

Spatial analyses reveal conservation benefits for cold-water corals and sponges from small changes in a trawl fishery footprint

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ABSTRACT: Spatial closures are an important component of regulations to protect cold-water corals and sponges from potential damage by bottom trawling. However, designing spatial closures can be challenging because the distribution of most cold-water coral and sponge habitat is unknown, and closures that overlap with fishing areas may reduce fishing opportunities and landings. In this paper, we examined trade-off relationships between bottom trawl fishery landings and the proportion of coral and sponge habitat protected by alternative spatial closure designs within Hecate Strait, British Columbia, Canada. We selected closures using a spatial optimization procedure involving 3 steps: (1) maximum entropy species distribution modelling to predict habitat suitability for Hexactinellida sponges and Alcyonacea and Pennatulacea corals, (2) matching habitat suitability predictions with spatially explicit estimates of bottom trawl landings value from at-sea observer data, and (3) Marxan spatial optimization to select closures that protect the most suitable coral and sponge habitat while minimizing losses in landings value. Our results suggest that the majority of coral and sponge habitat within Hecate Strait could be protected while maintaining existing fisheries value; spatial closures protecting up to 70% of the most suitable coral and sponge habitat resulted in negligible losses in trawl fishery landings. Protecting 99% of suitable coral and sponge habitats decreased landings value to 63% of its former total. Landings for rockfishes *Sebastes* and *Sebastolobus* spp. were the most sensitive to spatial closures, decreasing twice as much as average landings value for all groundfish species. By explicitly revealing potential trade-offs between fisheries and conservation objectives, our analysis provides a concrete starting point towards implementing spatial closures with increased transparency, credibility, and acceptability from stakeholders.

KEY WORDS: Bottom trawling · Cold-water corals and sponges · Conservation planning · Marxan · Maximum entropy · Species distribution modelling · Trade-offs

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INTRODUCTION

Cold-water corals and sponges are important components of seafloor ecosystems because they provide habitat structure, nursery areas, food resources, and refugia from predators (Turner et al. 1999, Baillon et al. 2012). These ecosystem services may contribute to fisheries productivity, yet they may also be impacted

by fishing activities (Sainsbury et al. 1997, Hiddink et al. 2006). Towing mobile fishing gear over the seafloor removes emergent epifauna (Watling & Norse 1998, Turner et al. 1999), causing long-lasting damage and degradation to corals and sponges (Kaiser et al. 2006, Williams et al. 2010). Many coral and sponge habitats are now designated as vulnerable marine ecosystems, which nations are called upon to

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protect from destructive fishing practices, by the United Nations General Assembly resolution 61/105.

Over the past decade, regulations concerning some bottom trawl fisheries have been implemented to reduce impacts on sensitive benthic species, including cold-water corals and sponges (Shester & Ayers 2005, Brock et al. 2009, Penney et al. 2009). Spatial closures are an important part of these regulations because they can prohibit trawling within sensitive habitat, thus minimizing destructive impacts from trawl gear (Auster et al. 2011). However, closures that overlap with fishing areas may be difficult to implement because of perceived losses in fishing opportunities and landings. Furthermore, conservation gains from closures may be negated if fishing effort and its ecological impacts are redistributed to other areas (Greenstreet et al. 2009). Freezing the fishery footprint is one approach to protecting benthic habitat while minimizing fisheries losses, which only allows bottom trawling within historically trawled areas. This approach minimizes impacts on the fishery because it only prohibits future spatial expansion (Hourigan 2009); however, its effectiveness at protecting coral and sponge habitat is generally unknown, and habitats remain vulnerable if they occur within the fishery footprint (Heifetz et al. 2009, Rieser et al. 2013).

Designing spatial closures that take into account the distribution of coral and sponge habitat along with fishery value could improve the acceptability of spatial closures and, hence, improve conservation outcomes (Penney & Guinotte 2013, Rieser et al. 2013). A major challenge in developing such closures is that cold-water corals and sponges often occur in patchy colonies spread over vast areas that are costly to survey, resulting in sparse sample coverage and ignorance of their distribution (Ross & Howell 2013). Species distribution models (SDMs) can help address this challenge by predicting coral and sponge distributions based on relationships between observed species occurrences and environmental variables (Tittensor et al. 2009, Knudby et al. 2013, Ross & Howell 2013). A fitted SDM can be used with environmental data layers to predict habitat suitability over broad areas that are difficult to survey directly (Franklin 2009).

In this study, we combine SDM predictions of cold-water coral and sponge distributions with spatially explicit fisheries data to develop and assess spatial closures for bottom trawl fisheries within the coastal region of Hecate Strait, British Columbia (BC), Canada. We develop closures over a range of coral and sponge conservation targets to estimate costs to the

trawl fishery and investigate potential trade-offs between fisheries and habitat conservation objectives. We also evaluate the conservation effectiveness of existing closures by determining their overlap with predicted coral and sponge habitats. Addressing these questions can inform the development of cost-effective measures to protect corals and sponges and help determine whether current closures provide sufficient protection (Penney & Guinotte 2013, Rieser et al. 2013). In addition, understanding the trade-offs associated with spatial closures can help balance fisheries and conservation objectives (Stewart & Possingham 2005, Klein et al. 2010) and lead to improvements in conservation outcomes (Gaines et al. 2010, Lester et al. 2013).

We use a spatial optimization approach that combines established methods in a novel and broadly applicable manner to design closures that minimize losses in fisheries landings while protecting predicted coral and sponge habitat. First, we create maximum entropy presence-only SDMs to predict habitat suitability for Hexactinellida sponges and Alcyonacea and Pennatulacea corals. We match these predictions with spatially explicit estimates of bottom trawl landings values based on at-sea observer data. Spatial optimization is then performed using Marxan (Ball et al. 2009) to select closures that protect a predetermined portion of the most suitable coral and sponge habitat while minimizing losses in landings value. We investigate trade-offs between fisheries value and protection of coral and sponge habitat by repeating the spatial optimization over a range of conservation targets to determine how landings value availability varies with the proportion of habitat protected.

METHODS

Study area

Our study area consists of Hecate Strait, BC, and the nearby regions of northern Queen Charlotte Sound and Dixon Entrance (Fig. 1). We focused on a subset of the BC coast so that regional high-resolution SDMs and spatial closures could be fitted. By applying high-resolution models, we hoped to reduce overestimation of habitat extent, which commonly occurs in coarse, large-scale SDMs (Rengstorf et al. 2013), while producing results at a spatial scale that is applicable to fisheries planning. We divided the study area into 31 032 grid cells of 1×1 km, which corresponded to the spatial scale of most envi-

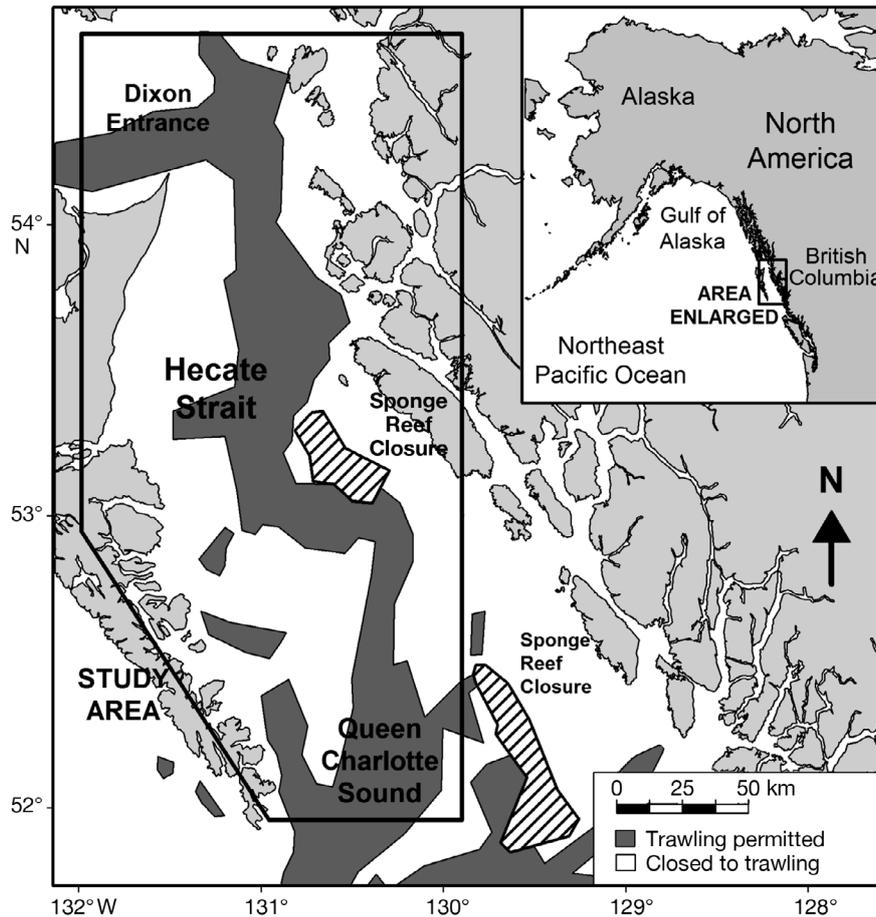


Fig. 1. Study area of Hecate Strait, northern Queen Charlotte Sound, and Dixon Entrance along with existing spatial closures for the British Columbia multi-species bottom trawl groundfish fishery. Spatial closures that restricted bottom trawling to dark grey areas were implemented in 2012. The sponge reef closures (hatched areas) were implemented in 2002 to protect large hexactinellid sponge reefs

ronmental predictors for SDMs, the precision of coral and sponge occurrence locations, and the scale at which fishery data were summarized.

We selected the Hecate Strait region of the BC coast because groundfish bottom trawling is the predominant fishery, and the area contains several groups of corals and sponges as indicated by occurrences from research surveys and incidental commercial catch (Finney & Boutillier 2010). The study area also contains a large, globally unique hexactinellid sponge reef, which has been closed to bottom trawling since 2002 (Fisheries and Oceans Canada 2013). In 2012, additional closures were implemented throughout the BC coast that restricted bottom trawling from expanding to unfished areas and decreased the fishery footprint by 20% coast-wide (Bodtker et al. 2013). These closures did not apply to other benthic fisheries in the study area, which may include longline, hook and line, crab trap, and shrimp beam trawl.

Biological and environmental data

Coral and sponge occurrence records originated primarily from research surveys but also from personal collections and museum records. We obtained records from Fisheries and Oceans Canada's (DFO) invertebrate general status report (P. D. Boutillier & G. E. Gillespie unpubl.) and from catch in DFO bottom trawl surveys within Hecate Strait and Queen Charlotte Sound (see Supplement 1 at www.int-res.com/articles/suppl/m528p161_supp.pdf). These fisheries-independent sources are not confounded with estimates of landings value.

We selected 10 physical and biological environmental variables as model predictors based on availability and relevance to coral and sponge biology. Predictors were derived from bottom salinity and temperature, non-tidal flow speeds, and bottom tidal currents adapted from a circulation model of the eastern North Pacific (Foreman et al. 2008) as well as

chl *a* bloom frequency, bathymetry, and slope (E. Gregr unpubl. data; see Supplement 1). Substrate type was not available for the entire study area, but informative proxies used in our analyses include bathymetry and slope (Yesson et al. 2012, Neves et al. 2014).

Coral and sponge distribution models

We used presence-only maximum entropy SDMs (version 3.3.3k; Phillips et al. 2006) to predict habitat suitability for the coral orders Alcyonacea (including Gorgonacea) and Pennatulacea and the sponge class Hexactinellida. We selected these groups because they were the most abundant coral and sponge occurrences within our study area (Finney & Boutillier 2010). Alcyonacea and Hexactinellida were modeled at their respective order and class levels because of uncertainties associated with species identification, but we divided the Pennatulacea order into the Halipteridae and Pennatulidae families and created SDMs for each family because occurrence records for this group were identified to a higher taxonomic resolution. Model evaluation also revealed that splitting Pennatulacea increased predictive accuracy compared to a single SDM with both families combined.

Models estimated a habitat suitability index (HSI) between 0 and 1, representing a relative measure of occurrence probability for each grid cell. We applied thresholds that transformed low HSI values to zero and excluded these lower quality cells as potential habitat for consideration in our spatial optimization of closures. This is analogous to applying a presence-absence threshold, except we retained HSI values above the threshold to provide additional information on habitat suitability for our spatial optimizations. We used the threshold value for each model that maximised the sum of specificity plus sensitivity (SSS) (Jiménez-Valverde & Lobo 2007). The SSS threshold is robust, generally resulting in a low rate of false negative and false positive prediction errors (Jiménez-Valverde & Lobo 2007; see our Supplement 2 at www.int-res.com/articles/suppl/m528p161_suppl.pdf for other methods we tested). To obtain HSI values for the Pennatulacea order, separate SSS thresholds were applied to model predictions for the Halipteridae and Pennatulidae families, and then HSI values in each grid cell were summed and rescaled between 0 and 1.

We evaluated SDM predictive accuracy by cross-validation and the area under the receiver operating characteristic curve (AUC). The AUC is a threshold-

independent measure of the probability that a randomly selected occurrence location will have a higher predicted HSI than a randomly selected background location (Fawcett 2006). An AUC value of 1.0 indicates perfect predictive accuracy, while a value of 0.5 indicates the model performs no better than random (Pearce & Ferrier 2000). We calculated the average AUC for each species group over 10 cross-validation models, which we created by excluding 10% of the occurrence records from model training and then calculating the AUC for these excluded occurrence records. Each of the 10 models excludes a different partition of the occurrence records, providing estimates of predictive accuracy based on occurrence data that were not used in model creation. Final SDMs used to estimate trade-offs included all available occurrence records.

Fisheries landings value

We estimated the spatial distribution of landings value for the bottom trawl groundfish fishery in Hecate Strait by multiplying landed weight and price for each fish species. We obtained annual prices per kilogram for trawl landings from DFO's Pacific catch statistics database. Spatially explicit catch weights were obtained from the PacHarvTrawl database and are based on at-sea observer estimates of location and composition for all trawl tows from 1996 to 2011 (Fisheries and Oceans Canada 2012). The weights and prices represent the 23 groundfish species managed with annual quotas, including 11 rockfish *Sebastes* spp. and *Sebastolobus* spp., 5 flatfish (family *Pleuronectidae*), 2 skates *Raja* spp., spiny dogfish *Squalus acanthias*, walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus*, lingcod *Ophiodon elongatus*, and sablefish *Anoplopoma fimbria*.

Because of privacy restrictions, catch weights were only available for grid and cell-year combinations that were fished by 3 or more vessels. Therefore, we obtained catch weights at 4, 2, and 1 km resolutions and interpolated weights that were missing. Missing weights were first interpolated from 4 to 2 km resolutions and then from 2 to 1 km resolutions. Catch weights unavailable at 4 km resolution could not be interpolated and were assumed to be zero because of the low number of vessels (<3) fishing within those cells. Consequently, losses in landings value due to spatial closures were underestimated. From 1996 to 2011, the percent of landed weight within privacy-restricted cells over

time ranged between 9 and 21 % of annual landed weight and averaged 13 %.

We summarized landings value by averaging over a range of years and summing landings values over the 23 groundfish species managed with quotas. Thus, a single estimate for each grid cell represented the mean annual landings value for all groundfish quota species combined. We calculated this mean annual landings value using all years of available data (1996 to 2011) and the 8 most recent years (2004 to 2011). These 2 ranges were selected to examine how temporal changes in the distribution of landings value affect trade-off predictions.

Spatial optimization of closures

We used Marxan reserve design software (Ball et al. 2009) to select spatial closures that protect a target portion of coral and sponge habitat while minimizing losses in landings value. Marxan determined spatial closures using stochastic optimization to minimize an objective function based on (1) the value of mean annual landings within closed cells and (2) a penalty for species groups that fall below their conservation target, as defined by the proportion of predicted coral or sponge habitat included within closed areas. For example, a conservation target of 0.5 required the summed HSI value of grid cells within closed areas to be $\geq 50\%$ of the summed HSI value over all cells; otherwise, a penalty was added to the objective function. Penalty values for each species were adjusted so that conservation targets were met under most optimization scenarios and the protected proportion of HSI was always within 5 % of the conservation target. Optimal spatial closures were determined for conservation targets ranging from 0 to 0.99, in 0.05 increments, applying the same conservation target to each coral and sponge group. We took the average of 500 near-optimal spatial closure solutions to integrate over stochastic effects within the optimization.

We used the spatial closure solutions for each conservation target to compute the remaining proportion of total landings value for all quota species combined and for each of the 23 quota species individually. This procedure revealed the trade-off relationships between fishery value and habitat conservation.

Spatial closure solutions were also generated with Pennatulacea excluded as a conservation target because these corals are associated with soft substrates that are easily trawled compared to the rocky, hard substrates that are more suitable for Alcyonacea and Hexactinellida. We hypothesized that spatial closures

would have a disproportionately negative impact on landings values when including Pennatulacea because of its association with soft substrates where more trawling occurs.

RESULTS

Species distribution models

The maximum entropy models for the Alcyonacea order, Hexactinellida class, and Halipteridae and Pennatulidae families (Fig. 2) had AUC values of 0.88, 0.88, 0.85, and 0.86, respectively, suggesting that all models fit the data well and have similar predictive accuracy. Comparisons of the distribution of HSI values suggest that Pennatulacea habitat is most widely distributed within the study area (Fig. 3), with a median HSI value of 0.23 for the combined Pennatulacea model compared to 0.040 and 0.074 for the Alcyonacea and Hexactinellida models, respectively.

There was high overlap in suitable habitat for Alcyonacea and Hexactinellida, as demonstrated by the proportion of grid cells sharing high HSI values. For example, 71 % of grid cells above the SSS threshold overlapped between the Alcyonacea and Hexactinellida models. By contrast, only 19 % of cells above the SSS threshold overlapped between Pennatulacea and Alcyonacea, while 32 % overlapped between Pennatulacea and Hexactinellida.

Fisheries landings value

The estimated total annual landings value of groundfish in the Hecate Strait bottom trawl fishery was CA \$6.6 million when averaged over all years (1996 to 2011) and \$4.7 million when averaged over recent years (2004 to 2011; Fig. 4). This decrease in landings value is attributable to declines from 7900 to 6500 tonnes in landed weight and CA \$1.21 to CA \$1.15 kg^{-1} in average price when averaging over all years compared to recent years, respectively.

A high proportion of landings value was concentrated over a small portion of the study area, especially when estimated using recent years (Fig. 5). There were no fisheries landings in over 78 % of grid cells when estimated using all years and in 90 % of grid cells using recent years. Grid cells within the 99th percentile of landings value covered 3103 km^2 and represented 35 % of total landings value over all years and 54 % of landings value over recent years.

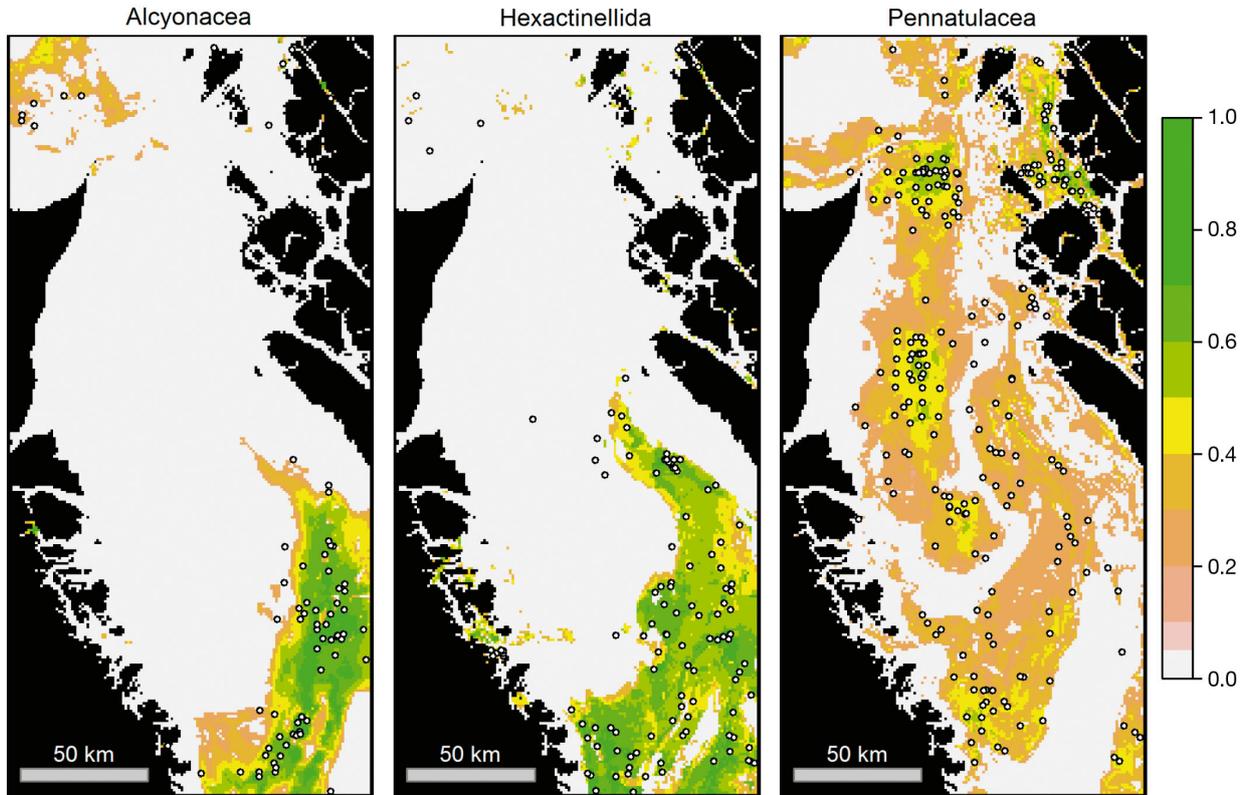


Fig. 2. Maximum entropy model predictions of habitat suitability for the coral orders Alcyonacea and Pennatulacea and the sponge class Hexactinellida. A threshold based on the maximum sum of specificity plus sensitivity has been applied to each model to convert low habitat suitability values to zero. Occurrence records used in model fitting are indicated by white circles. Habitat suitability for Pennatulacea represents the summed habitat suitability predictions for 2 families, Halipteridae and Pennatulidae, rescaled to a maximum value of 1

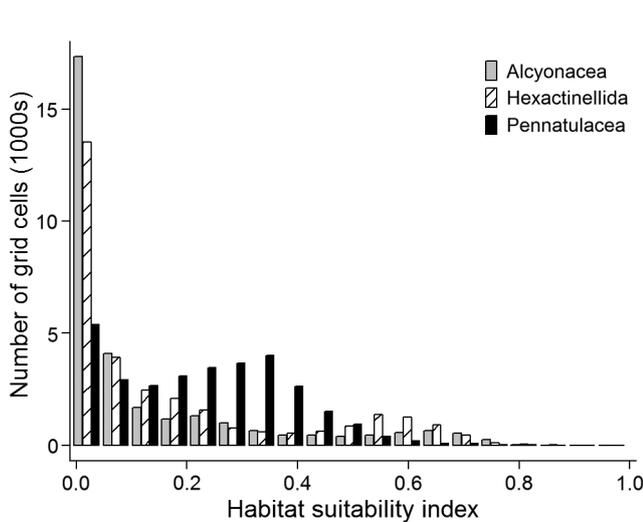


Fig. 3. Frequency distributions of habitat suitability predictions for the coral orders Alcyonacea and Pennatulacea and the sponge class Hexactinellida. A total of 31 032 grid cells of 1 × 1 km were included in each model. Habitat suitability for Pennatulacea represents the summed habitat suitability predictions for 2 families, Halipteridae and Pennatulidae, rescaled to a maximum value of 1

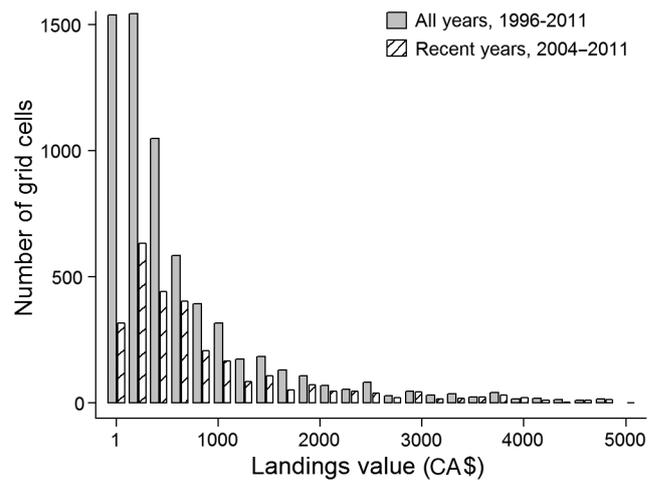


Fig. 4. Distributions of landed value for the bottom trawl groundfish fishery among grid cells within the study area, averaged over all available years of landings data and recent years only. Cells with zero landed value and landed value above 5000 were excluded to limit the plotting area and retain detail. There were 31 032 grid cells within the study area, with 78 and 90% of these grid cells containing zero landings value using all years of data and recent years, respectively

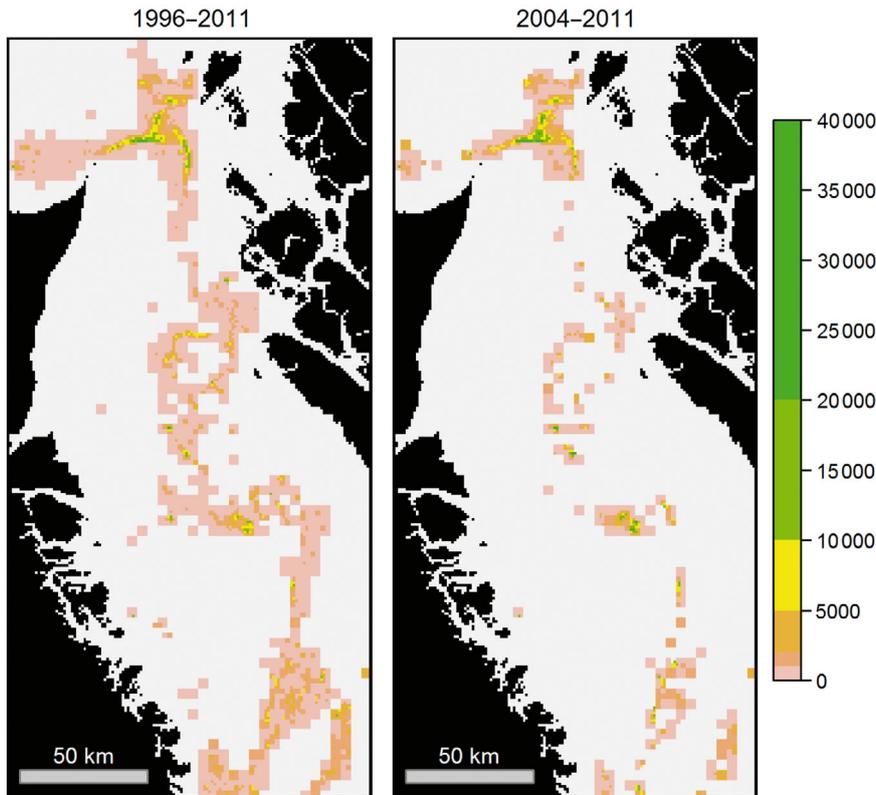


Fig. 5. Spatially explicit estimates of mean annual landings value (CA\$) for the bottom trawl groundfish fishery in Hecate Strait summed over all 23 groundfish species managed with quotas and averaged from 1996 to 2011 (left panel) and 2004 to 2011 (right panel). Each landings value shown represents a 1×1 km grid cell, with a total of 31 032 grid cells within the study area. White areas have zero landings value

Occurrence records within spatial closures

We measured the effectiveness of closures at protecting corals and sponges by determining the proportion of observed occurrence records within optimized spatial closures. If occurrence records are representative of true distribution patterns, and these proportions are near or above the conservation target, then spatial closures would likely accomplish their intended conservation objective. We also measured the proportion of the Hecate Strait hexactinellid sponge reef (Fig. 1) that was included within optimized closures. If the closures are accomplishing their conservation objective for Hexactinellida, then we would also expect this proportion to be near or above the conservation target.

We found that proportions of occurrence records protected within closures consistently equalled or surpassed the conservation target for Alcyonacea and Hexactinellida and equalled or were slightly below the conservation target for Pennatulacea (Fig. 6). The proportion of the hexactinellid sponge reef overlapping with optimized spatial closures also equalled or surpassed the conservation target and was within 0.05 of the proportion of Hexactinellida occurrence records within optimized closures across the entire range of conservation targets.

Trade-offs between fisheries landings and habitat protection

Trade-offs described in this section are based on spatial closures using landings value averaged over all years (1996 to 2011) and including Pennat-

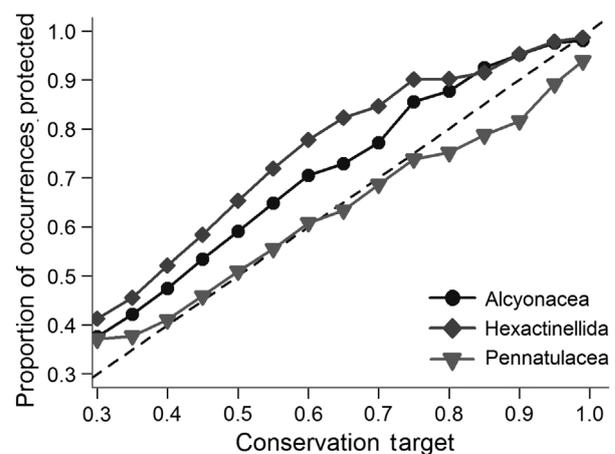


Fig. 6. Proportions of occurrence records for distribution modelling protected within Marxan optimized spatial closures over the upper range of conservation targets. Optimized closures used here were based on landings value estimated from 1996 to 2011 and included Pennatulacea as a conservation target. The dashed line shows where the proportion of occurrences protected equals the conservation target

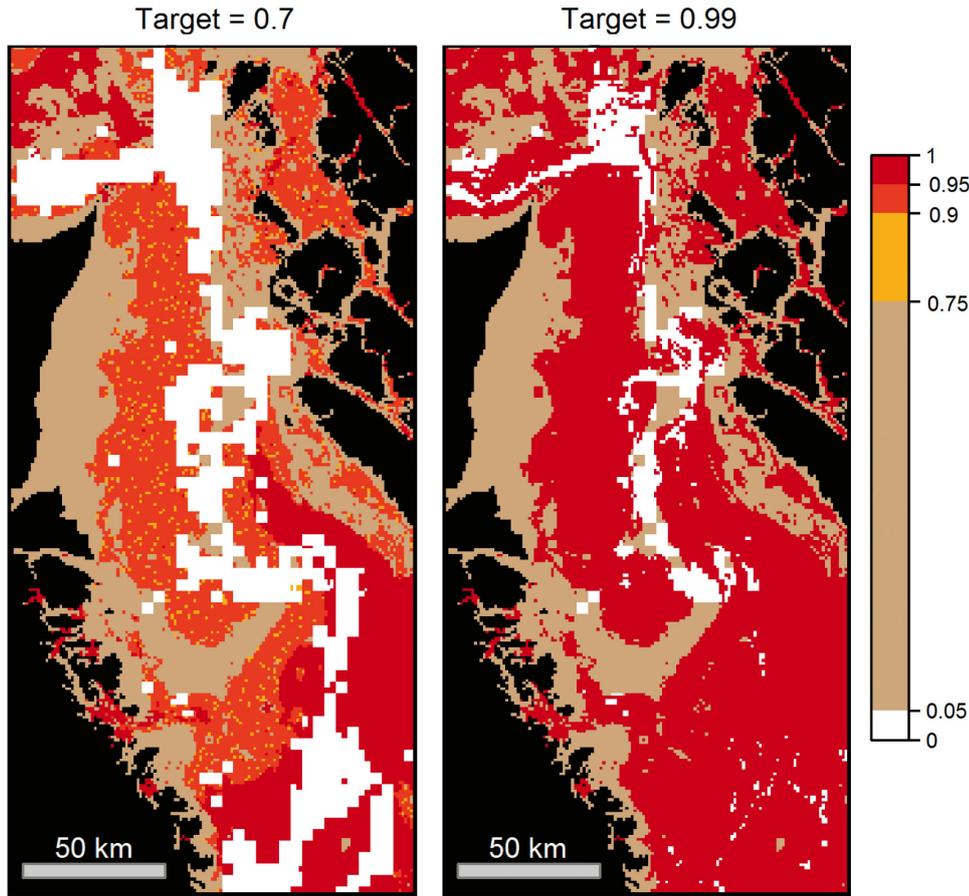


Fig. 7. Proportion of times each grid cell was closed out of the 500 spatial closure solutions produced by Marxan using conservation targets of 0.7 and 0.99. White areas were closed by less than 5% of the spatial closure solutions and represent areas of significant landings value. The proportions shown here estimate landings value by averaging over all years of data (1996 to 2011) and include Pennatulacea as a conservation target

ulacea as a conservation target, unless otherwise noted. There was negligible overlap between optimized spatial closures and fishing areas for conservation targets from 0 to 0.7 (Fig. 7); therefore, landings values remained at or near their maximum

over this range of targets (Fig. 8a). As conservation targets increased beyond 0.7, landings value decreased in an increasingly rapid manner. For example, spatial closures using conservation targets of 0.8, 0.9, and 0.99 decreased landings value to

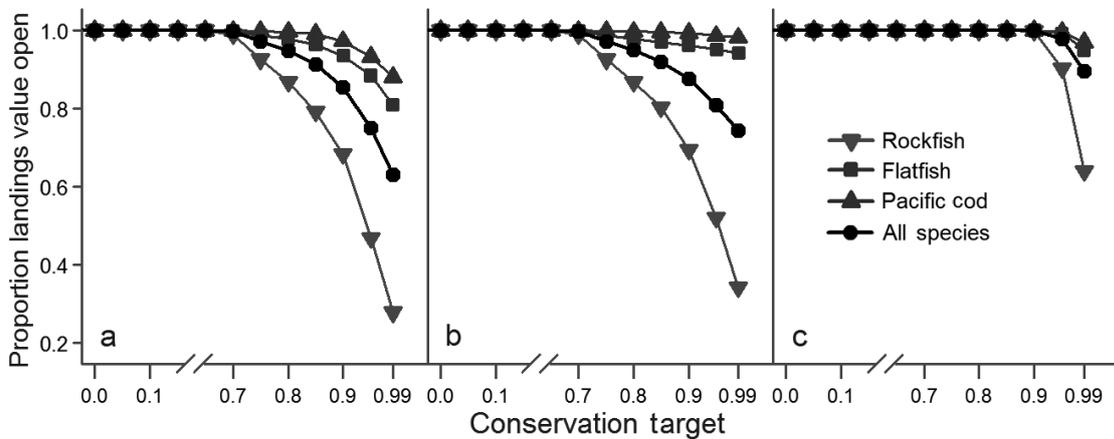


Fig. 8. Proportion of total landings value remaining open to trawling after applying spatial closures for coral and sponge habitat using conservation targets from 0 to 0.99. Landings value is shown for all 23 groundfish species added together (black line with circles), 11 species of rockfish *Sebastes* and *Sebastolobus* spp., 5 species of flatfish (Family Pleuronectidae), and Pacific cod *Gadus macrocephalus*. (a) Default scenario; landing value is estimated by averaging over all years of data (1996 to 2011) and Pennatulacea is included as a conservation target. (b) Pennatulacea is excluded as a conservation target. (c) Landings value is averaged over recent years of data (2004 to 2011) and Pennatulacea is included as a conservation target

94.8, 85.3, and 63.0% of the maximum value, respectively.

The proportion of landings value remaining at higher conservation targets differed among groundfish quota species (Fig. 8). Rockfish landings were most affected by spatial closures, while landings for flatfish were least affected. For example, spatial closures using a conservation target of 0.9 decreased landings value for rockfish to 70.2% of its maximum, compared to 92.6% for flatfish.

Excluding Pennatulacea as a conservation target had only a small effect on the landings value remaining after closures, except at conservation targets greater than 0.9 (Fig. 8b). For the highest conservation target of 0.99 and excluding Pennatulacea, landings value was decreased to 74.3% of its maximum, compared to 63.0% with Pennatulacea included as a target. Landings of flatfish and *Gadus macrocephalus* were more sensitive to Pennatulacea conservation compared to rockfish (Fig. 8a vs. 8b).

We estimated a higher proportion of landings value remaining after closures when the optimization procedure used landings averaged over recent years (2004 to 2011) compared to all years (Fig. 8c). Landings across all species remained at their maximum value up to a conservation target of 0.9 when using recent landings and only decreased to 89.6% of the maximum value for a conservation target of 0.99.

Predicted habitat within existing bottom trawl closures

The existing bottom trawl fishery closure within Hecate Strait (Fig. 1) covers 65% of our grid cells and overlaps with suitable habitat equivalent to conservation targets of 0.47, 0.51, and 0.57 for Alcyonacea, Hexactinellida, and Pennatulacea, respectively. The existing closure also reduced landings value to 97.5% of the maximum value averaged over 1996 to 2011. This small loss followed closure of the hexactinellid sponge reef and a few small areas at the edges of the original fishery footprint. By comparison, our spatial optimization found closure solutions up to a conservation target of 0.7, with landings value remaining at over 99% of its maximum.

DISCUSSION

Spatial fishery closures aimed at protecting sensitive cold-water corals and sponges may be difficult to implement broadly if the costs to fishery stakeholders

are perceived to be unacceptable. Costs to commercial fisheries may include losses in fishing opportunities, yield, and profits. These costs are rarely evaluated explicitly, yet they are often assumed to be significant. Our results, however, indicate that up to 70% of estimated coral and sponge habitat could be protected within Hecate Strait, BC, with negligible losses in bottom trawl fishery yield. By demonstrating these trade-offs using available empirical data at a scale relevant to fisheries planning, we provide a means of evaluating and improving spatial closures to protect vulnerable benthic habitat.

Trade-offs between fishery yield and habitat conservation depend on our assumptions about the fishery as well as SDM predictions of habitat suitability. Although we used high-quality, spatially explicit landings data to represent the potential costs of spatial closures, landings data alone, averaged over a particular window of time, may oversimplify the complexity of how value is generated by a multi-species groundfish trawl fishery. For example, actual costs could be lower if bottom trawl vessels mitigate closures by redistributing effort to remaining open areas (Klein et al. 2010) or by selling catch quotas to other non-trawl groundfish sectors (Fisheries and Oceans Canada 2013). Potential positive effects of closures on ecosystem productivity and fish spillover into adjacent fishing grounds could increase fishery yields, further offsetting actual costs (Sainsbury et al. 1997, Gaines et al. 2010).

Conversely, the costs of habitat protection could be higher if we accounted for operational constraints on closures as well as heterogeneity in species targeting behavior among trawl vessels. Predicted trade-offs between habitat protection and landings differed among groundfish quota species, with rockfish landings being most sensitive to spatial closures and flatfish landings being least sensitive. These sensitivities reflect the higher proportional overlap of rockfish species distributions with hard-bottom coral and sponge habitat (Stone 2006, Du Preez & Tunnicliffe 2011) compared to flatfish distributions over soft substrates that are less suitable for corals and sponges. Harvesters in the trawl fleet understand these distributional differences and are able to effectively target particular groundfish species based on available quota, market demand, and resource availability (Béné 1996, Branch & Hilborn 2008). Extensive spatial closures would reduce the ability of trawl vessels to target particular species and adapt to changes in regulations or market demand. This could impact fisheries profitability to a greater extent than indicated in our analyses. Our optimized spatial closures

also did not consider operational requirements for implementation, particularly the minimum patch size requirements for towing bottom trawl gear. Such practical constraints would reduce the efficiency of closures (Bodtker et al. 2013) and along with privacy restrictions on landings data may explain some of the differences in conservation efficiency between the existing Hecate Strait bottom trawl closures and the Marxan optimized spatial closures.

Accurate interpretation of SDM predictions and sources of uncertainty is critical in determining whether the conservation targets applied in this study are representative of actual conservation objectives or stakeholder values. Our presence-only SDMs likely represent the potential distribution of corals and sponges (where they could occur) rather than their realized distributions (where they actually occur) because we did not include absence records or non-environmental factors as model predictors (Jiménez-Valverde et al. 2008). Non-environmental factors, especially historical trawl exposure, could affect current coral and sponge density independent of other habitat features (Penney & Guinotte 2013). For example, areas repeatedly disturbed by trawling may contain fewer intact coral and sponge colonies (Watling & Norse 1998, Du Preez & Tunnicliffe 2011), but high habitat suitability may be predicted based on environmental conditions. Our SDMs demonstrated reasonable predictive power according to AUC values; however, such metrics may underestimate error in presence-only SDMs, especially if sampling effort is not spatially uniform (Yackulic et al. 2013). Error in SDM predictions may lead to differences between conservation targets and the actual proportion of coral and sponge habitat protected; therefore, accurately quantifying uncertainty and its implications for spatial closures (e.g. Tulloch et al. 2013) are important areas for further research.

Although our research focused on protection of cold-water corals and sponges from bottom trawling, it could be readily extended to include other bottom-contact fisheries, sensitive species, and habitat types. Spatial catch and effort are closely monitored for all trawl, longline, and trap fisheries operating within Hecate Strait, which means that the spatial distribution of landings value could be estimated for other bottom-contact fisheries. We considered bottom trawling because coral and sponge mortality is known to be high when contacted by this gear (Turner et al. 1999, Williams et al. 2010), while mortality caused by fixed gear fishing methods is less certain but thought to be lower (Kaiser et al. 2000). Concerns about fishing gear impacts on other species and habi-

tats could be addressed using additional conservation targets and distribution models. For example, conservation targets could include soft-sediment habitats adapted to low natural disturbance regimes because they can take years to recover from disturbances by bottom trawling (Kaiser et al. 2006). Predictions of benthic habitat sensitivity based on natural disturbance regimes and biological characteristics could also be developed (Hiddink et al. 2007, Kostylev & Hannah 2007) to evaluate spatial protection measures that minimize fishing impacts on benthic productivity (Jennings et al. 2012).

The fishing costs and conservation benefits of spatial closures are admittedly challenging to predict given the complexity of spatial fishery dynamics and the uncertainty associated with cold-water coral and sponge habitats. Despite these apparently large uncertainties, it is critical that we develop management systems that effectively balance conservation of vulnerable marine ecosystems with fishery economic objectives. Our analytic framework linking empirical data to SDMs and conservation objectives represents an adaptive process that can incorporate new information, SDM improvements, or alternative conservation objectives to improve conservation decision making (Sarkar & Illoldi-Rangel 2010). Empirical data could be improved by establishing presence-absence surveys, possibly in collaboration with commercial fisheries to reduce costs. SDMs could be adapted to use presence-absence as well as other environmental and non-environmental information (e.g. Chu & Leys 2010) to reduce uncertainty in predictions of coral and sponge habitat suitability. Modelling the targeting behavior and spatial dynamics of fishing effort is the greatest technical challenge because of the complex interactions among resource availability, market demand, and individual harvester preferences within an increasingly restrictive regulatory environment. Nevertheless, there is a high-quality database on groundfish fishing activity in BC that could be explored using choice modelling or machine-learning methods for complex decision making (e.g. Hutton et al. 2004). Research on harvester behavior and preferences could also reveal potentially valuable performance indicators that are more important to harvesters than landings value alone.

In conclusion, protection of vulnerable coral and sponge species could be improved by accurately estimating the fishery costs of spatial closures. Our modelling approach allowed us to produce novel estimates of losses in landings value for each groundfish species as well as compare the effectiveness of

Marxan optimized spatial closures to established trawl fishery closures. By examining a range of spatial closure options, our results show that habitat conservation costs to fisheries may not be as severe as previously thought, especially for moderate conservation objectives. Establishing a quantitative link between conservation objectives and fishing costs increases the transparency and credibility of conservation measures for corals, sponges, and other components of vulnerable marine ecosystems (Agardy et al. 2003, Rieser et al. 2013). It also provides a concrete starting point from which policymakers and stakeholders can discuss the barriers to implementing spatial closures that protect cold-water corals and sponges from bottom trawl fisheries.

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