form structurally complex reefs that can provide habitat for many invertebrate and fish species, and thereby enhance the biodiversity of the locations where these reefs exist (e.g., Henry and Roberts, 2007). Some of these reefs can extend large distances, covering areas of hundreds of square kilometres (Fosså et al., 2002; Hühnerbach et al., 2007), and

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have been shown to be significant sites of carbon and nitrogen mineralisation (Cathalot et al., 2015; De Froe et al., 2019). Other deep-water coral taxa also provide similar ecosystem functions and services, including species belonging to the Orders Alcyonacea (soft corals, sea fans, sea whips), Antipatharia (black corals), and Anthoathecata (hydrocorals) (Edinger et al., 2007; Love et al., 2007; Braga-Henriques et al., 2011).

Deep-water corals are vulnerable to a variety of human-related stressors (Roberts and Hirshfield, 2004; Roberts et al., 2006). Foremost among these stressors has been, and currently remains, the direct and indirect impacts of fishing; in particular, bottom-contact trawling, which can impact the presence or integrity of deep-water coral habitats (e.g., Reed et al., 2007). Bottom trawl fisheries are sometimes focused where deep-water corals are particularly abundant (e.g., seamounts) and the impact of bottom fisheries can be profound for seabed ecosystems supported by deep-water corals (Clark et al., 2016; Goode et al., 2020). A global analysis indicated that deep-water coral habitat on seamounts in many parts of the world is vulnerable to bottom trawling (Clark and Tittensor, 2010) and such coral-based ecosystems are considered by the United Nations as Vulnerable Marine Ecosystems and in need of protection from fishing on the high seas (FAO, 2009). Similarly, many nation states have recognised the threat posed to deep-water corals by bottom-contact trawling and have sought to identify and protect their habitat (Morato et al., 2010; Williams et al., 2020; Stephenson et al., 2021b).

Despite the protection that has been afforded to deep-water corals in some locations around the world, these types of corals are also vulnerable to future stressors, which current conservation measures may not protect them from. In particular, deep-water corals are thought to be under significant threat from climate-related stressors, through ocean warming and ocean acidification, and their associated changes in the chemical and physical properties of waters in the deep sea (Roberts et al., 2016). Specifically, changes in the depth of carbonate saturation horizons and other properties of bottom seawater, such as temperature and dissolved oxygen level, are predicted to result in unsuitable conditions for the settlement and growth of deep-water corals across large ocean areas (e.g., Guinotte et al., 2006). Given the ecological importance of deep-water corals for structuring benthic communities, it will be crucial to identify locations where these corals may persist under future climate change conditions to inform conservation planning (Tittensor et al., 2010; Morato et al., 2020), in particular to assess the efficacy of current protection measures and whether they require modification or additions (Anderson et al., 2022).

Multiple stressors operating in the deep sea can and may interact (Gao et al., 2020; Pinheiro et al., 2023), and these interactions may have synergistic, antagonistic or additive effects (Hewitt et al., 2016). Understanding how multiple stressors interact is a growing area of scientific research (e.g., Ban et al., 2014; Hewitt et al., 2016; Thrush et al., 2020; Pinheiro et al., 2023), and the need to account for multiple stressors in conservation planning has been recognised as an urgent imperative to mitigate the impacts of climate change on vulnerable species, communities, habitat and ecosystems (Hughes et al., 2017). However, there have been few practical examples of multiple stressors, including climate change, being quantitatively accounted for in marine conservation planning and actions (e.g., Kujala et al., 2013; Levy and Ban, 2013; Magris et al., 2015; Sala et al., 2021) and none that we know of for deep-water corals.

The waters around New Zealand are a global hotspot of biodiversity for deep-water corals; approximately one sixth of the worlds' deepwater coral species have been described from the region (Tracey and Hjorvarsdottir, 2019). However, they are frequently caught in commercial fisheries (Anderson and Finucci, 2022). The impact of trawling on deep-water corals has led to the inclusion of many taxa in New Zealand's threatened species classification (Freeman et al., 2014) and as protected species in New Zealand's Wildlife Act (1953), which prohibits the intentional damage or removal of deep-water corals. Nonetheless, current spatial protection measures do not afford high levels of protection for deep-water coral taxa (Anderson et al., 2022), and nor do they account for their vulnerability to future climatic conditions. Therefore, to ensure the conservation of these important organisms, in addition to understanding impacts from fishing, the distribution of deep-water corals under future climate conditions must be understood. In this paper we integrate several sources of impact to evaluate the future conservation needs for deep-water corals around New Zealand.

Anderson et al. (2022) developed habitat suitability models for twelve ecologically important taxa of deep-water corals, which were predicted under current and future seafloor environmental conditions. Future conditions were predicted using the New Zealand Earth System Model, which is specifically tailored for the South Pacific sector, and two greenhouse gas concentration trajectories following the Shared Socioeconomic Pathways SSP2-4.5 (4.5 W m⁻²) moderate increase trajectory, and the SSP3 – 7.0 (7.0 W m^{-2}) strong increase trajectory (Williams et al., 2016; Behrens et al., 2020). Here we use these spatial predictions to firstly assess the cumulative impact of bottom trawling on predicted current distributions of deep-water corals and then use these estimates, as well as the predicted distribution of these corals under different future climatic conditions (SSP2 - 4.5 and SSP3 - 7.0) to explore the effectiveness of illustrative examples of spatial marine protection. Given the substantial shifts in the location and decreases in area of the most suitable deep-water coral habitat by the end of the 21st century (Anderson et al., 2022), in combination with the cumulative impacts of bottom fishing, we posit that deep-water corals may be at high risk of local extinctions.

2. Methods

2.1. Overview of analysis

The study area extended over 2.1 million km² of the South Pacific Ocean within the New Zealand Territorial Sea (TS) and Exclusive Economic Zone (EEZ), herein referred to as the New Zealand marine environment, from 0 to 2000 m water depth (\approx 25–57°S; 162°E – 172°W; Fig. 1).

Using the habitat suitability models for deep-water corals predicted under current and future seafloor environmental conditions (Fig. 2, A and B respectively) from Anderson et al. (2022) we firstly assessed the cumulative impact of bottom trawling on predicted current distributions of deep-water corals (Fig. 2, C). We then explored illustrative examples of spatial marine protection developed using the decision-support tool *Zonation* and assess the effectiveness of protection relative to predictions of the current distribution of deep-water corals, and predictions of the distribution of habitat refugia for deep-water corals under future climatic conditions (Fig. 2, E). We also evaluated the possible economic effects of protection on the fishery using a simple metric of fishing value (measured as kg km⁻² catch of demersal fish) (Fig. 2, D). Specifically, we explored the effectiveness of levels of possible protection developed under two scenarios:

Scenario 1. Spatial prioritisation analyses to identify areas for marine protection using only predictions of current deep-water coral distributions (given the impact of fishing). This scenario aims to emulate the existing process for designation of marine protected areas and explores the risks associated with protection measures that *do not account* for multiple stressors or consider climate refugia.

Scenario 2. Spatial prioritisation analyses to identify areas for marine protection using both predictions of current deep-water coral distributions (given the impact of fishing) and future predictions under different future climatic conditions (SSP2 – 4.5 and SSP3 – 7.0). This scenario aims to explore the synergies in the protection measures that *do account* for multiple stressors and the future and uncertain spatial distributions of deep-water corals.



Fig. 1. The New Zealand marine environment (Exclusive Economic Zone, black dashed line). Water depth and feature names used throughout the text are displayed.

2.2. Ensemble habitat suitability modelling of deep-water coral distribution

Habitat suitability models were recently constructed by Anderson et al. (2022) for twelve coral taxa protected under New Zealand legislation, comprising four species of the order Scleractinia (reef-forming stony corals), four groups of the order Alcyonacea ('gorgonian' octocorals), and two genera each of the order Antipatharia (black corals) and Family Stylasteridae (Class Hydrozoa, stylasterid hydrocorals) (Table S1, Supplementary Materials). Given the importance of these layers in our analyses, a brief overview of the methods is provided here but see Anderson et al. (2022) for a comprehensive description of model inputs, construction, and results.

The selection of coral taxa was based on the level of available sample data as well as the conservation status of the taxa and their importance for providing structural habitat. Sample presence data was compiled from a combination of research surveys, commercial fishing records, museum records, and online databases. Absence data for each taxon model comprised a random selection of sampling locations, equal to the number of presence records, from a master dataset of over 60,000 survey stations, excluding locations where the modelled taxon was recorded (referred to as "target-group background" data, Phillips et al., 2009).

The environmental variables used in the models were a combination of temporally fixed and dynamic parameters. Fixed variables included bottom depth and physical seabed characteristics derived from bathymetry, such as slope and benthic position index (BPI), along with substrate type (percent mud, sand, and carbonate) derived from sediment sampling (for further information on these variables see Anderson et al. (2022)). Dynamic variables were produced as outputs from New Zealand Earth System Model (NZESM), a highly complex model of the climate system specifically tuned to the New Zealand region and capable of estimating past, current and future environmental conditions (Williams et al., 2016; Behrens et al., 2020). Models were trained on current conditions (mean values for 1995–2014) then fitted to these and future conditions (mean values for 2080–2099) under two alternative emissions pathways (SSP2-4.5 and SSP3 – 7.0) to predict present and future habitat suitability.

Two methods were applied, Random Forests (Breiman, 2001) and Boosted Regression Trees (Elith et al., 2006), with the outputs from each combined to produce ensemble predictions of habitat suitability separately for each taxon. Spatially explicit estimates of model uncertainty were made using a bootstrap approach, whereby models were re-run



Fig. 2. Infographic showing examples of spatial data layers and how these were combined in spatial prioritisations for Scenario 1 and 2. **(A)** Predicted habitat suitability index (HSI, 0–1) for the reef-forming coral species *Goniocorella dumosa* under current climatic conditions (1995–2015) and associated spatially explicit uncertainty (standard deviation of the mean HSI). **(B)** Future predicted HSI (0–1) for climatic conditions under a moderate greenhouse gas concentration trajectory (SSP2-4.5, 2080–2100) and under a strong greenhouse gas concentration trajectory (SSP3 – 7.0, 2080–2100). **(C)** Estimate of condition (0–1) of seafloor taxa and resulting predicted habitat suitability of reef-forming coral species *Goniocorella dumosa* after accounting for the impact of bottom fishing. **(D)** Observed fish catch (kg km⁻²) from deep-water fisheries in New Zealand (1995–2015), and predicted fish catch under future climatic conditions SSP2-4.5 and SSP3 – 7.0 (2080–2100). **(E)** Illustrative example outputs from the spatial prioritisation of deep-water corals for Scenarios 1 and 2.

200 times using data randomly selected from the sample presence and absence records. Model ensembling incorporated a two-part weighting process, comprising equal contributions from the overall performance of each model type (spatially cross-validated AUC values) and the uncertainty measure (coefficient of variation, CV) in each cell for each model type (Stephenson et al., 2021b). Habitat suitability predictions for current (e.g., Fig. 2, A) and future climatic conditions (e.g., Fig. 2, B), as well as associated spatially explicit uncertainty, are available for all study taxa in the Supplementary Materials (Figs. S1–S12).

2.3. Spatially explicit impact of bottom fishing

The impact of bottom trawling on deep-water corals was estimated using the MSRP method (Mormede et al., 2017; Rowden et al., in review); the naming of this approach was based on the first initials of its authors: Mormede/Sharp/Roux/Parker. In this method, impact values are defined as the proportion of vulnerable benthic taxa damaged or destroyed in a single passage of a bottom trawl. Impact values were determined for three functional groups of benthic fauna (large, erect, hard, sessile (LEHS); small, fragile, encrusting (SFE); and deep, burrowing infauna (DBI)) across a wide range of target fisheries and vessel, ground gear, and bottom types (Rowden et al., in review). The MSRP method is based on adjusting area-swept polygons of recorded trawls for each gear type, then sectioning the polygons to assign to individual cells of a 1×1 km grid. The total impact per cell is then calculated by overlapping the sectioned polygons in each cell in a random manner such that impact is represented by a cumulative proportional area on a scale of 0-1, with 0 being a completely unimpacted state and 1 being completely impacted. The MSRP method does not allow for any recovery over time, therefore it may overestimate the impact of bottom trawling, although this over-estimate may only be small for slow-growing taxa such as deep-water corals since their recovery time may take decades or more (Clark et al., 2019; Baco et al., 2020).

Estimates of fishing impact on deep-water coral taxa were based on their morphological traits applied to the LEHS and SFE groupings (Fig. S13, Supplementary Materials), multiplied with their current-day predicted habitat suitability to produce impact adjusted deep-water coral taxa habitat suitability estimates (e.g., Fig. 2, C, but see Figs. S14 - SA25, Supplementary Materials for all impact adjusted deepwater coral taxa habitat suitability estimates). The reduction of predicted habitat suitability following the discounting of fishing impacts was calculated and summarised in histograms for each taxon.

2.4. Spatially explicit current and future value to the fishery

Spatial layers representing the current value to the fishery was derived by combining the trawl footprint from the deep-water fisheries across New Zealand from 1989 to 2019 with associated demersal fish catches (kg km⁻²). The trawl footprint, the proportion of each cell in a grid contacted by the combined swept area of all bottom trawls carried out within it, and the demersal fish catch data, were derived from records of all deep-water commercial fishing operations during this period (Baird and Mules, 2021). This measure of value to the fishery does not account for market value of different taxa, but rather represents a gradient of productivity and biomass of fish that are presumed to be a good relative proxy for economic value.

Given the many unknowns and uncertainty associated with estimating value of fish in the future (and under different possible climatic conditions), it was decided to simply predict the distribution of catch (kg $\rm km^{-2}$) into the future by assuming that there was a relationship between catch and environmental conditions in current conditions (Soykan et al., 2014). A model predicting the spatial distribution of catch was constructed by randomly selecting observed spatial distribution of catch (20,000 random samples) and estimating the relationships of catch with co-variables (distance to port and the environmental variables used to predict the habitat suitability models) using a hurdle model approach (e. g., as in Dedman et al. (2015)). That is, a binomial model was used initially to predict the probability of occurrence of a vessel fishing a location, followed by a separate model with a Gaussian distribution to the catch where presence was recorded.

To produce parsimonious models, a variable selection method was implemented. In the first instance, a Random Forest model was fitted to the presence/absence of a fishing vessel and separately to fish catch using the extended Forest package in R (Liaw and Wiener, 2002). This method accounts for any co-linearity in predictor variables when determining the relative importance of each predictor variable in the model through the implementation of a conditional approach to variable importance calculation (Ellis et al., 2012). Only variables with a relative influence >5% were retained (Müller et al., 2013; Jouffray et al., 2019). This approach allowed predictors that may have localised importance, but with low overall importance, to be retained whilst removing any very low, or negatively contributing environmental variables (Stephenson et al., 2023).

Binomial models of presence/absence of fishing vessel and gaussian models of demersal fish catch were fitted with temporally static predictor variables (distance to port, water depth, seafloor slope and seafloor rugosity) and current day estimates for temporally dynamic predictor variables from the NZESM (Anderson et al., 2022). Spatial predictions from the binomial and gaussian models were hurdled (multiplied) to provide spatial estimates of catch (kg km⁻²). The predictive performance of the models was assessed using 5000 samples which were completely independent and randomly selected from observed distribution of catch. The binomial model had excellent predictive power with an AUC 0.96 and predicted distribution of catch from the hurdle model compared to independent evaluation data had a high Pearson's correlation of 0.75. Binomial and gaussian models were predicted using variables from the NZESM (and were hurdled) to produce spatial prediction of catch under future climatic conditions (SSP2-4.5 and SSP3 - 7.0, Fig. 2, D, and Fig. S27, Supplementary Materials).

2.5. Spatial prioritisation analysis

The effectiveness of illustrative examples of spatial marine protection were explored using the spatial prioritisation tool *Zonation* (Moilanen et al., 2009). *Zonation* initially assumes that the entire area of interest (study area) is protected, sequentially removing in a stepwise fashion those cells making the lowest contribution to the representation of a full range of biodiversity features (Moilanen et al., 2014), in this case, deep-water coral distribution layers. For all analyses presented here, the Core Area Zonation (CAZ) algorithm was used for 'Prioritisation' (Moilanen, 2007). This rule prioritises representativeness of all biodiversity features as opposed to other rules that can be used which maximise biodiversity hotspots or target prioritisation of individual biodiversity features. The resulting output is a single map of deep-water coral prioritisation, with areas identified from the highest to lowest priority in terms of conservation value.

2.5.1. Outputs from the spatial prioritisation analyses

Spatial prioritisations were presented as maps that identified the top 10%, 20% and 30% priority conservation protection areas for deepwater coral distributions. Other Zonation outputs included the proportion of each taxon's range protected across the range of prioritisation (i. e., 0-100% of total area selected collated into tables). At each priority conservation protection level (top 10%, 20% and 30%), the ranges of individual taxa contained within these areas were extracted providing information on the extent of protection for each taxon. The performance of spatial protection can broadly be evaluated according to whether a greater proportion of the taxon's range is protected than the proportion of the area protected (e.g., as a rule of thumb if taxon X has \geq 5% of its range protected within the top 5% priority areas, this could be considered an efficient protection solution for taxon X). In addition, the proportion of each taxon's range protected at each protection level (i.e., 10%, 20% and 30%) were also calculated for habitat suitability distribution values with a threshold at 0.7 which represent highly suitable habitat; we refer to these areas as 'core habitat' (Tong et al., 2013). Core habitat was considered an important measure because these represent areas which are most likely to contain deep-water corals (Tong et al., 2013), yet may not occur in the same locations under future climatic conditions (Anderson et al., 2022).

2.5.1.1. Scenario 1 – Single stressor scenario. Spatial prioritisation analyses using only current predictions of deep-water corals (given the impact of fishing). Deep-water coral distributions under current climatic conditions (1995-2014), accounting for the predicted impact of bottom fishing, were spatially prioritised for conservation value. Furthermore, associated uncertainty estimates for each deep-water coral distribution were used to prioritise areas where predictions of deep-water coral distribution were more certain using the 'Info-Gap Analysis' option in *Zonation* (Moilanen and Wintle, 2006) with a weighting value of $\alpha = 0.2$ (Rowden et al., 2019; Stephenson et al., 2021a). Taxa-specific weightings can be applied to distribution layers in the spatial prioritisation to reflect higher perceived value of prioritising areas suitable for particularly important taxa. The reef-forming corals (Order Scleractinia) were given a higher weighting (5 x weighting of other taxa) in the spatial prioritisation to reflect their perceived higher biodiversity value, e.g., Scleractinia reefs can provide habitat for diverse and functionally important ecosystems (following weightings and rationale detailed in Rowden et al. (2019)).

To assess whether areas identified as having high conservation value from the spatial prioritisation using current-day predicted distributions overlapped with future distributions (i.e., may provide climate refugia), predicted distribution of deep-water corals under different future climatic conditions (SSP2 – 4.5 and SSP3 – 7.0) were included in the spatial prioritisation with a weighting of zero. That is, the inclusion of zeroweighted distributions had no influence on the spatial prioritisation but the overlap of these distributions with the identified high priority conservation value areas could be calculated.

2.5.1.2. Scenario 2 – Multiple stressor scenario. Spatial prioritisation analyses using both current predictions of deep-water corals (given the impact of fishing) and future predictions under different future climatic conditions (SSP2 - 4.5 and SSP3 - 7.0). Zonation settings used for Scenario 1 were used also for Scenario 2. However, future predictions of deep-water corals (SSP2 - 4.5 and SSP3 - 7.0) were given taxa weightings (i.e.,

these layers had an influence on the spatial prioritisation). Similarly to current-day predictions, the relative taxa weighting of reef-forming corals (Order Scleractinia) was five-times greater than for other taxa under future climatic conditions. Taxa weightings were the same between future distributions under SSP2 - 4.5 and SSP3 - 7.0 conditions. Taxa weightings of future predictions were progressively increased from 0.25, 0.5, 1.0 relative to current distributions in exploratory analyses. Final weightings of future predictions were set to equal those of current distributions because there was little penalty to the efficiency of the spatial prioritisation of current layers with increasing weighting of future predictions, but a large increase in efficiency in the spatial prioritisation of future layers. Furthermore, a spatial prioritisation where each climatic scenario has equal weighting between current conditions and future conditions SSP2 - 4.5 and SSP3 - 7.0 was felt to best represent the uncertainty as to which conditions may eventuate. That is, the incorporation of multiple possible future conditions in this manner could be seen as a precautionary assumption.

2.5.2. Estimated impact of conservation protection on value to the fishery

Finally, across both scenarios, the impact that levels of conservation protection may have on distribution of a simple value to the fishery metric was assessed by including a measure of current day and predicted future (predicted under different future climatic conditions: SSP2 – 4.5 and SSP3 – 7.0) catch (measured as kg km⁻² fish) as zero-weighted layers in both Scenario 1 and 2. That is, the value to the fishery metrics had no influence on the spatial prioritisation but the overlap of these distributions with the identified high priority conservation value areas could be calculated.

3. Results

3.1. Predicted impact of fishing on deep water coral distributions

Accounting for the historical impact of bottom fishing resulted in decreases in all predicted current-day habitat suitability for deep-water coral taxa (Fig. 3). However, a subset of taxa was predicted to have been particularly strongly impacted by bottom fishing (i.e., many moderate high value habitat suitability areas were reduced) based on the higher predicted susceptibility to fishing impacts (i.e., large, erect, hard and sessile fauna) and the overlap of predicted deep-water coral distribution with the observed distribution of bottom trawl fishing. For example, the branching reef-forming corals (Order Scleractinia) Goniocorella dumosa and Madrepora oculata, the hydrocorals Stylaster spp. and Errina spp. were predicted to lose more than 30% of the areas with habitat suitability values greater than 0.7 (dashed black lines in Fig. 3, Table S2 in Supplementary materials). Loss of areas with moderate to high value habitat suitability was particularly obvious in spatial predictions. For example, impact adjusted habitat suitability of Goniocorella dumosa was predicted to be restricted to offshore areas (Fig. 4, B), whereas unimpacted habitat suitability was also high in coastal regions off the North and South Islands of New Zealand (Fig. 4, A). Goniocorella dumosa is presented here as an example taxon because it is considered a key habitat-forming stony coral in the study area, but see also impact adjusted habitat suitability for the 11 other taxa in the supplementary materials (Figs. S14-S25).



Fig. 3. Histogram of predicted habitat suitability (0–1) for deep-water coral taxa under current climatic conditions (1995–2014, light grey) and accounting for the predicted impact of bottom fishing (grey). Dark grey represents the increase in low predicted HSI value cells following fishing impacts. The secondary y-axes (and dashed lines) represent the proportional difference between predicted habitat suitability (0–1) for deep-water coral taxa under current climatic conditions and the predicted habitat suitability accounting for impact of bottom fishing.



Fig. 4. Predicted habitat suitability (0–1) for *Goniocorella dumosa* (reef-forming coral) A) under current climatic conditions (1995–2014), and B) following inclusion of estimates of seafloor condition, i.e., impact of bottom trawling (i.e., Fig. S13). Predicted habitat suitability under current climatic conditions and following inclusion of estimates of seafloor condition for all other taxa are available in the supplementary materials (Figs. S14–S25).

3.2. Spatial prioritisation analysis

In Scenario 1 (Fig. 2, E), the proportion of the impact adjusted current distributions of deep-water corals, was very high for all taxa in the top 10, 20, 30% conservation areas for protection (Fig. 5, A). The median protection for taxa was 0.42, 0.62 and 0.75 for the top 10, 20 and 30% priority conservation areas respectively (Fig. 5, A, Table S3, in supplementary materials). Protection levels of the zero-weighted (i.e., the overlap of) predicted distributions for deep-water corals under future climatic conditions (SSP2 - 4.5 and SSP3 - 7.0) were lower across the conservation priority protection levels (Fig. 5, A). Despite a wider spread in the proportion protected, all but a few taxa of deep-water corals were well represented under future climatic conditions (i.e., the proportion of the taxon's distribution which is protected is equal to or greater than the proportion of the particular conservation priority level area) (Fig. 5, A, Table S3, in supplementary materials). Those taxa that were not well represented under both future climatic conditions and across all protection levels included the black coral Leiopathes spp. And the bubblegum coral Paragorgia spp. (LEI and PAB in Fig. 5, A), while the branching coral Goniocorella dumosa was not well represented in the top 20 or 30% priority areas under the more severe climate change scenario represented by SSP3 - 7.0 (GDU in Fig. 5, A).

Despite the promising result in the relative efficiency of the spatial conservation prioritisation, the proportions of taxa distributions at each protection level were based on predicted distributions, which in many cases were far smaller under future climatic conditions (Table S4, supplementary materials). For several taxa there were drastic declines in core habitat (i.e., areas where the habitat suitability \geq 0.7, see coloured taxon abbreviations in Fig. 5). For example, the core habitat of *Goniocorella dumosa* under future climatic conditions represents 1% and 14%

of current distribution for SSP2 - 4.5 and SSP3 – 7.0 respectively, noting that for some taxa an increase in core habitat is predicted (Fig. 4 and Table S4 in supplementary materials, Anderson et al., 2022). Core habitat for taxa predicted under current climatic conditions are well represented in the spatial prioritisation of Scenario 1. However, core habitat for most taxa under future climatic conditions were not well represented in Scenario 1 (red cells in Table 1). This finding is due to both the reduction in extent, and the limited overlap between, core habitat predicted from current climatic conditions to those from future climatic conditions (Anderson et al., 2022).

The proportion of deep-water coral distributions predicted under future climatic conditions (SSP2 - 4.5 and SSP3 - 7.0) were higher for most taxa at all protection levels (top 10, 20, 30% conservation priority areas) compared to Scenario 1 (Fig. 5, B compared to Fig. 5, A). Differences in the proportion of impact adjusted current distributions of deep-water corals were negligible between Scenario 1 and 2 (Fig. 5, A and B). All taxa distributions (predicted under current and future climatic conditions), at all protection levels, were well represented by the spatial prioritisation of Scenario 2 (i.e., the spread of the protection values is tighter for Scenario 2 compared to Scenario 1, Fig. 5; see values in Table S3, supplementary materials), including much higher levels of protection for most taxa whose distributions are predicted to contract (e. g., red, orange and yellow in Fig. 5). Specifically, core habitats for taxa under future climatic conditions, despite still being lower than those from current-day predictions, were better represented across all taxa in Scenario 2 (Table 1).

Despite 100% protection of many of the core habitats predicted under future climatic conditions across protection levels, for some taxa, this still represents a reduction of 86–99% of the core habitat protected compared to that expected under current climatic conditions (Table 1).



Fig. 5. Boxplots showing the median (horizontal black line), interquartile range (box), 5th and 95th quantile (whiskers) of the proportion of taxa distributions protected in top 10% (unshaded), 20% (light grey) and 30% (dark grey) of the spatial prioritisation analysis for Scenario 1 (A) and Scenario 2 (B) under current and possible future climatic conditions (SSP2 – 4.5 and SSP3 – 7.0). Proportion protected for each taxon is indicated by the 3-letter taxon abbreviation: BTP: *Bathypathes* spp., CLL: *Corallium* spp., ERO: *Enallopsammia rostrata*, ERR: *Errina* spp., GDU: *Goniocorella dumosa*, ISI: *Keratoisis* spp. and *Lepidisis* spp., LEI: *Leiopathes* spp., MOC: *Madrepora oculata*, PAB: *Paragorgia* spp., PMN: *Primnoa* spp., STL: *Stylaster* spp., SVA: *Solenosmilia variabilis*. The percentage of core habitat (defined as habitat suitability values \geq 0.7) under future climatic conditions compared to current day predictions is shown as coloured text where red-yellow indicates a decline in core habitat under future climatic conditions, grey is about the same, and blue - green indicates an increase in core habitat under future climatic conditions compared to current day core habitat. Exact values of percentage of core habitat under future climatic conditions materials.

Table 1

Core habitat (km²) of deep-water coral taxon distribution within priority areas (top 10%, 20%, and 30% priority areas) under current climatic conditions and absolute percent increase (blue cells)/decrease (red cells) of core habitat area (km²) under future climatic conditions (SSP2 – 4.5; SSP3 – 7.0) compared to current climatic conditions for Scenario 1 (Single stressor scenario) and 2 (Multiple stressor scenario). Taxa abbreviations used: BTP: *Bathypathes* spp., CLL: *Corallium* spp., ERO: *Enallopsammia rostrata*, ERR: *Errina* spp., GDU: *Goniocorella dumosa*, ISI: *Keratoisis* spp. and *Lepidisis* spp., LEI: *Leiopathes* spp., MOC: *Madrepora oculata*, PAB: *Paragorgia* spp., PMN: *Primnoa* spp., STL: *Stylaster* spp., SVA: *Solenosmilia variabilis*.

Scenario	Climatic conditions	Priority area	ВТР	CLL	ERO	ERR	GDU	ISI	LEI	мос	РАВ	PMN	STL	SVA
Scenario 1	Current	Top 10 % priority area	31001	35975	31993	37724	7826	50678	15475	30869	42956	76068	19405	99080
		Top 20 % priority area	56618	64137	31993	90003	7826	95415	15475	30869	76698	158447	21186	193651
		Top 30 % priority area	62550	80732	31993	129307	7826	121672	15475	30869	90011	223141	21186	205558
	SSP2 - 4.5	Top 10 % priority area	-63	-16	-17	-18	-100	-99	-100	-87	-100	-99	5	-78
		Top 20 % priority area	-60	-25	-10	-22	-100	-99	-100	-86	-100	-99	18	-79
		Top 30 % priority area	-62	-22	-7	-25	-100	-98	-100	-84	-100	-99	26	-77
	SSP3 – 7.0	Top 10 % priority area	-62	65	40	2	-94	-100	-94	-49	-100	-54	120	-30
		Top 20 % priority area	-69	80	74	-6	-93	-100	-91	-45	-100	-51	242	-18
		Top 30 % priority area	-69	114	136	-1	-93	-100	-90	-42	-100	-41	348	-5
Scenario 2	Current	Top 10 % priority area	28495	29772	29159	21578	7826	32943	12003	28964	21978	46528	14199	58866
		Top 20 % priority area	43584	43920	31993	44474	7826	65002	15475	30869	47235	100684	20202	117238
		Top 30 % priority area	54341	54869	31993	71872	7826	87555	15475	30869	65185	149666	21186	170482
	SSP2 - 4.5	Top 10 % priority area	-46	-3	35	-20	-99	-81	-52	-70	-97	-91	26	-44
		Top 20 % priority area	-48	-16	75	-14	-99	-86	-63	-72	-99	-93	34	-53
		Top 30 % priority area	-50	-21	80	-16	-99	-89	-63	-72	-99	-94	55	-67
	SSP3 – 7.0	Top 10 % priority area	-43	64	99	35	-86	-93	-12	-17	-97	-26	143	-6
		Top 20 % priority area	-53	80	205	33	-86	-93	5	-11	-99	-26	203	-8
		Top 30 % priority area	-58	95	306	27	-86	-94	14	-11	-99	-24	300	0

This finding is particularly concerning for taxa such as the branching coral *Goniocorella dumosa* which was already predicted to have a restricted core habitat under current climate conditions following the impacts of bottom trawling (approximately 7800 km² of the core habitat predicted to currently exist after accounting for the impacts of bottom trawling cross the New Zealand marine environment), and which is predicted to be reduced to approximately 50–1070 km² under future climatic conditions (under SSP2 – 4.5 and SSP3 – 7.0 respectively).

3.3. Impact of conservation protection on value to the fishery

Broad spatial patterns in current and future predicted demersal fish catch were similar, although catch was predicted to be reduced in all but a few areas where some localised increases were predicted in the future (Fig. 2, D and Fig. S27, Supplementary Materials). For Scenario 1, using predictions of current-day deep-water coral distributions, the proportion

Table 2

Proportion (%) of the current fish catch (kg km⁻²) from deep-water fisheries in New Zealand and predicted fish catch under possible future climatic conditions (SSP2 – 4.5 and SSP3 – 7.0) in the top 10%, 20% and 30% of the spatial conservation protection prioritisation for Scenario 1 (Single stressor scenario) and Scenario 2 (Multiple stressor scenario).

	Scenario	1		Scenario 2					
	Current	SSP2 - 4.5	SSP3 - 7.0	Current	SSP2 - 4.5	SSP3 - 7.0			
Top 10%	0.5	5.9	3.5	6.8	11.7	7.7			
Top 20%	2.3	11.3	12.7	13.9	20.9	16.9			
Top 30%	8.1	20.7	25.0	19.9	28.9	25.5			

of fish catch (kg km^{-2}) from deep-water fisheries in New Zealand which would be lost under the different protection levels increased from 0.5% to approximately 8% under current climatic conditions (Table 2). Similarly, the proportion of predicted fish catch lost under possible future climatic conditions (SSP2 - 4.5 and SSP3 - 7.0) were also predicted to increase with increasing protection levels. However, these proportions were much larger under future climatic conditions than for current climate conditions (Table 2). For example, if the top 30% priority conservation areas identified in Scenario 1 were closed to fishing, current value to the fishery was expected to decline by 8% but decline by 21% and 25% under future climatic conditions (SSP2 - 4.5 and SSP3 -7.0 respectively) (Table 2). Similar results were found for Scenario 2, using predictions of future deep-water coral distributions, albeit the proportional losses in value to the fishery were much higher across both current and future climatic conditions (particularly for current fish catch which would decline by 20% in Scenario 2 compared to 8% for Scenario 1, Table 2).

4. Discussion

Globally, ecosystems and the biodiversity they support are subjected to increasing anthropogenic pressures that can negatively impact ecosystem condition and functioning (Díaz et al., 2019). In marine environments, fisheries, pollution, and eutrophication are currently thought to be responsible for much of the observed ecosystem degradation, yet environmental changes caused by global climate change are predicted to be of the same magnitude as all current pressures to date combined (Wåhlström et al., 2022). This issue may be particularly problematic in New Zealand as the region is also a hotspot of climate change (Rickard et al., 2016; Law et al., 2018). For deep-water corals around New Zealand, substantial shifts in their location and decreases in their extent are predicted by the end of the 21st century (Anderson et al., 2022), which, in combination with the impacts from bottom fishing, mean deep-water corals may be at a high risk of local extinctions. In this paper, an initial exploration of the effectiveness of possible levels of spatial protection under single and multiple stressor scenarios were assessed for: protecting the estimated current distribution of deep-water corals; providing habitat refugia under future climatic conditions; and the possible economic effects of spatial protection for corals on the fishery. We highlight learnings that we argue are crucial considerations for effective spatial planning and which are equally applicable for conservation efforts of other marine taxa.

4.1. Multiple stressors on deep-water coral distributions

Deep-water coral distributions in the New Zealand marine environment were predicted to be negatively impacted by bottom trawling to varying degrees, based on biological traits (grouped here into functional groups), and the spatial overlap between deep-water coral distributions and the distribution of fishing, similar to several other studies (Roberts and Hirshfield, 2004; Clark et al., 2016; Goode et al., 2020). Habitat for all deep-water corals examined here was predicted to be negatively impacted by bottom fishing, but some taxa were predicted to be strongly impacted (i.e., a large reduction in core habitat for: *Goniocorella dumosa*, *Madrepora oculata, Leiopathes* spp., *Errina* spp. and *Stylaster* spp.).

In contrast, the effects of climate change on deep-water coral distributions have been found to be more varied (Morato et al., 2020; Anderson et al., 2022). Some taxa were predicted to have decreased core habitats under both SSP2 and SSP3 scenarios (i.e., *Bathypathes* spp., *Goniocorella dumosa, Keratoisis* spp. and *Lepidisis* spp., *Madrepora oculata and Paragorgia* spp.). A smaller number of deep-water coral taxa were predicted to have increased core habitats (i.e., highly suitable habitat where HSI > 0.7 for *Enallopsammia rostrata* and *Stylaster* spp.). Finally, some deep-water coral taxa were predicted to have a mixed response, with decreased core habitat in one climate scenario but increased core habitat in the other climate scenario (i.e., *Corallium* spp., *Errina* spp., *Leiopathes* spp., *Primnoa* spp. and *Solenosmilia variabilis*).

Impacts of multiple stressors on species' distributions can be positive (e.g., in this study, increase in suitable habitat), negative (e.g., decrease in suitable habitat) or mixed (e.g., an increase in suitable habitat due to one stressor, but a decrease in suitable habitat due to another). One key aspect of managing multiple stressors (whether positive, or negative) is whether they have synergistic or antagonistic effects. That is, where the combined effect of multiple stressors is either greater or smaller (respectively) than what is expected additively (Hewitt et al., 2016). Understanding whether there are synergistic effects are of particular importance for effective management since actions to reduce one stressor may provide additional benefits by simultaneously reducing the synergistic effect (Ban et al., 2014; Rullens et al., 2022). In contrast, if there are antagonistic effects, management actions that reduce one stressor may be ineffective.

The modelling approach used here does not provide information on whether synergism or antagonism occurs because the model used to predict future distribution under climate change scenarios is temporally static and there is no inclusion of the connectivity among populations over time. That is, predictions of suitable habitat are based on environmental conditions without regard for demographic processes such as reproduction or population dynamics (Elith and Leathwick, 2009). The approach used here, will likely over-estimate future habitat suitability for those taxa predicted to be impacted by bottom fishing (all taxa in this study, but noting that some marine taxa are thought to have positive relationships with bottom fishing, e.g., predator-scavengers, Lambert et al. (2017)).

Despite this shortcoming, we can still conclude whether there are positive, negative or mixed effects from bottom fishing and climate change. Combined negative effects present the most ecological risk, whilst combined positive effects represent the least risk irrespective of synergism or antagonism (Rullens et al., 2022). In combination, bottom

trawling and climate change were predicted to have a cumulative negative impact on the distribution of several deep-water corals, particularly for reef-forming corals (e.g., Goniocorella dumosa and Madrepora oculata), but also the black coral Bathypathes spp. and Leiopathes spp., bamboo corals Keratoisis spp. and Lepidisis spp., and bubble gum coral Paragorgia spp. For example, core habitat of Goniocorella dumosa was predicted in our models to be reduced from $33,488 \text{ km}^2$ to 7826 km² due to bottom fishing and was then predicted to be further reduced to 1074 km² or 50 km² by the end of the 21st century under different future climatic conditions (SSP2 - 4.5 and SSP3 - 7.0 respectively). Bottom trawling and climate change may have mixed effects on several deep-water coral taxa: precious coral Corallium spp., hydrocoral Errina spp., the seafan Primnoa spp. and reef-forming coral Solenosmilia variabilis. A small number of taxa were predicted to have increased core habitat under both future climate change scenarios, which may result in increased suitable area despite impacts from bottom fishing: the reef-forming coral Enallopsammia rostrata and the hydrocoral Stylaster spp. (acknowledging that this conclusion is uncertain since our approach does not explicitly consider the interaction between bottom fishing and climate change on the impact in the spatial predictions). Given the combined negative impacts of bottom fishing and climate change, it may be important in future work to use modelling approaches that allow interaction types (synergism, antagonism, or additive) to be explored; for example, by accounting for connectivity (Beger et al., 2022) applied to impact-adjusted distributions (from bottom fishing) for predictions under future climatic conditions (e.g., using methods that can account for demographic processes, Evans et al., 2016).

In addition to considerations of changes in extent (increases or decreases) of core habitats due to multiple anthropogenic stressors, a key issue for conservation planning under a changing climate is whether locations of future predicted core habitat occur in the same locations as current-day (Morato et al., 2020; Anderson et al., 2022). Here we show that there are substantial predicted shifts in location of core habitats under future climatic conditions (under both SSP2 and SSP3) (in line with findings from Anderson et al., 2022). Therefore knowledge of changes in extent and location of deep-water coral distributions under future climate scenarios are important in designing effective conservation areas (Anderson et al., 2022). Below we further outline considerations to ensure appropriate conservation actions using impact adjusted distributional data in spatial planning.

4.2. Accounting for cumulative impacts in spatial planning

The effect of anthropogenic stressors on species' distributions are rarely accounted for in species distribution modelling (Elith and Leathwick, 2009), yet predictions that account for historic impacts are likely to represent more realistic (reduced) estimates of current distribution (Bowden et al., 2021). Given the potential for strongly altered distributions of deep-water corals resulting from the impacts of bottom fishing and climate change, as shown here, it is particularly important to consider impact-adjusted habitat suitability layers in spatial planning processes to avoid the possibility of ineffective conservation measures (Moilanen et al., 2011). That is, to avoid the protection of areas which previously had high habitat suitability, but which may no longer be of high conservation values due to the impact of bottom fishing. In addition, the impact-adjusted habitat suitability estimates have the added benefit that they can be used to identify possible areas that may support recovery or active restoration. For example, areas impacted by bottom fishing that have suitable environmental conditions for deep-water corals and a suitably close (or connected) source of deep-water coral larvae may be suitable areas for recovery should bottom fishing cease (Baco et al., 2020; Williams et al., 2020; Clark et al., 2022a). Furthermore, the importance of these potential areas of recovery increases if they overlap with areas that remain environmentally suitable under future climatic conditions (Beger et al., 2022).

In the single stressor scenario (Scenario 1) we accounted for the

historic impacts of bottom trawling but still undertook the 'usual' process for identifying priority conservation areas whereby only currentday species' distributions informed the spatial prioritisation (e.g., Rowden et al., 2019). We show that, despite the top 30% of priority areas for conservation protecting a high proportion of current predicted distribution of deep-water corals, both in terms of the protection of the overall distribution and core habitat areas, these areas did not provide strong protection for deep-water corals under future climatic. This finding is particularly important in regard to the Target 3 of Kunming-Montreal Global Biodiversity Framework, which calls for at least 30% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem functions and services, to be effectively conserved and managed through ecologically representative, well-connected and equitably governed systems of protected areas and other effective area-based conservation measures. Given the reduction in distributions due to fishing impacts, and the drastic decline in core habitat areas for many deep-water coral taxa under future predicted climatic conditions, our results demonstrate that there are considerable risks associated with effectiveness of protection measures that do not account for current and future stressors in line with findings from other studies (e.g., Sala et al., 2021).

We argue that it is crucial that multiple stressor scenarios (Scenario 2) are used that allow for future species' distributions and core habitats to be considered and maximised in the spatial planning process to avoid implementing protected areas which do not contain suitable future habitat (i.e., climate refugia). Similarly to Kujala et al. (2013) and Sala et al. (2021), we found that a spatial prioritisation which simultaneously accounted for present and potential future distributions of species (in our case deep-water corals), could identify efficient conservation areas for future distributions with only marginal reductions in present-day conservation values. The gains in proportion of future deep-water coral distributions were small in our study but may be particularly valuable for conservation given the increased coverage of the core habitats which were predicted to be greatly reduced due to bottom fishing and future climate change.

Successful establishment of marine protected areas depends on the early establishment of agreed conservation goals, objectives and methods (e.g., Fernandes et al., 2009; Spalding and Hale, 2016; Álvarez-Romero et al., 2018; Fitzsimons and Wescott, 2018; Sala et al., 2021). Obtaining this agreement includes consultation with established resource users such as commercial and recreational fishers who will be affected by the implementation of protection (Capitini et al., 2004; Jones, 2007); failure to achieve 'buy-in' can easily undermine an otherwise effective design process (e.g., Capitini et al., 2004; Christie, ; Gladstone, 2014). The use of multi-criteria spatial planning approaches that explicitly consider competing resource uses, including biodiversity protection, fishing, and/or energy generation (e.g., Leathwick et al., 2008; Yates et al., 2015; Sala et al., 2021) can play an important role in building this acceptance (Melià, 2017). Here we explored the possible impact that a conservation approach may have on current and future fishing value but without including the value to the fishery as a trade-off (i.e., the analysis did not seek to minimize the impact on the value to the fishery).

Overall, the potential loss to the current day value of the fishery was low when only accounting for current-day deep-water coral distributions in the single stressor scenario (maximum 8.1%, Scenario 1). However, with the inclusion of future deep-water coral distributions in the multiple stressor scenario (Scenario 2) we predicted an increased cost to current day value to the fishery (maximum 19.9%). In addition, the future cost to the fishery under possible future climatic conditions (SSP2 – 4.5 and SSP3 – 7.0) was predicted to be even higher (i.e., maximum 28.9 and 25.5% respectively). These higher losses suggest that these deep-water fisheries may be increasingly vulnerable under future climate change. However, despite these likely increased costs to the fishery from possible conservation protection, both Scenarios 1 and 2 would still be considered 'efficient' in that the proportion of lost value to the fishery was, in all but two cases, less than the proportion of protected area. This finding may also highlight the overlap of fishing with important core habitats for deep-water corals (Clark et al., 2016) which represent both the highest conservation value for current and future distributions of deep-water corals and may also represent areas that actively support the fish populations targeted by deep-water fisheries (Clark et al., 2022b). Effective management needs to consider both habitat protection and fisheries production (Clark and Dunn, 2012). Thus, implementation of any spatial planning for deep-water corals would have to consider the interplay between conservation goals and fishery values (Sala et al., 2021), and should be undertaken as part of an open stakeholder engagement process which may include further scenario testing and different weightings of spatial layers (e.g., Rowden et al., 2019).

4.3. Considerations of risk and uncertainty in spatial planning

Failure to acknowledge sources of uncertainty can lead to poor management decisions (Link et al., 2012; Regan et al., 2005) and misleading results in spatial planning processes (Moilanen et al., 2006; Stephenson et al., 2021a). Here, several sources of uncertainty were assessed (acknowledging these were not exhaustive). Associated uncertainty estimates for each of the current and future deep-water coral distribution estimates provides an important indication of the variability in the modelling estimates (Leathwick et al., 2006). Whereas the inclusion of deep-water coral distributions under multiple future climatic conditions (SSP2 and SSP3) provide different possible future outcomes based on the (uncertain) decision making for globally reducing greenhouse gas emissions (Kujala et al., 2013; Magris et al., 2015). The inclusion of these sources of uncertainty in a quantitative manner results in the most certain areas with the highest conservation value being prioritised in the solutions, but also allows the spreading of risk given it is unclear which future distributions may eventuate. That is, decision-making can be improved by exploring risks and trade-offs associated with different climate scenarios (Kujala et al., 2013).

Given the uncertainty in future predictions, one way of reducing the risk of ineffective spatial protection of deep-water corals in the future would be to protect large enough areas to most likely capture current and future predictions. For example, if the top 30% conservation priority areas identified in this study were to be protected (based on the spatial prioritisation of the multiple stressor scenario, Scenario 2), 57%–90% of current deep-water coral distributions and 52%-100% or 38%-90% of future deep-water coral distributions (SSP 2 and SSP 3 respectively) would be captured. The high proportion of taxa' ranges and core habitat included in this level of protection would provide the greatest certainty that these important taxa are conserved now and into the future considering both historic and future anthropogenic impacts. However, it is acknowledged that it may not be practicably feasible to protect all of the top 30% conservation priority areas identified by our study. These areas are too dispersed and sometimes too small to be effectively managed as part of a national-scale marine protected area network, but their identification can nonetheless provide the first step in a process toward the future conservation of deep-water corals in the New Zealand marine environment.

5. Conclusions

The predicted combined impacts of bottom trawling and climate change (SSP2 – 4.5 and SSP3 – 7.0) on the distribution of suitable habitat for deep-water corals were used to explore the effectiveness of illustrative examples of spatial marine protection. Accounting for combined impact of multiple stressors, including climate change, in marine conservation planning and actions has received little attention in the literature; yet it is a crucial consideration. We demonstrate that when designing protection using current day predictions of suitable coral habitat alone (which is akin to the "usual approach"), spatial marine

protection was unlikely to provide adequate conservation for deep water-corals in the future due to distribution shifts associated with climate change and fishing. However, in the analyses where we accounted for future distributions of suitable coral habitat, areas were identified which may provide climate refugia for corals whilst still providing efficient protection for current distributions (despite being impacted by bottom trawling). Despite the large, predicted reductions in core habitats for many deep-water corals from the cumulative impacts of fishing and climate change, the approach exemplified here provides a means to maximise the likelihood of designing marine protected areas that effectively protect biodiversity values under a range of climatic conditions. The potential loss to the current day and predicted future areas of value to the fishery were assessed but was not used to influence the spatial prioritisation analysis. Clearly the possible loss of fishing grounds to marine protected areas that prohibit fishing is an important social-economic consideration and implementation of any spatial planning would have to consider the interplay between conservation goals and fishery values which should be undertaken as part of an open stakeholder engagement process. Our results demonstrate that there are considerable risks associated with developing effective marine protected areas that do not account for current and future stressors in a combined framework. We illustrate the approach with deep-water corals in New Zealand, although this approach is equally applicable to other marine taxa and other locations.

CRediT authorship contribution statement

Fabrice Stephenson: Conceptualization, Methodology, Formal analysis, Validation, Investigation, Data curation, Supervision, Funding acquisition, Visualization, Writing - original draft, Writing - review & editing. Ashley A. Rowden: Conceptualization, Methodology, Writing original draft, Writing - review & editing, Supervision. Owen F. Anderson: Conceptualization, Methodology, Formal analysis, Validation, Investigation, Data curation, Writing - original draft, Writing review & editing. Joanne I. Ellis: Conceptualization, Supervision, Funding acquisition, Visualization, Writing - original draft, Writing review & editing. Shane W. Geange: Conceptualization, Methodology, Writing - review & editing. Tom Brough: Conceptualization, Methodology, Validation, Visualization, Writing - review & editing. Erik Behrens: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - review & editing. Judi E. Hewitt: Conceptualization, Methodology, Writing - review & editing. Malcolm R. Clark: Conceptualization, Methodology, Writing – review & editing. Dianne M. Tracey: Conceptualization, Methodology, Writing - review & editing. Savannah L. Goode: Formal analysis, Visualization, Writing - review & editing. Grady L. Petersen: Visualization, Writing - review & editing. Carolyn J. Lundquist: Conceptualization, Methodology, Validation, Writing - review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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