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Developing quantitative methods for the assessment of risk to benthic habitats from bottom fishing activities using the test case of holothurians on the Chatham Rise

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TABLE OF CONTENTS

EXECUTIVE SUMMARY 1

1. INTRODUCTION 2

2. METHODS 2
   - 2.1 Data 3
   - 2.2 Indicator taxa approach 4
   - 2.3 Distribution modelling 4
   - 2.4 Impact calculations 5
   - 2.5 Spatial population modelling 5

3. RESULTS 6
   - 3.1 Distribution modelling using BRT 6
   - 3.2 Distribution modelling using VAST 7
   - 3.3 Fishing impact overlap 8
   - 3.4 Spatial population model 8

4. DISCUSSION 9
   - 4.1 Distribution modelling 9
   - 4.2 Fishing impact overlap 11
   - 4.3 Spatial population modelling 11

5. MANAGEMENT IMPLICATIONS 12

6. ACKNOWLEDGMENTS 12

7. REFERENCES 12

TABLES AND FIGURES 15

EXECUTIVE SUMMARY

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This study developed a method to assess risk to benthic habitats from fishing, using holothurians on the Chatham Rise as a case study. A spatial population distribution layer was developed. This layer and the bottom-contacting trawl footprint were then used in a Bayesian spatial population model to calculate the biomass trajectory and spatially and temporally explicit impact overlap statistics for the taxon. Species susceptibility was either assumed or estimated within the population model. The spatial population model tool can also be used to test the impact of alternative spatial management scenarios on the taxon. Further expanding this method to other indicator taxa will allow the management of risk at the community level.

Spatial distribution plots of holothurians were derived using two alternative methods: boosted regression trees which use environmental variables to derive distributions, or spatio-temporal analyses of univariate data which use correlates between space and time to derive distributions. Data used were trawl survey catches over the 2007–16 years, or deep-towed video camera counts from 2007 and 2017. Spatial delta generalised linear mixed models are expected to be more suitable for this application because they provide estimates of absolute biomass in each year data are available, subject to trawl catchability. Moreover, using camera-based counts might allow the estimation of trawl catchability for those species.

The biomass distributions developed were then used alongside spatial trawl footprint data to calculate three impact metrics: impact levels, impact overlap with the population, and trawl exposure. These metrics provide different pieces of information, with the impact overlap metric integrating the susceptibility of the taxon to trawling, the location of the impact, and the taxon biomass distribution. These impact metrics require assumptions about the susceptibility of the taxon to trawling, on trawl catchability, and / or on the biomass distribution of the taxon. The trawl footprint was split between fish / squid trawls or scampi trawls because they are expected to have different impacts on benthic taxa.

Developing a spatial population model required further knowledge than was needed to calculate the impact metrics, specifically in terms of taxon biology (e.g., growth, reproduction, and movement). A model was developed and was fitted to the biomass estimates developed using the spatial distribution models discussed above. The model allowed the investigation of alternative assumptions: we tested the impact of changing natural mortality, taxon susceptibility and trawl selectivity as well as movement hypotheses. Results showed that in this instance trawl selectivity had the biggest impact on the biomass trajectories. Although the data available were insufficient for the model to estimate the taxon susceptibility with any certainty, it was still useful to provide bounds on those parameters.

The quantitative method investigated showed potential usefulness for management in its current form. It is likely to be applicable to a range of taxa from data collected during the trawl surveys. For more cryptic taxa or in areas where no trawl survey data are available, further method development might be required, and a relative impact assessment might be achievable. Applying this method to a number of taxa (such as within a broad taxonomic group of those that constitute a habitat or community) might allow a holistic approach to benthic risk assessment and management.

1. INTRODUCTION

Quantitative methods currently used in Australia (Mazor et al. 2017) evaluate the benthic impacts of fishing at the species level (i.e., they are population-based assessments). For management purposes however, habitat-level impact and risk evaluation may be more relevant, with the additional advantage that it more realistically conveys community-scale complexities. One way to achieve this may be to quantitatively evaluate the risk of fishing impacts on indicator species. Indicator species are key biological elements of an ecosystem. Assessing fishing impacts on indicator species may serve to evaluate the fundamental condition of the environment without having to capture the full complexity of the system (Whitfield & Elliott 2002). Benthic indicator species may be defined as those taxa that are most responsive (and respond most negatively) to habitat disturbance (e.g., habitat-forming emergent taxa), so that changes in their individual abundance and distribution, and estimates of impact and risk due to fishing, will reflect changes at the scale of the habitat (e.g., Lundquist et al. 2013, Hewitt et al. 2014).

The aim of the project was to develop spatially-explicit quantitative methods to estimate fishing impact and risk on benthic indicator taxa. These methods include spatial distribution modelling, spatially explicit impact assessment, and spatial population dynamics modelling, and build on previous work carried out in New Zealand (e.g., Mormede & Dunn 2013). The scope of work focused on:

1) investigating spatial density estimation methods, here boosted regression trees (BRT) and spatio-temporal analysis of univariate data (using the package VAST) on a candidate indicator taxon and impact estimation (using both a reference impact and projection type approach); and
2) provision of recommendations for application to other candidate indicator taxa.

A case study of the Chatham Rise Area in depths of 250–1250 m (Figure 1) was developed using holothurians (class Holothuroidea) as the candidate indicator taxon.

2. METHODS

We define the following terms, noting that equations and descriptions of those parameters are further detailed in this section:

Catchability (q): The likelihood that a particular taxon occurring within the doorspread of the trawl will be retained by the fishing gear and retrieved on board the vessel. Catchability is only used to convert the trawl survey catches into absolute abundance distributions.

Fishing footprint (f): the area of the seafloor contacted by trawl gear during 1990–2016, using doorspread and trawl tracks, converted to a percentage footprint per cell and year.

Trawl exposure (Mazor et al. 2017): the product of a spatially explicit taxon biomass and a spatially explicit fishing footprint, expressed as a percentage of the total taxon biomass exposed (equation 3).

Vulnerability (V): the likelihood that a particular taxon occurring within the footprint will be fatally impacted or destroyed in a single fishing event (ranges 0 to 1).

Bottom fishing impact mortality (I): the product of taxon vulnerability and fishery footprint resulting in mortality, expressed as a percentage of the taxon biomass present at the site (equation 1).

Fishing impact overlap (I_o): the product of a spatially explicit taxon distribution (as a percentage of its total biomass) and spatially explicit bottom fishing impact mortality, yielding spatially explicit estimates of cumulative fisheries impact (equation 2).

Status: The spatially explicit proportion of the initial biomass remaining.

Risk: The consequences of impact at an ecosystem or population scale.

2.1 Data

A number of different datasets were prepared and considered for analyses: trawl survey data, fishery-dependent observer data, commercial fisheries effort (footprint) data, environmental data layers, video (deep towed imaging system or DTIS), and other fishery-independent research survey data. An initial look at the extent of the distributions of benthic invertebrates in the Chatham Rise study area (see Figure 1) from research trawl surveys and fishery-dependent observations (Figure 2 and Figure 3), resulted in the choice of holothurians as the test taxon for the methodology investigated here (see Section 2.2).

For BRT modelling, a dataset of holothurian presence data for the Chatham Rise study area (2007–2017) was collated from research trawl survey data (primarily from RV *Tangaroa)*; from biodiversity survey data; and from scientific observer data from commercial trawl effort. Although the data represent different sampling methods, the combination ensured that we had a large enough dataset to suit the requirements of BRT and to test the methodology. Data prior to 2007 were not used due to concerns about the potential variability in recording holothurians. Differences in reporting meant that 'presence' rather than weight or numbers was used as the measure of distribution. The 'presence' data were combined with a fuller dataset of sampling stations to provide a presence/absence dataset. This latter dataset included observer sampling effort from 2008–2010 when the observers were detailed specifically to collect benthic data from commercial trawling; the research trawl survey data from the Chatham Rise January trawl survey of over 20 years of data collection; from Chatham Rise biodiversity surveys since the 1950s; and from two recent biodiversity voyages (DTIS data from 2007 and 2017).

For VAST modelling, a dataset of holothurian biomass data collected between 2007 and 2017 on the RV *Tangaroa* surveys on the Chatham Rise was used. An alternative VAST model used the video survey (DTIS) data of two Chatham Rise surveys carried out in 2007 and 2017 (voyages TAN0705 and TAN1701). Preliminary analyses showed that in-situ and land-based post-processed data were not comparable. Therefore, only post-processed data of counts of individual holothurian sightings were used. Each tow was split in sections of 5 minutes length and treated as independent observations. We assumed an average towing speed of 0.5 m/s and 1.5 m frame width for the 2007 survey, and an average towing speed of 0.3 m/s and 3.2 m frame width for the 2017 survey (Bowden 2011, Bowden et al. 2017).

The fishery footprint data generated using the method described by Baird & Wood (2018) for the 1990–2016 fishing years were used for the trawl impact layer. This trawl footprint represents the area of the seafloor contacted by trawl gear during 1990–2016. This method used groomed, bottom-contacting trawl data within a spatially enabled database and applied a doorspread value (defined by the reported target species) to each trawl track (the straight line between the start and finish positions) to generate a swept area per tow. An overlay of these swept areas provided the footprint which is then summarised at the scale of a 5 × 5 km grid to provide both the area of the combined seafloor covered by the combined swept areas of all bottom-contacting trawls and the total number of tows with bottom contact in a cell. Note that tows generally contact a number of cells, as split by the 5-km cell grid, and that the maximum footprint area within a cell is 25 km^2, that is, 100% of the seafloor within a cell. Two sets of annual footprint data were generated: one representing bottom-contacting tows that targeted fish or squid species, and another for tows targeting scampi. The impact of scampi trawl gear on holothurians is expected to be different from that of trawl gear used for other species.

Environmental data were made available from earlier analyses undertaken to predict the preferred environmental space of some protected coral species in New Zealand (Tracey et al. 2011b, Baird et al. 2013, Anderson et al. 2014). The 'best' BRT model was then predicted over a 1 × 1 km grid of the relevant environmental predictors to produce a predicted distribution of the preferred environmental space for this set of holothurian species. The variables offered to the final model and their relevance to the species distribution are detailed in Table 1.

2.2 Indicator taxa approach

A number of benthic species or species groups were identified that could be used as candidate indicator taxa for the case study area and allow consideration of habitat level outcomes using the spatially explicit risk assessment methods developed in this project (Table 2). The list of suggested benthic indicator taxa was developed based on literature (Gordon 2009, Tracey et al. 2011a, Williams et al. 2014). The spatial distribution of samples for the groups of interest based on observed fishery records and all trawl survey records are shown in Figure 2 and Figure 3 respectively. Holothurians were chosen as a test case for developing risk assessment methods because there are more records of holothurians in the trawl survey database (relative to other taxa), they are distributed throughout the Chatham Rise, and they tend to be closely associated with soft substrate habitat with high organic content, which is the dominant substrate on Chatham Rise, and hence they may be representative of soft and productive soft sediment areas.

The class Holothuroidea comprises many diverse taxa and little is known of their biology. Expert advice provided by N. Davey, NIWA (pers. comm.) was used to identify holothurian genera or species that would be suitable for inclusion in this analysis (i.e., epibenthic holothurians and some swimming species that settle on the substrate to feed) (Table 3). Very little is known of the biology of holothurians, and the class comprises many diverse taxa (under 47 different possible species codes). The biological parameters used in this analysis are summarised in Table 4 and are based on expert knowledge (N. Davey, pers. comm.). Where possible, the impact of alternative parameter values was tested.

2.3 Distribution modelling

Two distribution modelling methods were carried out: Boosted Regression Trees (BRT) and spatio-temporal analysis of univariate data (spatial delta generalised linear mixed models) using the package VAST (Vector Autoregressive Spatio-Temporal model, Thorson & Barnett 2017).

Boosted Regression Tree (BRT) analyses were carried out using presence / absence data from fishery observer data and Chatham Rise trawl and biodiversity surveys to assess the probability of the presence of holothurians in the domain area. The final dataset was restricted to observations within the 250–1250 m study area shown in Figure 1. BRT uses recursive binary splits within a tree structure to explain the relationship between the response variable and the predictor variables, with ‘boosting’ improving the model performance through a combination of many simple models (Elith et al. 2008). The BRT models used a binomial error distribution (family Bernoulli) to predict the probability of occurrence of the taxon of interest. Analyses were conducted using the R statistical package and gbm libraries and functions (Ridgeway 2007, Elith et al. 2008, Leathwick et al. 2008, Elith & Leathwick 2013, R Core Team 2017). Two of the primary factors that control the BRT model fit – the ‘learning rate’ and the number of trees – were optimised within the model. The third factor, the number of interactions that determine a split (‘tree complexity’) was set to a moderate level of 3, where 1 is no interactions. The ‘best’ model was then applied to a 1 × 1 km grid of the relevant environmental predictors to produce a predicted distribution of the habitat suitability for this set of holothurian species. The variables offered to the final model and their relevance to the species distribution are detailed in Table 1; the full suite of variables tested are detailed in Table 5. Several models were run with different levels of interactions, and the best model chosen based on the AIC value (Akaike 1974). Where an environmental variable was shown to have no significant effect on the probability of presence of the taxon, it was not offered to the final model. All other settings not mentioned above were set at the default given in gbm (Ridgeway 2020).

VAST is specifically designed for survey data. It uses a delta-generalised linear mixed modelling framework which separately models the probability of having non-zero catches (likelihood of positive catches), and positive catch rates. VAST allows for spatial as well as temporal correlation in the models, vessel covariates, environment covariates, and may cater for a number of different model functions (e.g., lognormal, gamma, zero-adjusted negative binomial, etc). These options were investigated and the final model chosen based on the AIC value (Akaike 1974). As part of this project, VAST was applied to the annual January Chatham Rise trawl survey data from 2007 to 2016 (note that the survey became biennial in 2014 and so no survey was conducted in 2015), and video survey data from 2007 and 2017 as two separate models. VAST was further developed to allow for user-defined spatial projections so that the predictive modelling could be carried out in the same projection as the footprint. This required VAST to run in grid configuration (rather than the default mesh configuration) to align VAST predictions with the trawl footprint grid.

2.4 Impact calculations

The bottom fishing impact mortality I was calculated as the mortality from fishing at the cell level for each year:

$$I = 1 - \prod\nolimits_{tows}(1 - f_t \times V_F) \tag{1}$$

where f_t is the tow-by-tow footprint at time t, and V_F the vulnerability of holothurians per fishery type, assumed constant in time and space. The trawl footprint is available as the total footprint per cell and year (t_t) and the number of tows carried out in the same period. Therefore, the tow-by-tow footprint was assumed equal between tows in each cell and year and calculated as the total footprint for the cell and the year divided by the number of tows carried out in that same cell and year. For methods development, vulnerabilities were arbitrarily set to 0.1 for fish / squid tows and 0.8 for scampi tows (Table 4). These values were based on expert knowledge (N. Davey, pers. comm.).

The fishing impact overlap metric I_o was then calculated as the proportion of the total biomass impacted in each cell and year:

$$I_o = I \times \frac{B_t}{\sum_{cells} B_t} \tag{2}$$

Holothurian densities in space and time are required to calculate the impact overlap metric, with B_t the biomass in any given cell at time t. The annual density values predicted using VAST were used to calculate the annual impact overlap metric. An index of population impact was also calculated in each year, by summing the cell-based impact overlap metrics. These values could be compared with a reference F value if available.

Gear exposure was also calculated, following Mazor et al. (2017):

$$Exposure = \frac{\sum_{cells} B_t \times p_t}{\sum_{cells} B_t} \tag{3}$$

where p_t is the non-cumulative proportion of each cell impacted by fishing in any year, calculated assuming a random location of trawl within cells:

$$pf_t = 1 - e^{-t_t} \tag{4}$$

2.5 Spatial population modelling

An age-based Bayesian spatial population model of holothurians on the Chatham Rise was developed using the software SPM (Dunn et al. 2012). The SPM software was further developed for this project to allow a trawling mortality event, with a vulnerability parameter (estimable) and annually varying layers representing the trawl events for each fishery. In this instance, a single cumulative trawling footprint is provided to the model for each year and fishery, ignoring how many times the tows might have overlapped, which means that at this stage the impact is under-estimated. Future development of the software could include tow-by-tow footprint or accounting for the number of tows carried out to capture the exponential decay of the population with repeated tows.

The spatial resolution was 25 × 25 km cells, lined up with the grids of the trawl footprint data and identical to the resolution of the distribution models using VAST. Each cell was assumed independent, with no movement between cells. The alternative assumption of diffusive movements between cells was tested. The population model comprised ages 1 to 15 and a single class of mature animals. The biological parameters used in the model are described in Section 2.2 and summarised in Table 4. Recruitment was assumed local to each cell, with recruit initial distribution proportional to the biomass distribution in 2009 (because it was the highest biomass and the distribution was stable between years). The option of global recruitment was also tested, whereby the recruitment is distributed throughout the Chatham Rise, as might happen with broadcast spawners and ocean circulation.

The annual trawl footprint from 1990 to 2016 was used as input to the model driving bottom fishing impact mortality. The footprint was split between the two fisheries: scampi or fish / squid tows to allow for differing vulnerabilities to differing fishing gear, and input as a percentage impact on all holothurians present in the cell. For each year and cell, the trawl footprint value of each fishery was multiplied by the taxon vulnerability for that fishery to calculate the percentage mortality of holothurian in that cell. For example, if 20% of cell x was within the footprint of a scampi trawl in year y and the vulnerability of holothurians to scampi trawls was 0.8, then a bottom fishing impact mortality of 0.16 (0.8 * 0.2) was applied to holothurians in that cell and year.

The annual spatial biomass estimates from the VAST distribution modelling, including error values, were used as observations of holothurian biomass in space and time to which the model was fitted. As the distribution modelling was based on trawl data, a trawl catchability q was applied and assumed at 0.2. A generic process error of 30% was also applied above and over the annual cell-based error calculated by VAST.

The model was used as a simulator or as an estimator. As a simulator, the model estimated initial recruitment, and provided biomass trajectories given different assumptions on some of the critical parameters: vulnerability, catchability, and natural mortality. As an estimator, the two values of vulnerability for the two fishery groupings were estimated, and MPD profiles were carried out to evaluate the ability of the model to estimate those parameters.

3. RESULTS

3.1 Distribution modelling using BRT

A number of models were tested, using the Bernoulli distribution, at least 1000 trees, and a number of variables that were considered potentially of use and that were not highly correlated. The final model had a tree complexity of 3 and yielded an Area Under the Curve (AUC) of 0.79, with 19% of the deviance explained. Nine variables were offered to the final model, and the percentage contribution of each variable to the final model ranged between 6 and 16% (Table 6).

Figure 4 shows the predicted distribution (probability of occurrence) for holothurians, as indicated by the final BRT model, where areas in orange and red indicate most likely areas of suitable habitat, and those in green indicate areas of less suitable habitat. It further indicates areas where the predicted habitat has a lower probability, despite concentrations of positive holothurian samples, and vice versa. The coefficient of variation associated with the BRT predictions is presented in Figure 5.

Many of the models tested in this analysis had similar results in terms of the contribution of the main variables (i.e., those with the most contribution in each model), despite a range of different variables included for testing (Table 7). None of the substrate variables (percentage of sand, mud, gravel, rock) were included because they consistently contributed only a small amount to the overall result. When depth was included in some models, any variables highly correlated with depth were not offered to the model; similarly, when those variables were included, depth was excluded. Overall, the environmental variables considered had limited explanatory power in predicting the spatial occurrence of holothurians over the Chatham Rise.

3.2 Distribution modelling using VAST

Models using VAST were carried out with the trawl survey data only, or the DTIS data only. The optimised models (with the lowest AIC score) used a poisson-link delta model for presence-absence and lognormal model for the biomass. The addition of environmental covariates did not improve the fits to the data. We note that these choices did not change the predictions much, and model selection was based on the AIC value of the models (Table 8) and qq-plots (e.g. see Figure 10).

Distribution modelling using trawl survey data

The finest model resolution computationally achievable considering the available trawl survey data and related sampling design was a grid of 25 × 25 km; which was lined up with the trawl footprint 5 × 5 km grid. Although this was the finest possible grid resolution, the model fits were similar to those obtained using coarser grids; thus, it might be more suitable to use a coarser grid where fewer cells are derived from neighbours (with no data, see Figure 6). The trawl survey catchability was assumed constant through the years, which is a reasonable assumption considering that the same vessel and gear were used in all years. The model predicted the annual distribution of densities of holothurians for the survey years (Figure 7) as well as the CV of those densities (Figure 8). The total biomass over the surveyed years was relatively variable, but within the uncertainty (Figure 9). Fits to the data were adequate (Figure 10), and so was the distribution of data in the domain (Figure 11). The density and CV of density for each cell and year was independent of the number of samples in each cell and year (Figure 4). We note that no more than four samples were available per cell-year combination, and no more than 16 in each cell for all years combined.

A model without temporal correlates was carried out: the predictions in each year were independent of the predictions in the other years. This model performed very similarly to the base model, both in terms of AIC (Table 8) and biomass distribution, indicating that the survey could provide a biomass distribution of holothurians over time without extensive extrapolation between years. The robustness of the model to outliers was also tested by removing the few large outliers in the data. The AIC dropped considerably as expected (Table 8) but the predictions were identical, showing that the model was robust to outliers.

Distribution modelling using DTIS data

The finest model resolution computationally achievable with the video survey data was a grid of 50 × 50 km (at smaller scales the model failed to compute). This grid was lined up with the trawl footprint 5 × 5 km grid. The model predicted annual distribution of densities of holothurians for the two years in which a survey was available (Figure 12) as well as the CV of those densities (Figure 13). The total biomass increased multiple folds between 2007 and 2017 (Figure 14) despite taking into consideration the change in the size of sampling between the two years due to change in hardware. Fits to the data were adequate (not shown), and so was the distribution of data in the domain (Figure 15). The density and CV of density for each cell and year increased with the number of samples in each cell and year (Figure 16). We note that no more than seven samples were available per cell-year combination (Figure 16), and no more than 30 in each cell for all years combined. Each sample represents a five-minute recording of DTIS data.

Comparison between VAST predictions using DTIS or trawl survey data

The results from the VAST predictions using DTIS or trawl survey data were compared for 2007, the only overlapping year in this study. The predictions using the trawl survey data were aggregated to the

50 km × 50 km cells used for the predictions using DTIS data. DTIS data were provided in numbers and trawl survey data in kilograms. To make these comparable, an average holothurian weight of 250 g was used, based on data collected during the 2018 trawl survey (R. O'Driscoll, NIWA, pers. comm.). Results are presented as a distribution of the relationship, akin to a distribution of trawl survey catchability if one assumes the DTIS data have a 100% detection rate. In this case, the mean catchability of the trawl used onboard RV *Tangaroa* during the Chatham Rise surveys was estimated at 0.07 (Figure 17).

Comparison between BRT and VAST predictions

The predictions from the BRT model were averaged for each cell of the VAST model; and the predictions from the VAST model were averaged over all years predicted. We note that BRT predictions spanned from 0.004 to 1 as it predicts the probability of presence, and VAST predictions from 0.01 to 42 as it predicts the expected absolute abundance, although the averaging reduced the upper limits to approximately 0.75 and 1.7 respectively (Figure 18). The relationship between those mean values was found significant ($p^2 = 2e^{-11}$) with a slope of 1.88, whereby VAST predicted twice as high a density of holothurians as BRT. This difference is likely to be due to the assumption that the probability of presence calculated using BRT is proportional to the density. Moreover, the scatter plot suggested that the relationship is likely to be driven by a relatively small number of large values rather than the bulk of the data (Figure 18).

3.3 Fishing impact overlap

The fishing impact overlap is defined as the product of the bottom fishing impact mortality and the percentage of biomass present in each cell (equations 1 and 2). Therefore, the impact overlap is insensitive to the trawl catchability assumption made when calculating the biomass distribution. The estimates obtained by VAST using the trawl survey data were used. The impact overlap is also determined by the values of vulnerability used for the two fisheries, assumed here 0.8 for the fishery targeting scampi and 0.1 for all bottom trawl fisheries targeting any fish or squid. As such, the impact overlap presented is only for illustration purposes as a relative index.

The spatial and temporal fishing impact overlap for each fishery is shown in Figure 19 and Figure 20; and for both fisheries combined in Figure 21. The trend in time is summarised in Figure 22. Results show that the higher-level effects are mostly localised and driven by the scampi fishery, as expected with such a high vulnerability of holothurians to the scampi trawl gear. The total impact over time has remained steady in the last eight years.

Trawl exposure (Mazor et al. 2017) is defined as the product of the taxon abundance and the trawled proportion for each cell, summed over all cells and divided by the total taxon biomass (equation 3). The trend in trawl exposure in time is shown in Figure 23. Results show that the exposure to the scampi fishery is low compared with that of fish / squid fishery. The exposure index doesn't take into consideration the differences in vulnerability between the two fisheries, but it can show a trend in the exposure to each fishery over time.

3.4 Spatial population model

Summaries of the model runs and their outcome including negative log likelihoods are detailed in Table 9. The best fits were obtained using a model with local recruitment (independent between cells) and with no diffusion movement between cells (models R1, R2, R5, and R5.1). When diffusion was estimated within the model, a diffusion close to zero was estimated (model R5). The best fits were obtained for 2009 and 2012 onwards, with both over- and under-estimations in the other years (Figure 24).

This simulation model was used to investigate the effect of changing the vulnerability of holothurians to the two types of fishing gear, and of different values of catchability and natural mortality (Table 9 and Figure 25). In each case the initial recruitment was re-estimated within the model to fit to the biomass data. Increasing the vulnerability of holothurians to the scampi fishery from 0.1 to 0.9 reduced the current biomass by less than 5 percentage points with a much worse fit to the data (models R2 and R2.1). Increasing natural mortality from 0.3 to 0.5 also had only limited impact on the biomass trajectory but improved the fit to the data (model R4.1). Estimating natural mortality within the model provided a value of 0.68 (model R6.2). On the other hand, changing the trawl catchability from 0.2 to 0.5 had a dramatic impact on the predictions since trawl catchability is a direct scalar to biomass estimates fitted in the model and therefore initial biomass. We note that this high value is highly unlikely because the negative log likelihood increased dramatically (model R3.1), and an external estimate using VAST models comparing trawl and camera data was only about 0.07 (Figure 17).

The spatial population model developed was also used to estimate the vulnerability of holothurians to trawling for the two fisheries included in the model (model R2.2, R3.2, and R4.2). The ability of the model to estimate those parameters was tested by running an MPD profile on these two parameters. Results show that these parameters were poorly estimated, but unlikely to have values over 0.13 for fish tows and 0.3 for scampi tows (Figure 26). These two parameters were independently estimated from each other, in that the value estimated for the second parameter was constant regardless of the value fixed for the parameter of interest (not shown). Bayesian estimations of these parameters were attempted, however the MCMC chains quickly settled to local minima, and each new MCMC chain run settled at different values. These values were consistent with the MPD profile, with values for vulnerability to fish trawls between 0.06 and 0.17, and values for vulnerability to scampi trawls between 0.10 and 0.18.

A final model was carried out bringing together the optimum parameter values at this stage of the process: a survey trawl catchability of 0.07, natural mortality estimated at 0.68, and holothurian vulnerabilities of 0.15 for fish and squid gear and 0.3 for scampi gear. The total biomass trajectory presents the least depletion over time of the scenarios tested (Figure 25, right panel), but the model still presents high levels of localised depletion (Figure 27).

4. DISCUSSION

Progress was made in the development of spatially-explicit quantitative methods for the assessment of benthic impacts from bottom-contact fishing activities using an indicator species approach. Method development and testing were implemented in a case study example focusing on New Zealand's Chatham Rise fishery ecosystem and holothurians as a candidate indicator taxon. Two spatially-explicit population distribution modelling methods were investigated and compared, and the results combined with an aggregated fishing footprint to create overlap metrics. Spatial population models were developed to evaluate the effect of the assumptions on the biomass trajectory, and these can be used to evaluate the levels of localised depletion and management scenarios in the future.

4.1 Distribution modelling

Any characterisation of a species distribution is determined by the quantity and quality of the available data, including the extent of the sampling effort. Two types of distribution modelling methods were tested: BRT, a random-forest type method, and VAST, a mixed-modelling method. The predictions from both methods provided roughly similar distributions over the Chatham Rise and both can provide estimates of variance which can be propagated to the spatial population modelling. They have quite distinct advantages and disadvantages.

BRT is highly data intensive, and therefore the trawl survey and fishery-dependent observer data from all years had to be pooled to provide a single distribution representative of the distribution of the taxon over that period of time. This approach relies on the implicit assumption that species distribution was constant over the time scale of our observations, and that the probability of occurrence indexes abundance. On the other hand, predictions were made at a finer spatial resolution corresponding to the scale of the environmental variables, 1 km^2 in this instance. But the precision of BRT is likely to be misleading. BRT modelling assumes that there is a relationship between the environmental data and the distribution of the taxa involved, therefore predictions could be made in areas where no or little biological data were available. Furthermore, it represents potential suitable habitat rather than realised habitat. Although this can be advantageous for species where data are spatially limited, it also means spurious results can be obtained, as shown in some differences between BRT and VAST outputs, or when model outputs were then ground-truthed (e.g., Anderson et al. 2016). This may be related to the time-varying nature of the relationships between environmental variables and species occurrence for example, which is not considered in the model structure. In the case of holothurians, the environmental variables considered explained only a small fraction of the modelled probability of occurrence on the Chatham Rise. This suggests that other factors not considered in this study might determine the probability of occurrence for the species group, or that the distribution of holothurians is only loosely related to environmental drivers. Alternatively, the use of a species group may have masked species-specific environmental relationships affecting occurrence and distribution. We note that BRT may also provide a relative index of abundance, in which case any impact assessment using BRT outputs will be itself relative.

VAST provides a direct scale-up of the survey data collected and does not require the assumption of a relationship between the taxa distribution and the environment (although environmental covariates can be added). As a result, VAST should be used to predict distributions outside of the area where data are available with extreme caution. On the other hand, this method may be used to test the assumption of constant distribution over time, and to relax any assumptions of realised spatial distributions being determined by temporally consistent environmental forcing. VAST models can assume a spatial correlation, temporal correlation, or both. In this instance, removing the temporal correlation did not change the outputs significantly to the model using trawl survey data, which indicates that the survey itself has been capturing holothurian distribution consistently over time. This result gives us confidence that the survey data can be used to estimate and monitor holothurian distribution, despite not being designed for holothurians. On the other hand, VAST is also data and computationally intensive, which results in coarser predictions, at 25 × 25 km squares in this instance. The main advantages of VAST over BRT for this application are that: 1) VAST can provide annual biomass distributions when data are available; and 2) VAST provides absolute biomass values (dependent on the trawl survey catchability of course). Another advantage not yet considered is that VAST can be run on multiple species simultaneously. Multispecies applications make it possible to assess the strength of inter-specific correlations in space and time, which may serve to define or refine species groups or species assemblages for use as candidate indicator taxa. The principal disadvantage of VAST is that it usually relies on fisheries-independent survey data and its use is limited to the survey area. Expanding to fisheries-dependent data would require careful investigations. Further investigation of the models and optimisation of settings will be required, in particular with regards to the size of the cells and quantity of data in each cell driving the predictions. Note that the difference in the estimated biomass between 2007–2008 and the 2009–2016 period may be an artefact of differences in sampling linked to improved taxonomic resolution and sampling of the entire catch since 2009–2010.

We recommend that VAST is better adapted than BRT to provide biomass distribution layers for quantitative assessment of benthic impacts as proposed here, as long as sufficient data are available. When predictions outside of the surveyed areas are required, BRT is an alternative that might allow a relative impact assessment to be carried out. Other methods in development might provide alternative options for predictive modelling in the future.

Comparing the results of models using either trawl survey data or DTIS data has the potential to provide estimates of trawl survey catchability (including a distribution of the likely catchability) that can be propagated to the spatial population modelling. Assumptions had to be made in this instance to convert numbers to weights. The scale of the observations is also very different: from a trawl of 0.4 km^2 swept area or more, to a DTIS five-minute segment with a 0.0003 km^2 swept area. We speculate that should a suitable estimation of holothurian size from DTIS data or of holothurian numbers and length-weight relationships from trawl survey data be possible, VAST might be able to estimate a distribution of potential trawl catchability if we assume DTIS catchability is one (we see and record all animals present). Future recording of holothurians in numbers as well as weights during trawl surveys, and the construction of a length-weight relationship for these taxa, might provide data required to refine such analysis.

4.2 Fishing impact overlap

Given a fishing footprint, taxon vulnerability to fishing, and taxon biomass distribution, a fishing overlap metric can be calculated in space and time for the taxon of interest. The fishing impact calculation is straight forward and can be compared to a reference *F* to evaluate the cumulative impact of fishing activities on benthic indicator taxa, with some measure of uncertainty. The development of reference *F* levels for benthic taxa however, remains challenging and subject to methods development. A better option may be to develop acceptable thresholds for fishing impact overlap in space. Impact overlap allows managers to map the extent and magnitude of fishing impact in space and time, identify hotspots of impact by fishery groups, and trends of impact with time (provided biomass distributions are available in time). Quantitative impact mapping does not require population structure assumptions, which have yet to be demonstrated for benthic taxa, and at this stage remain unsupported by data.

However, the scale of the impact calculation is driven by taxon vulnerability to the various trawling activities, values which are usually expert-based and difficult to quantify. Methods based on functional traits and re-sampling of the available biological information in time and space are worth investigating to inform vulnerability. Bycatch composition and trends in observer data from different fishing activities also carry information that might be useful in this context. If biomass is available through time, then the change in the fishing impact over time can be a useful management tool in itself, especially if the association between the indicator taxa and a specific habitat type can be demonstrated and used to infer habitat-level impacts and acceptable impact thresholds.

Other metrics such as the fishing impact or the trawl exposure can also be computed and provide different information which might be complimentary to the fishing impact overlap. However, those two metrics do not include all the parameters such as taxon biomass distribution (fishing impact) or taxon vulnerability (trawl exposure).

4.3 Spatial population modelling

Spatial population modelling was successful in providing alternative biomass trajectories given a range of assumptions, and for providing spatial plots of the levels of localised depletion. We showed that trawl survey catchability had the strongest influence on the potential impact of fishing on the taxon of interest, as the results from the spatial distribution modelling anchors the biomass trajectory in that time-frame. The data available were not sufficient in this instance to estimate taxon vulnerability accurately within the spatial population model. However, the model provided likely upper bounds to those values (0.13 and 0.3 for fish / squid and scampi fisheries respectively). We note that further assumptions had to be made in the spatial population model, mostly pertaining to biological characteristics of the taxon of interest (growth, reproduction, movement, etc.). The optimised model given the assumptions showed a low level of depletion at the stock level, but high levels of localised depletion. We note those values are under-estimated as the method currently doesn’t consider the number of times the footprint might have been impacted.

Spatial population models could also be developed for multiple species in a predictive capacity to investigate the effect of alternative management plans over an ensemble of species.

5. MANAGEMENT IMPLICATIONS

The quantitative method investigated showed potential usefulness for management in its current form. It is likely to be applicable to a range of taxa where data were collected during the trawl surveys. For rare taxa or in areas where no trawl survey data are available, further method development might be required, and a relative impact might be achievable. Applying this method to a number of taxa might allow a more holistic and reliable approach to quantifying habitat-level benthic impacts, and effectively managing the risk from fishing activities to benthic communities. A multi-indicator approach would serve to integrate the idea that benthic community integrity is a determinant of benthic ecosystem function, and that community-level impact monitoring will ensure effective conservation and management of benthic habitats (Hewitt et al. 2011, Lundquist et al. 2013, Hewitt et al. 2014).

We recommend the method and inputs be further developed. In particular:

- Fishing footprint be extrapolated in the years prior to 1990 to obtain a full time-series, or simulations carried out using the spatial population model to ascertain the impact of ignoring the footprint prior to 1990.
- Biological data be collected and life and functional traits characteristics be investigated for taxa of interest, and vulnerability of those to various fisheries be developed in conjunction with model estimates.
- The SPM modelling platform developed further to allow trawling impact using multiple tow.
- Investigate means to better estimate trawl catchability. It might be achievable using trawl survey and DTIS data in a single VAST model for each taxon. For holothurians it would require further data collection and / or analysis to convert DTIS and / or trawl surveys to a single unit (biomass or numbers). For species where numbers were collected on trawl surveys, VAST might allow this calculation directly, with uncertainty. Other methods might be possible.
- The same approach be applied to the other taxa of interest. We note that the spatial distribution modelling using VAST offers the potential to estimate the distribution of multiple species concurrently, drawing on the information of more common species to infer that of less common species. SPM can model multiple species at once, including interactions between species if suitable, to show the results of alternative management scenarios at once for all species.
- For further management purposes, reference *F* values could be developed, and alternative management scenarios can be tested. A multi-species approach should also be developed to integrate the results from multiple taxa together.

6. ACKNOWLEDGMENTS

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TABLES AND FIGURES

Table 1: Brief description of the final environmental data variables included in the BRT model, and their relevance (after Tracey et al. 2011).

Variable	Relevance
cdom	Dissolved organic matter: measure of food availability
depth	Depth: measure or changes in variables such as salinity, temperature, pressure, and nutrients
dynoc	Dynamic topography: Relative sea surface height (proxy for surface current velocity)
poc	Particulate organic carbon flux: measure of food availability
slope	Sea floor slope (degrees) derived from bathymetry: may indicate more localised processes, especially water flow, food supply, and sedimentation, as well as being a rough proxy for substrate
sstgrad	SST gradient: location of frontal zones where primary productivity can be concentrated/particulate matter flux enhanced, and which may provide barriers to larval dispersal
tempres	Residuals from the GLM relating bottom water temperatures to depth: influences on physiological processes such as reproduction and dispersal potential
tidal	Tidal current speed: maximum depth-averaged tidal current speed that indicates areas of current flow
vgpm	Vertically-generalised productivity model: measure of potential food source

Table 2: Initial list of potential benthic indicator taxa for the Chatham Rise study area.

Species or species group		Habitat association	Functional type (living position, mobility, feeding, size)
Solenosmilia variabilis	Coral	Hard substrata, deeper, small hills, habitat-forming	Erect, sessile, suspension, large
Goniocorella dumosa	Coral	Hard substrata, shallower, habitat-forming	Erect, sessile, suspension, small / medium
Hyalascus n. sp.	Sponge	Soft sediment, shallower	Erect, sessile, filter, large
Pennatulacea spp.	Seapens	Soft sediment	Erect, sessile, suspension, small / medium
Echinoidea spp.	Sea urchins	Soft sediment	Surface, mobile, deposit / grazer, small / medium
Holothuroidea spp.	Sea cucumbers	Soft sediment, more productive sediments	Surface, mobile, deposit, small / medium

Table 3: List of holothurian taxa identified as present in the holothurian dataset. These taxa are all considered to live on the substrate, or at least feed from the substrate surface; none are thought to live in the substrate sediment.

Currently known taxonomy	Taxon
C. Holothuroidea	O. Holothuriidae
C. Holothuroidea	C. Holothuroidea
O. Dendrochirotida, F. Cucumariidae	*Neoamphicyclus*
O. Dendrochirotida, F. Cucumariidae	*Neocucumella*
O. Dendrochirotida, F. Cucumariidae	*Plesiocolochirus ignavus*
O. Dendrochirotida, F. Phyllophoridae	*Neothyonidium armatum*
O. Dendrochirotida, F. Phyllophoridae	*Pentadactyla longidentis*
O. Dendrochirotida	F. Psolidae
O. Dendrochirotida, F. Psolidae	*Psolus*
O. Dendrochirotida, F. Psolidae	*Psolus antarcticus*
O. Dendrochirotida, F. Psolidae	*Psolus squamatus segregatus*
O. Elasipodida	*Enypniastes eximia*
O. Elasipodida	F. Laetmogonidae
O. Elasipodida, F. Laetmogonidae	*Laetmogone*
O. Elasipodida, F. Laetmogonidae	*Laetmogone violacea*
O. Elasipodida, F. Laetmogonidae	*Pannychia*
O. Elasipodida, F. Laetmogonidae	*Pannychia moseleyi*
O. Elasipodida	F. Psychropotidae
O. Holothuriida, F. Mesothuriidae	*Zygothuria*
O. Holothuriida, F. Mesothuriidae	*Zygothuria lactea*
O. Molpadida, F. Caudinidae	*Paracaudina alta*
O. Molpadida, F. Caudinidae	*Paracaudina chilensis*
O. Persiculida, F. Pseudostichopodidae	*Pseudostichopus*
O. Persiculida, F. Pseudostichopodidae	*Pseudostichopus mollis*
O. Persiculida, F. Pseudostichopodidae	*Pseudostichopus peripatus*
O. Synallactida, F. Synallactidae	*Bathyplotes*
O. Synallactida, F. Synallactidae	*Bathyplotes moseleyi*
O. Synallactida, F. Synallactidae	*Bathyplotes sulcatus*

Table 4: Biological parameters used for the class Holothuroidea.

Function	Parameter name	Value used
Age-length parameters	L_{inf}	100 mm
	k	0.3
	t_0	0
Length-weight parameters	a	1
	b	3
Natural mortality	M	0.3
Fishing vulnerability	V_{fish} for fish tows	0.1
	V_{scampi} for scampi tows	0.8
Beverton-Holt recruitment	h	0.75

Table 5: Brief description of the environmental data variables offered to the BRT model.

Variable	Description
aou	Apparent oxygen utilisation
arag	Aragonite saturation state
botni	Bottom nitrate
boto2sat	Bottom saturated O_2
botoxy	Bottom oxygen concentration
botpho	Bottom phosphate
botsal	Bottom salinity
botsil	Bottom silicate
botspd	Bottom current
bottemp	Bottom temperature
calc	Calcite saturation
cdom	Colour dissolved organic matter
depth	Bathymetry
disorgm	Dissolved organic matter
domnc	Dominant sediment type
dynoc	Dynamic topography
gravelrf	Proportion of gravel
midlat	Latitude of cell midpoint
midlon	Longitude of cell midpoint
mudrf	Proportion of mud
poc	Particulate organic carbon flux
rockrf	Proportion of rock
sandrf	Proportion of sand
slope	Slope derived from bathymetry
smt	0 = not on an underwater feature (UTF); 1 = on an UTF
sstgrad	Sea surface temperature gradient
tempres	Bottom temperature residuals
tidal	Tidal current strength
vgpm	Primary productivity

Table 6: The contribution of each environmental variable offered to the model of family Bernoulli, using a tree complexity of 3, and over 1000 trees. The result had an AUC of 0.79 and 19% deviance explained. See Table 1 for description of the variables.

Variable	vgpm	dynoc	tempres	tidal	depth	cdom	sstgrad	poc	slope
% contribution	16.38	14.78	13.55	12.00	10.91	9.88	9.70	6.43	6.36

Table 7: A small sample of BRT model outputs from a pared-down set of environmental variables where those that were confounded or contributed less than 3% were ignored in later runs. All models required at least 1000 trees and several different interaction levels were tested for each set of variables. The variables are listed in alphabetical order.

Model	Interactions	Variables	Deviance (% explained)	AUC
M1	2	botoxy,botsal,botspd,bottemp,disorgm,dynoc,sstgrad, tidal,vgpm	18	0.76
M2	2	botni,botsil,botsal,bottemp,calc,cdom,disorgm,dynoc, poc,sstgrad,tidal,vgpm	17	0.73
M3	5	cdom,depth,dynoc,poc,slope,smt,sstgrad,tempres, tidal,vgpm	19	0.79
M4	5	botoxy,botsal,botspd,bottemp,disorgm,dynoc,sstgrad, tidal,vgpm	19	0.78
M5	3	cdom,depth,dynoc,poc,slope,sstgrad,tempres, tidal,vgpm	19	0.79

Table 8: Summary of models carried out with VAST and their AIC value used for model selection.

Model	Presence – absence model	Abundance modelling	Other attributes	AIC
R1	Mixed effect	Lognormal		1 909
R2	Poisson link	Lognormal		1 892
R3 (base)	Poisson link	Gamma		1 860
R4	Poisson link	Gamma	No temporal correlation	1 868
R5	Poisson link	Gamma	Exclude outliers	1 760

Table 9: Summary of the spatial population models, parameters, and their negative log likelihood (NLL) value used for model selection. ** denotes the negative log likelihood is not comparable to other values.

		Estimated (* is not estimated)					Fixed	
		R_0	Vf_{ish}	V_{scampi}	diffusion	NLL	q	M
TESTING RECRUITMENT AND DIFFUSION								
R1	global recruitment	$48.6\ e^{6}$	0.01	0.00	–	-2 117**	0.2	0.3
R2	local recruitment	600	0.08	0.12	–	245	0.2	0.3
R5	R2 with diffusion	591	0.08	0.14	0.0001	245	0.2	0.3
R5.1	R5 fix diffusion at 0.5	120	0.00	0.30	0.5*	23 224	0.2	0.3
SIMULATION								
R2.1	effect of U, only estimate R_0	655	0.1*	0.9*	–	24 575	0.2	0.3
R3.1	effect of q, only estimate R_0	531	0.1*	0.9*	–	338 419	0.5	0.3
R4.1	effect of M, only estimate R_0	1 656	0.1*	0.9*	–	18 279	0.2	0.5
ESTIMATION								
R2	local recruitment	600	0.08	0.12	–	245	0.2	0.3
R3.2	check effect of q	143	0.01	0.57	–	5 595	0.5	0.3
R4.2	check effect of M	1 104	0.02	0.29	–	-1 796	0.2	0.5
OPTIMISED MODEL								
R6.2	Local recruitment	36 383	0.15*	0.30*	–	–1 857	0.07	0.68

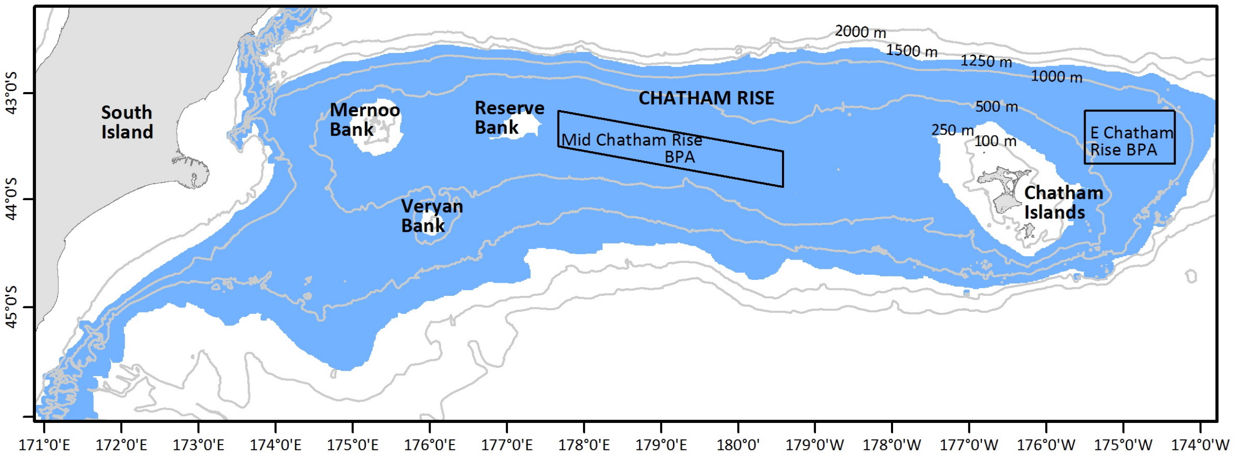


Figure 1: Location of the main topographic features of the Chatham Rise that extends east of the South Island, to depths of at least 2000 m. The blue area denotes the area covered by 1-km cells that are within the 250–1250 m study area (n = 231 471 cells). The black rectangles show the location of Benthic Protection Areas (BPA) created as no-bottom trawl zones in 2007 (www.mpi.govt.nz).

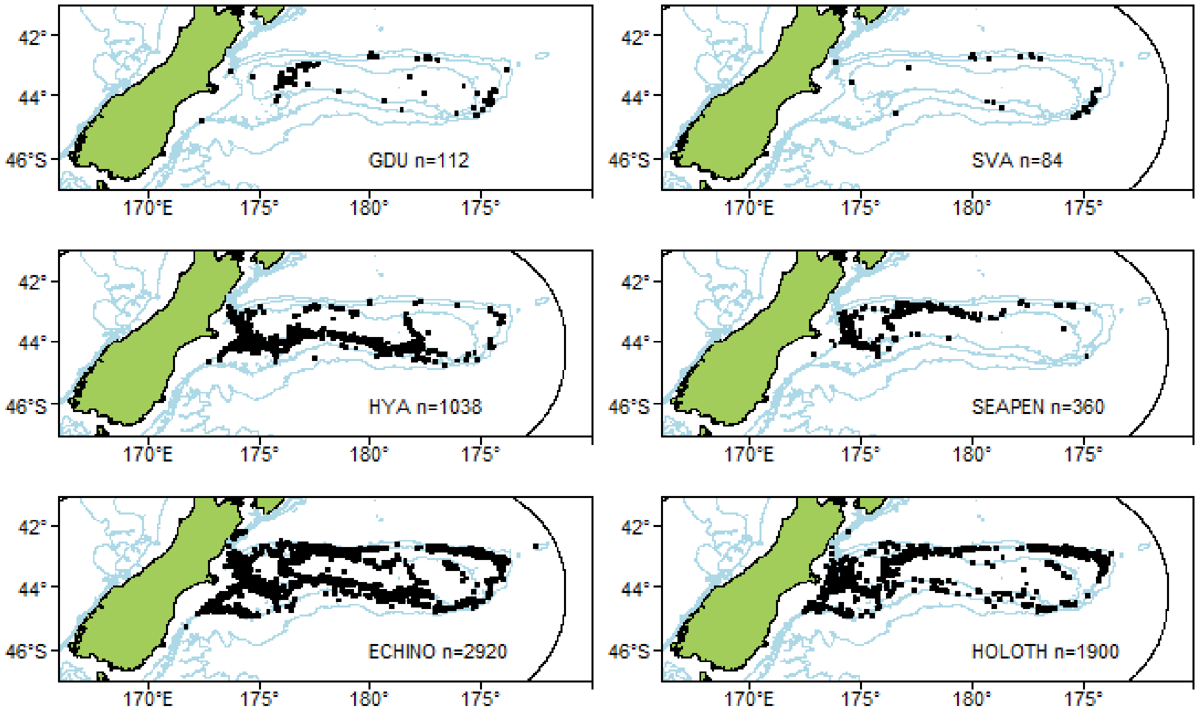


Figure 2: Locations of start positions of observed fishing events with records of invertebrate bycatch, for fishing years 1997–2017. Species represented are *Goniocorella dumosa* (GNU), *Solenosmilia variabilis* (SVA), *Hyalascus* sp. (HYA), seapen, echinoderms (ECHINO), and holothurians (HOLOTH).

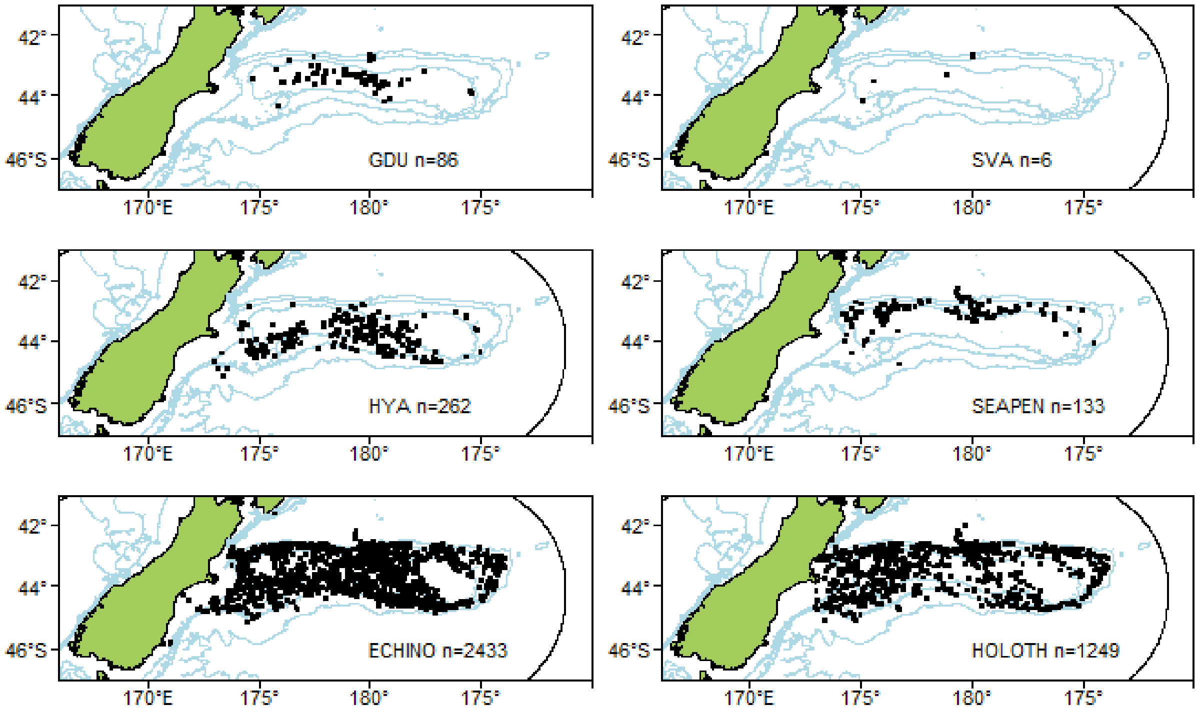


Figure 3: Locations of start positions of trawl survey tows with records of invertebrate bycatch, for fishing years 1973–2017. Species represented are *Goniocorella dumosa* (GNU), *Solenosmilia variabilis* (SVA), *Hyalascus* sp. (HYA), seapen, echinoderms (ECHINO), and holothurians (HOLOTH).

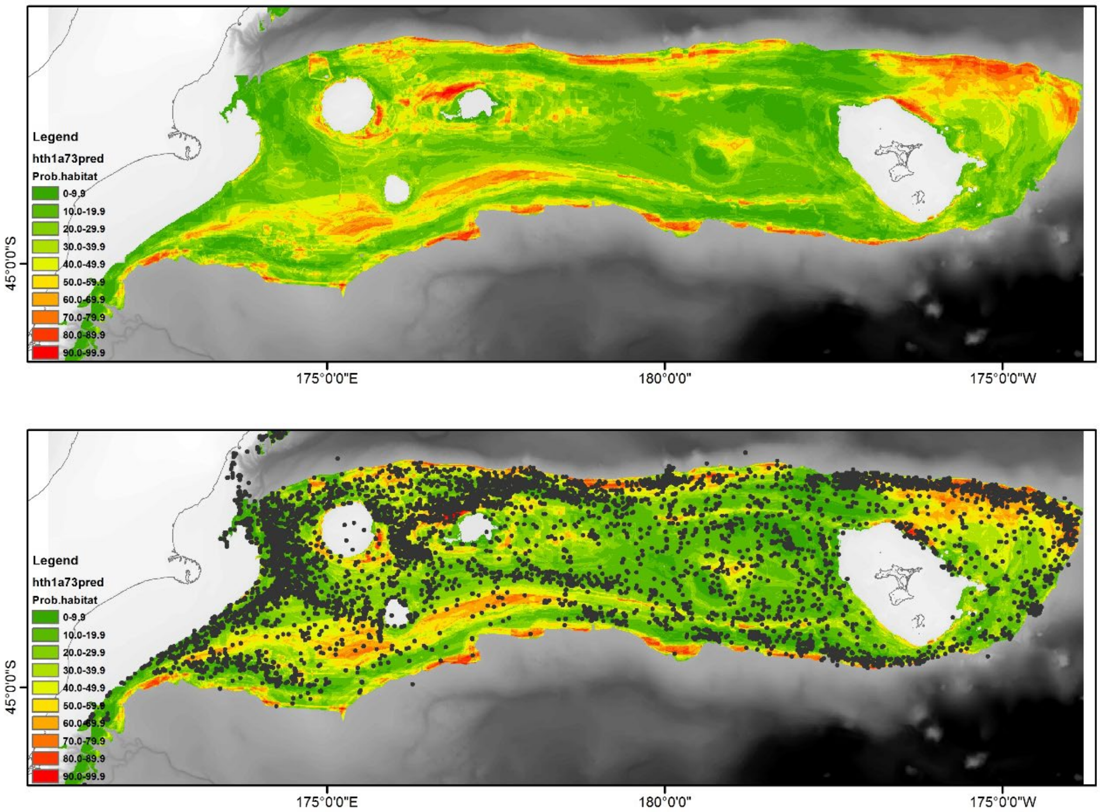


Figure 4: **The final predicted distribution of environmental space or suitable habitat for surface-dwelling holothurians, as indicated by the BRT model (upper) and the predicted distribution overlaid with the points indicating samples where holothurians were present (lower).**

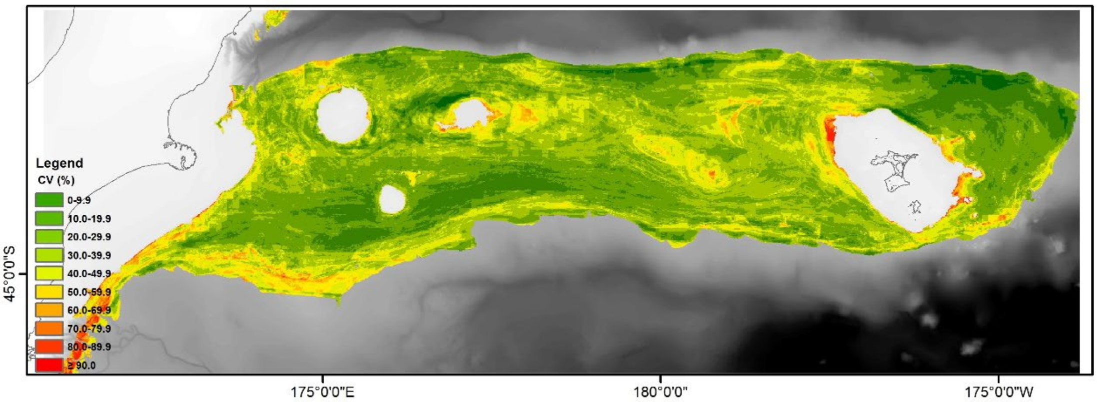
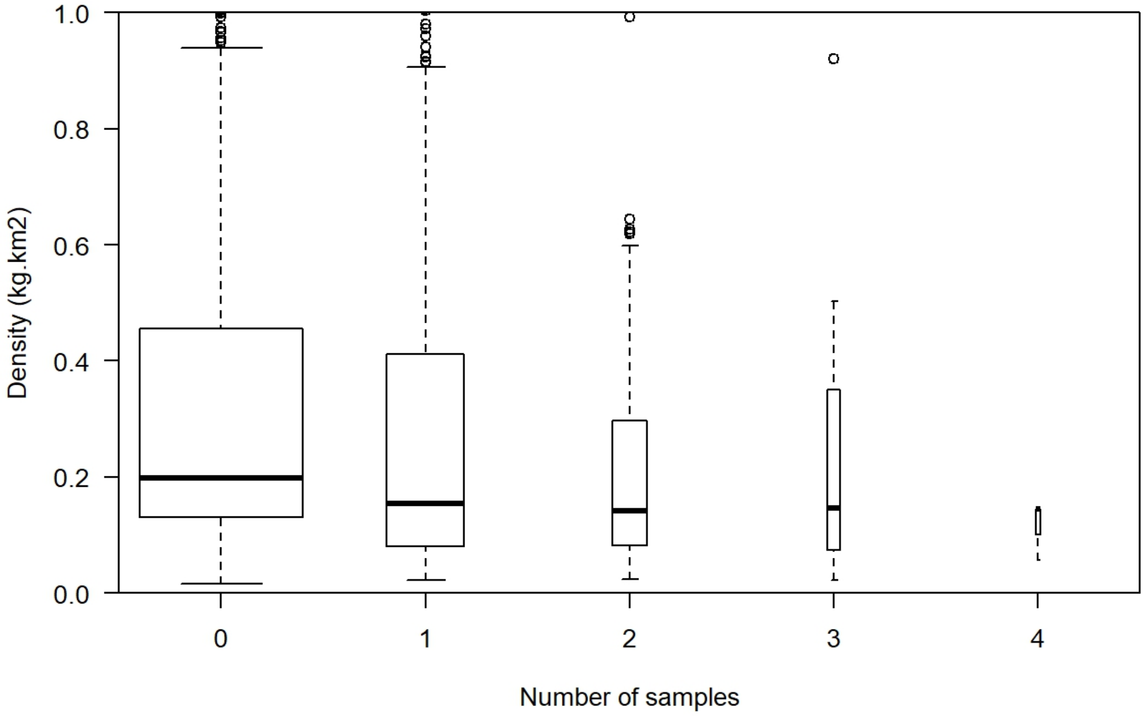


Figure 5: **The CV of the final predicted distribution of environmental space or suitable habitat for surface-dwelling holothurians, as indicated by the BRT model.**



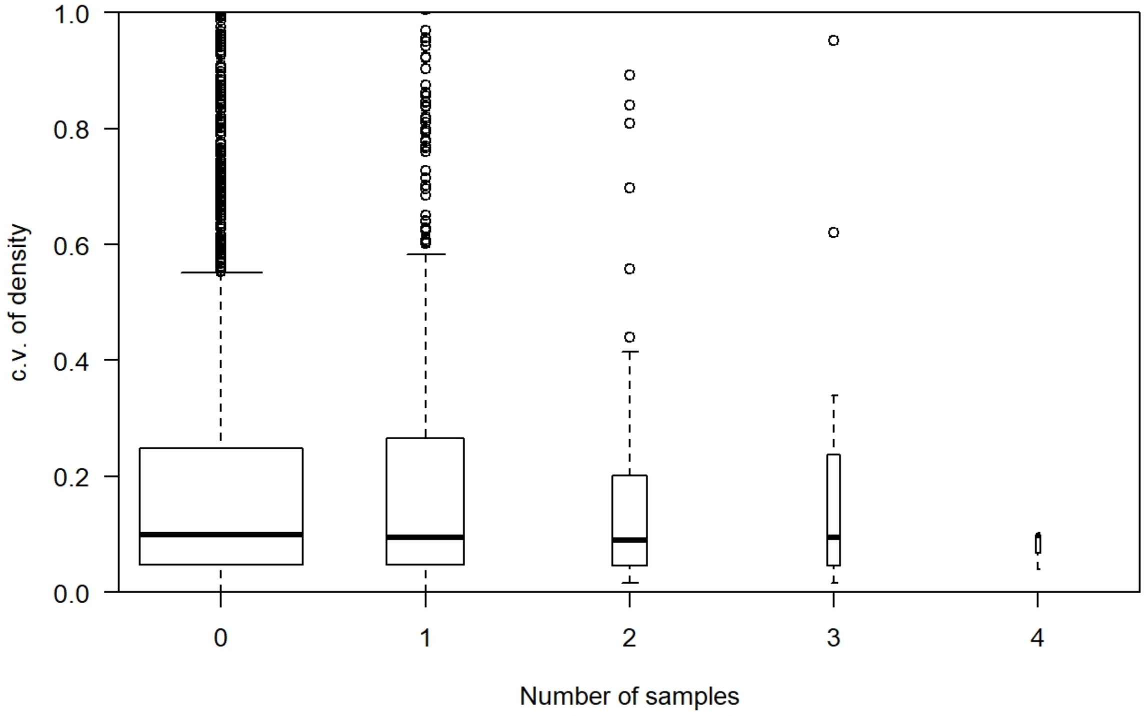


Figure 6: **Density estimates and CV of density estimates by number of samples in each cell and year combination for the model using survey data. The width of the bars are proportional to the square root of the number of observations.**

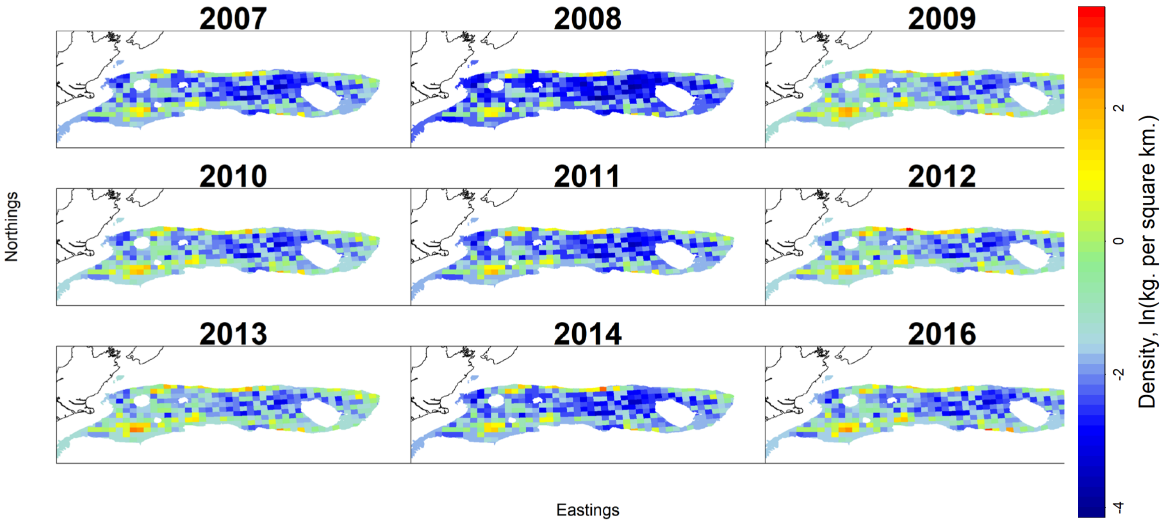


Figure 7: Densities of holothurians as predicted by VAST using trawl survey data.

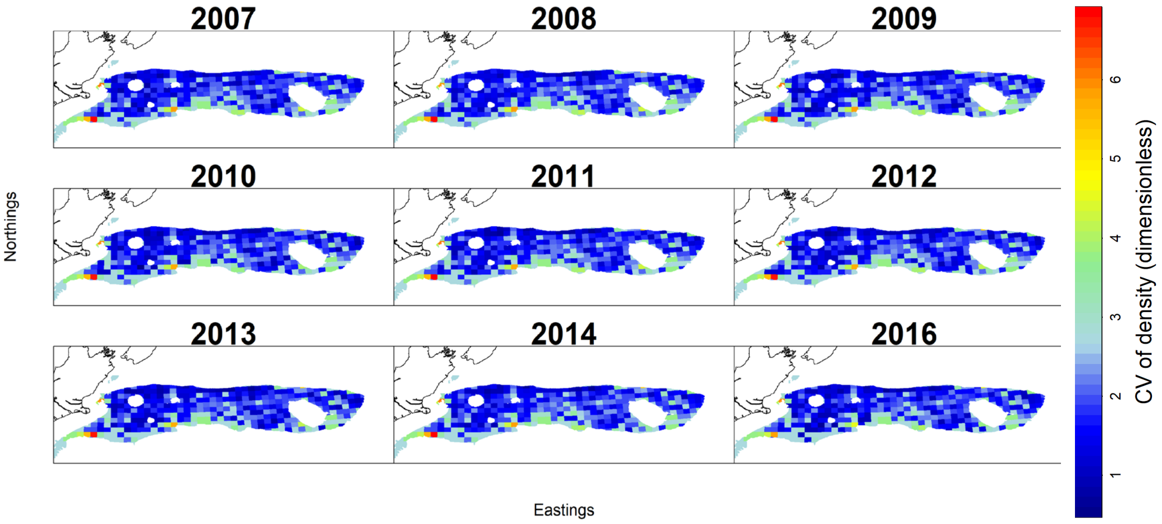


Figure 8: CV of densities of holothurians as predicted by VAST using trawl survey data.

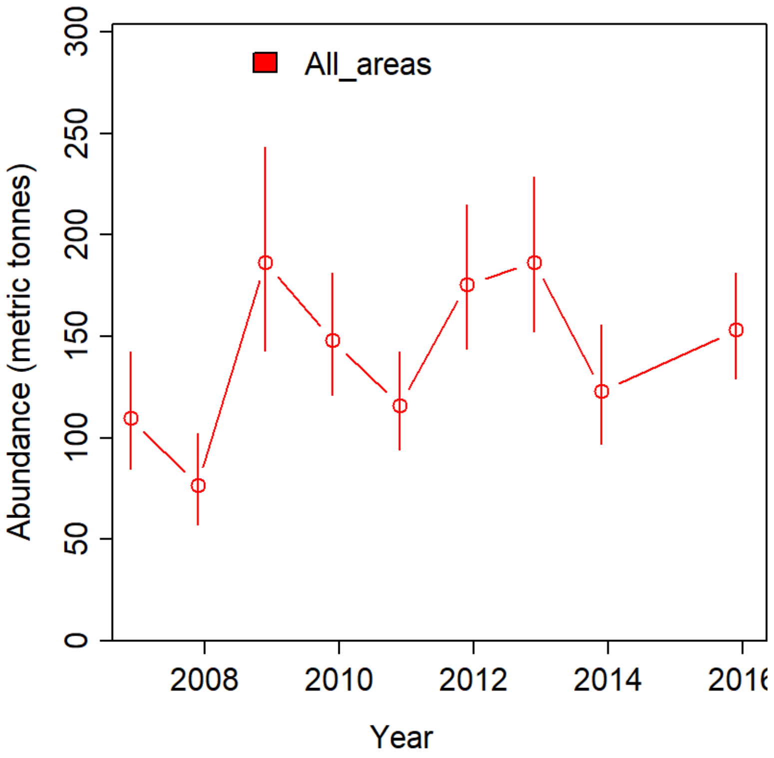


Figure 9: Biomass trend of holothurians over the entire Chatham Rise as predicted by VAST using trawl survey data. Note the abundance is relative to catchability, assumed 1 here.

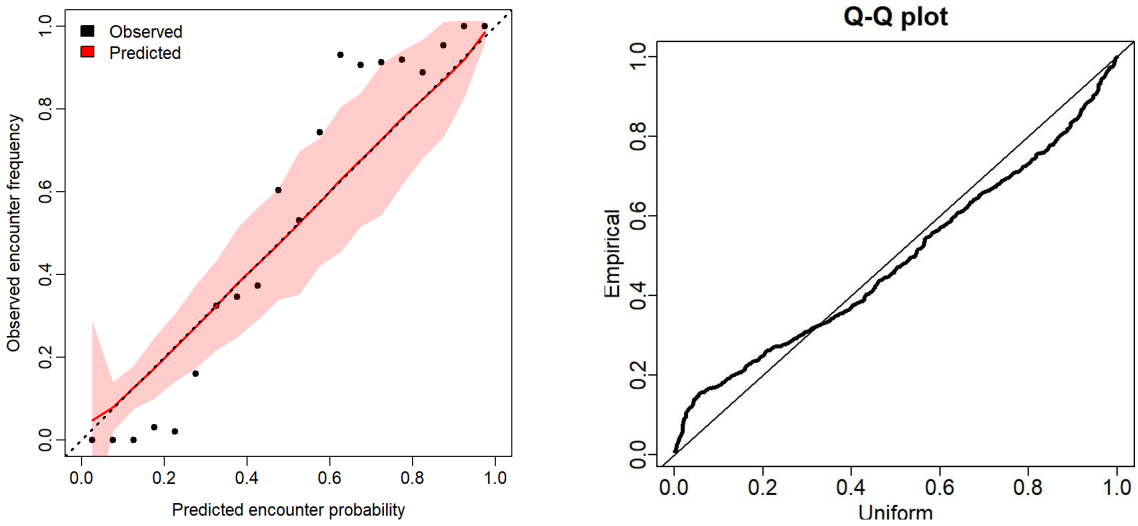


Figure 10: Model diagnostics for the VAST model using trawl survey data, probability of presence on the left and abundance on the right.

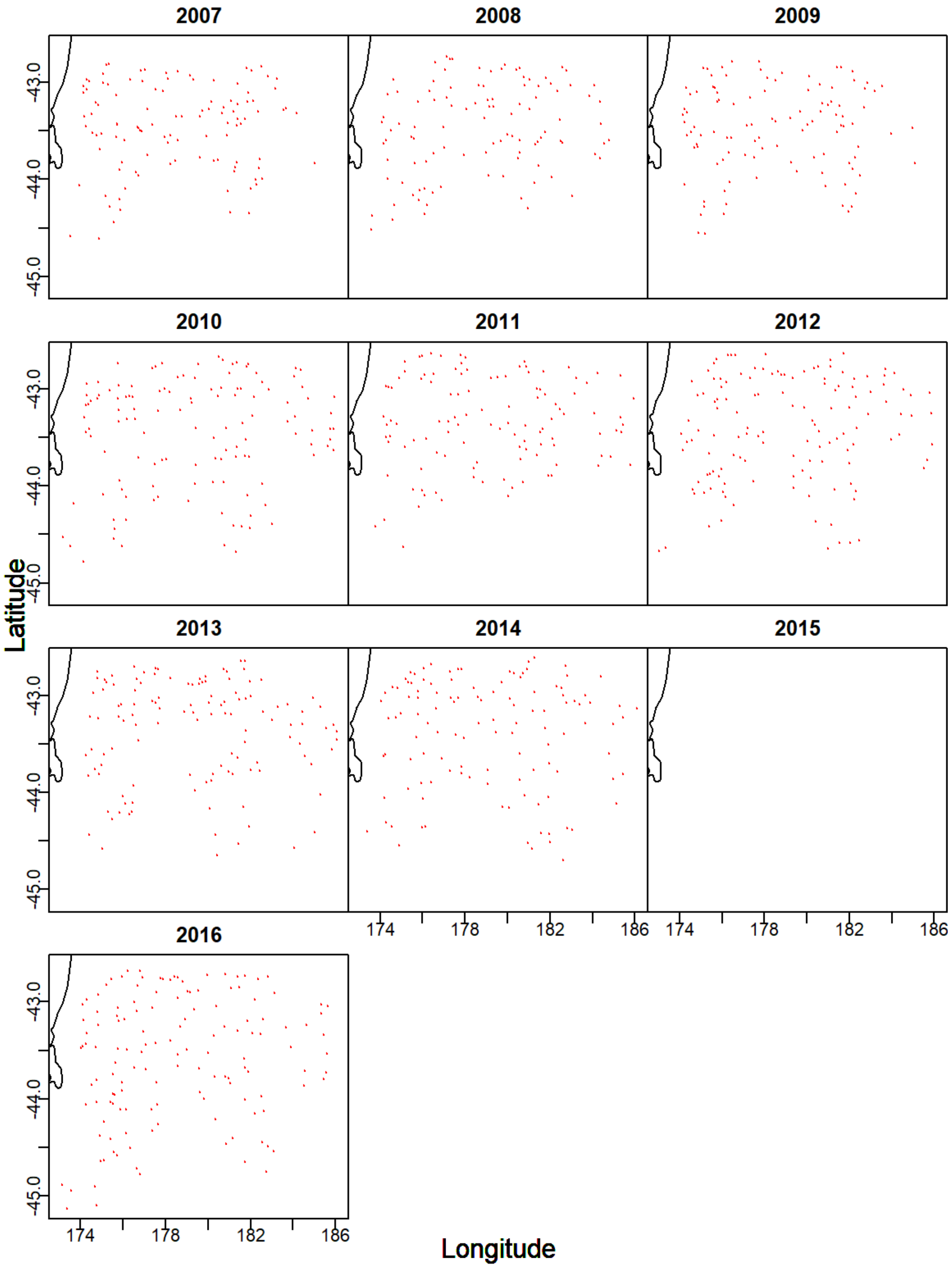


Figure 11: Data distribution in the domain over time for the VAST model using trawl survey data. We note that no trawl survey was carried out in 2015 because the surveys became biennial.

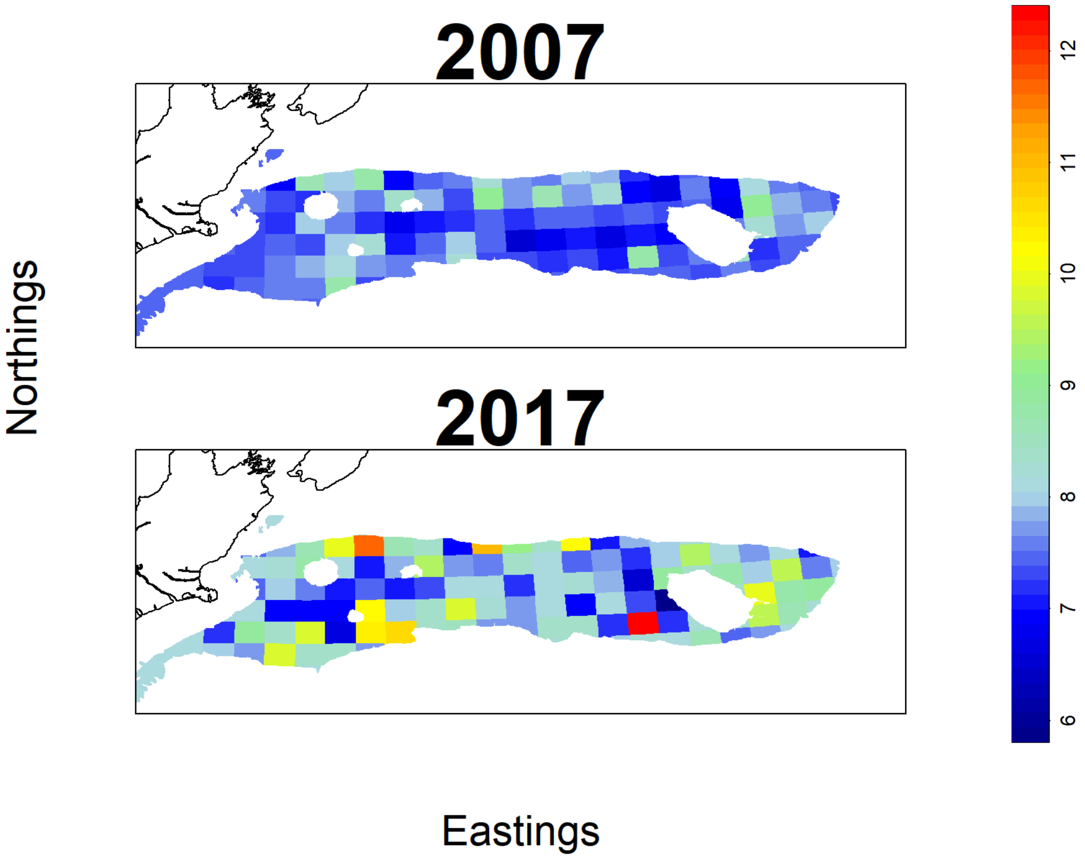


Figure 12: Densities of holothurians as predicted by VAST using DTIS data. Scale in log of numbers per square km.

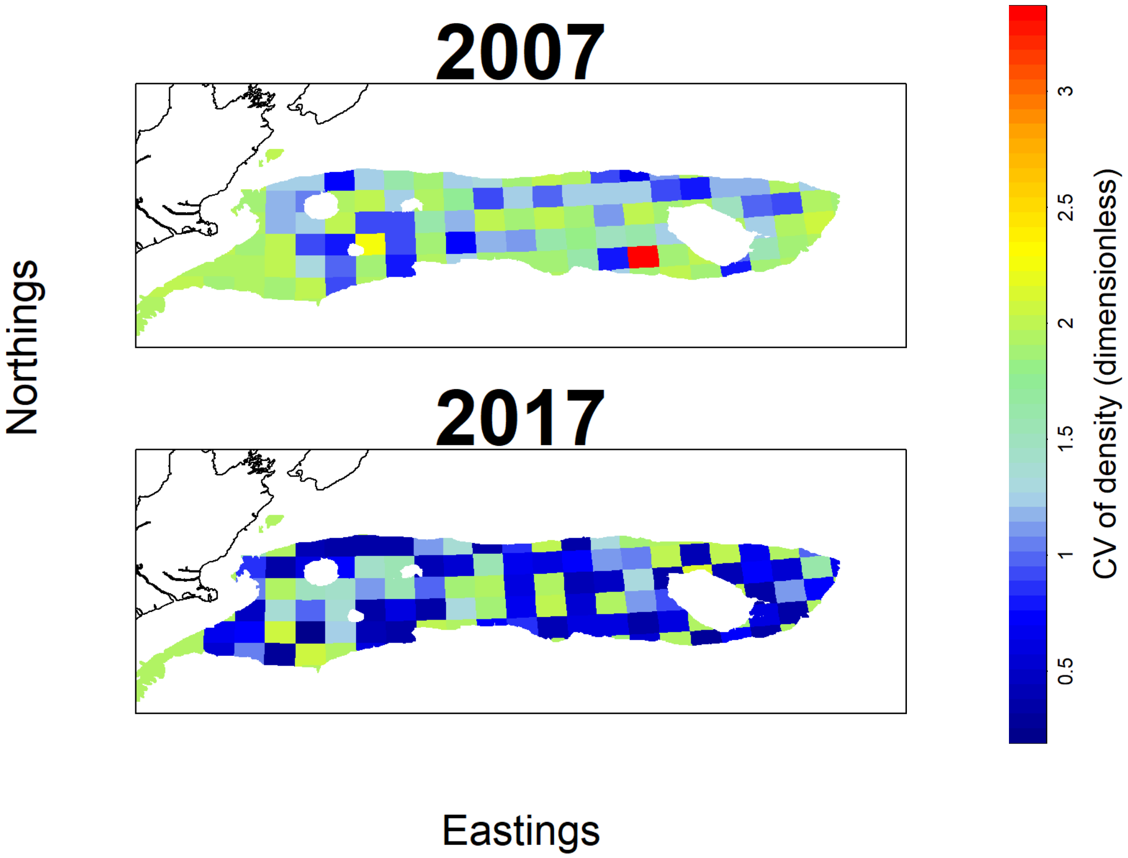


Figure 13: CV of densities of holothurians as predicted by VAST using DTIS data.

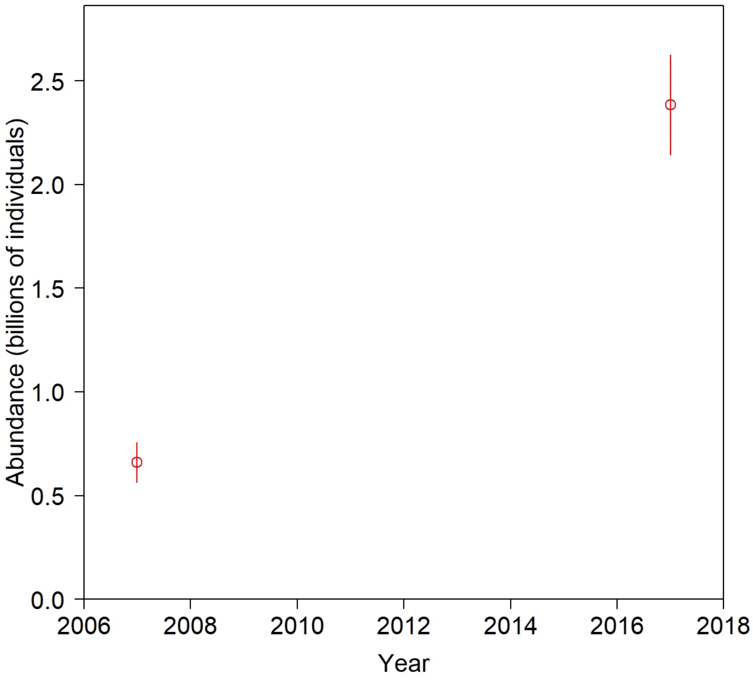


Figure 14: Biomass trend of holothurians over the entire Chatham Rise as predicted by VAST using DTIS data. Note the abundance is relative to catchability, assumed 1 here.

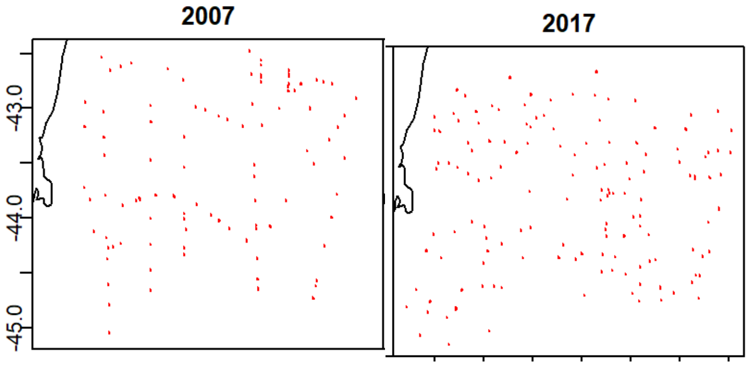
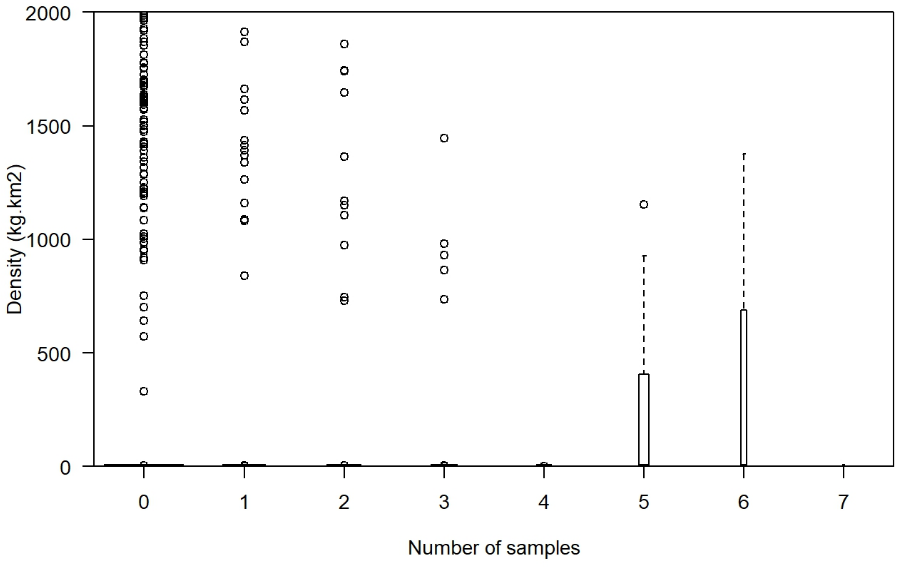


Figure 15: Data distribution in the domain over time for the VAST model using DTIS data.



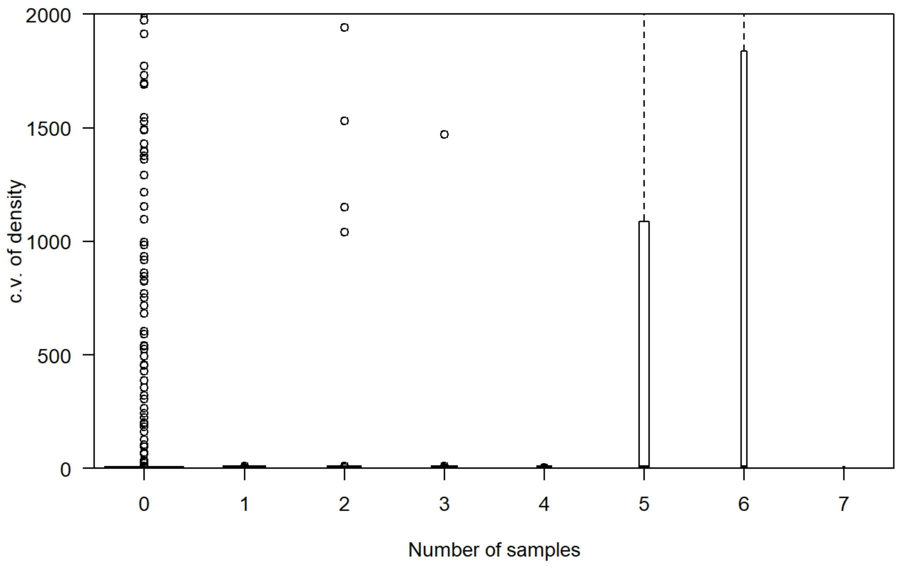


Figure 16: Density estimates and CV of density estimates by number of samples in each cell and year combination for the model using DTIS data. The width of the bars are proportional to the square root of the number of observations.

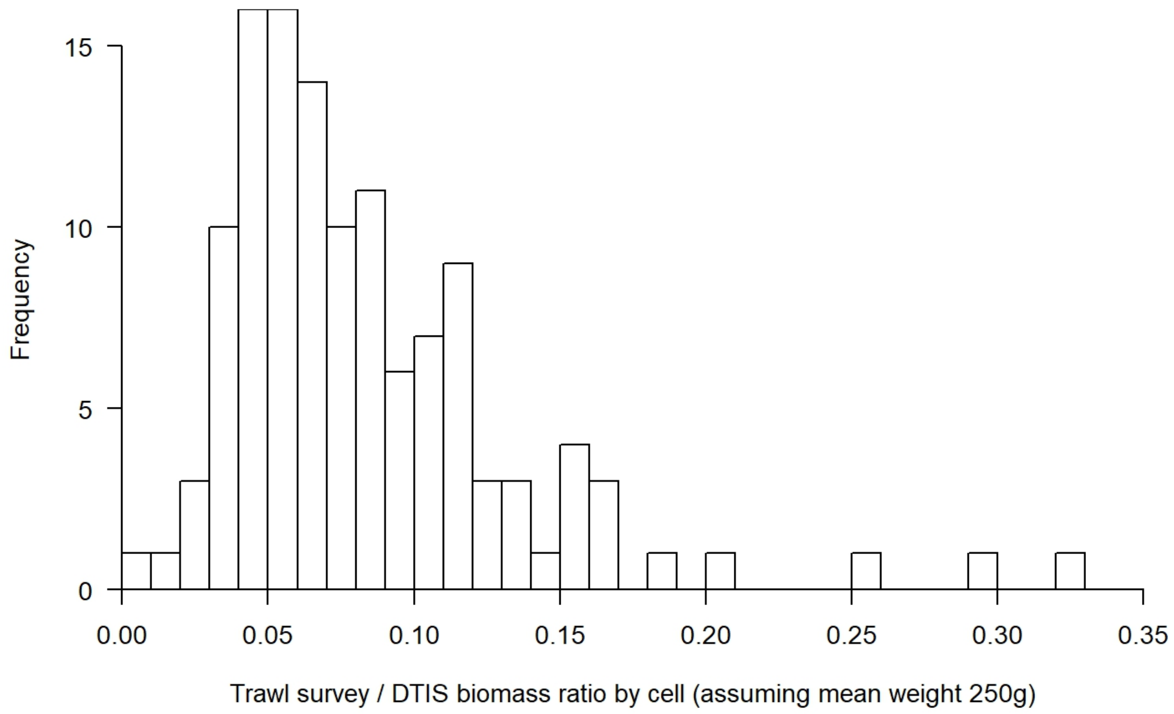


Figure 17: Comparison between VASTdensity predictions using trawl survey data or DTIS data: ratio of trawl survey to DTIS biomass by cell assuming a mean holothurian weight of 250 g.

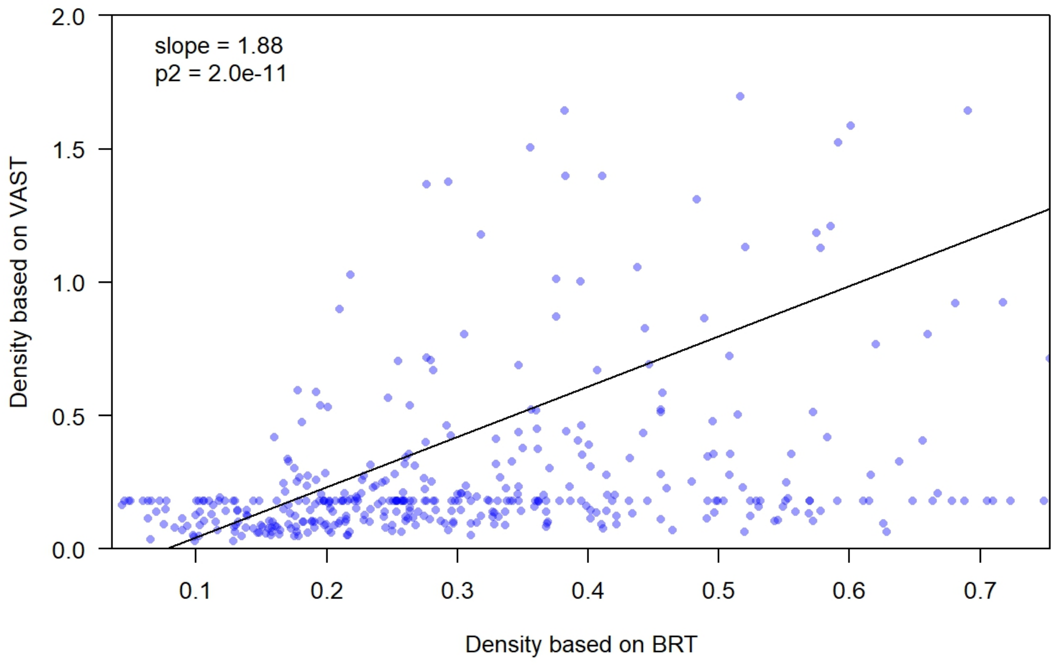


Figure 18: Comparison between BRT and VAST density predictions. BRT results are averaged for each VAST cell, and VAST results are averaged over all years predicted. The slope and its significance are also shown.

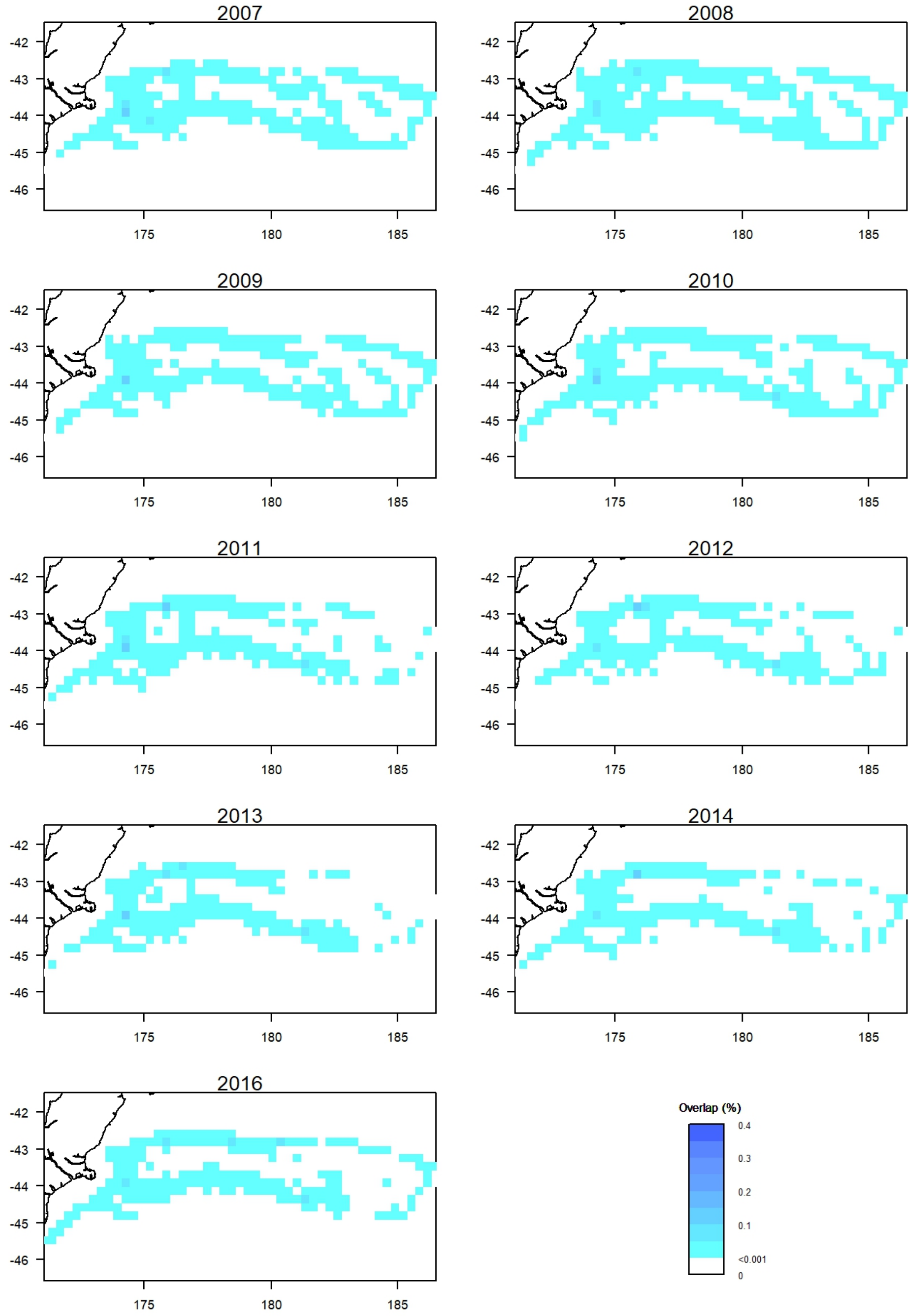


Figure 19: Example of fishing impact overlap in space and time for the fish / squid fisheries, in percentage of total biomass impacted. The scale is identical in all plots and in all plots of Figure 20 and Figure 21.

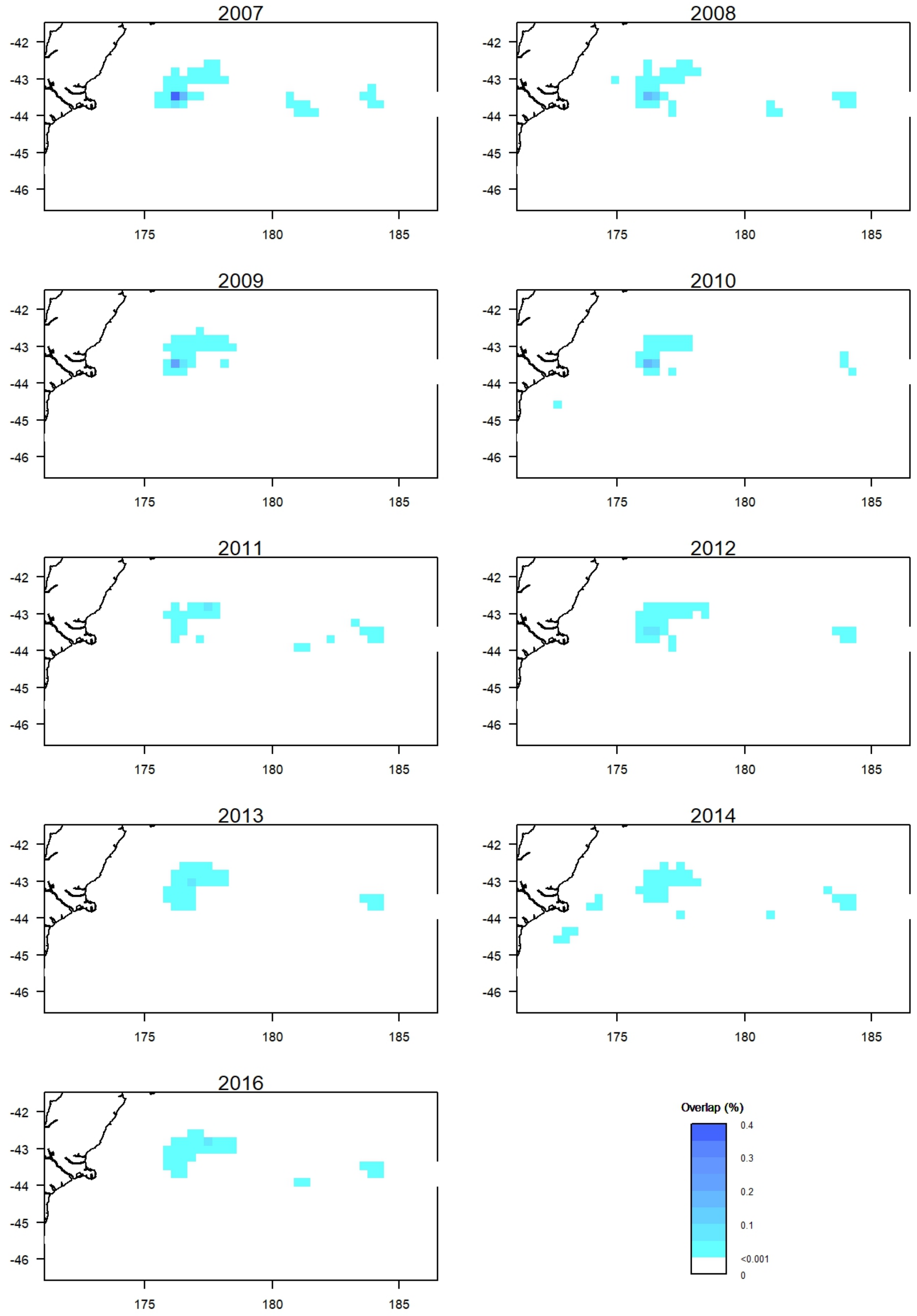


Figure 20: Example of fishing impact overlap in space and time for the scampi fisheries, in percentage of total biomass impacted. The scale is identical in all plots and in all plots of Figure 19 and Figure 21.

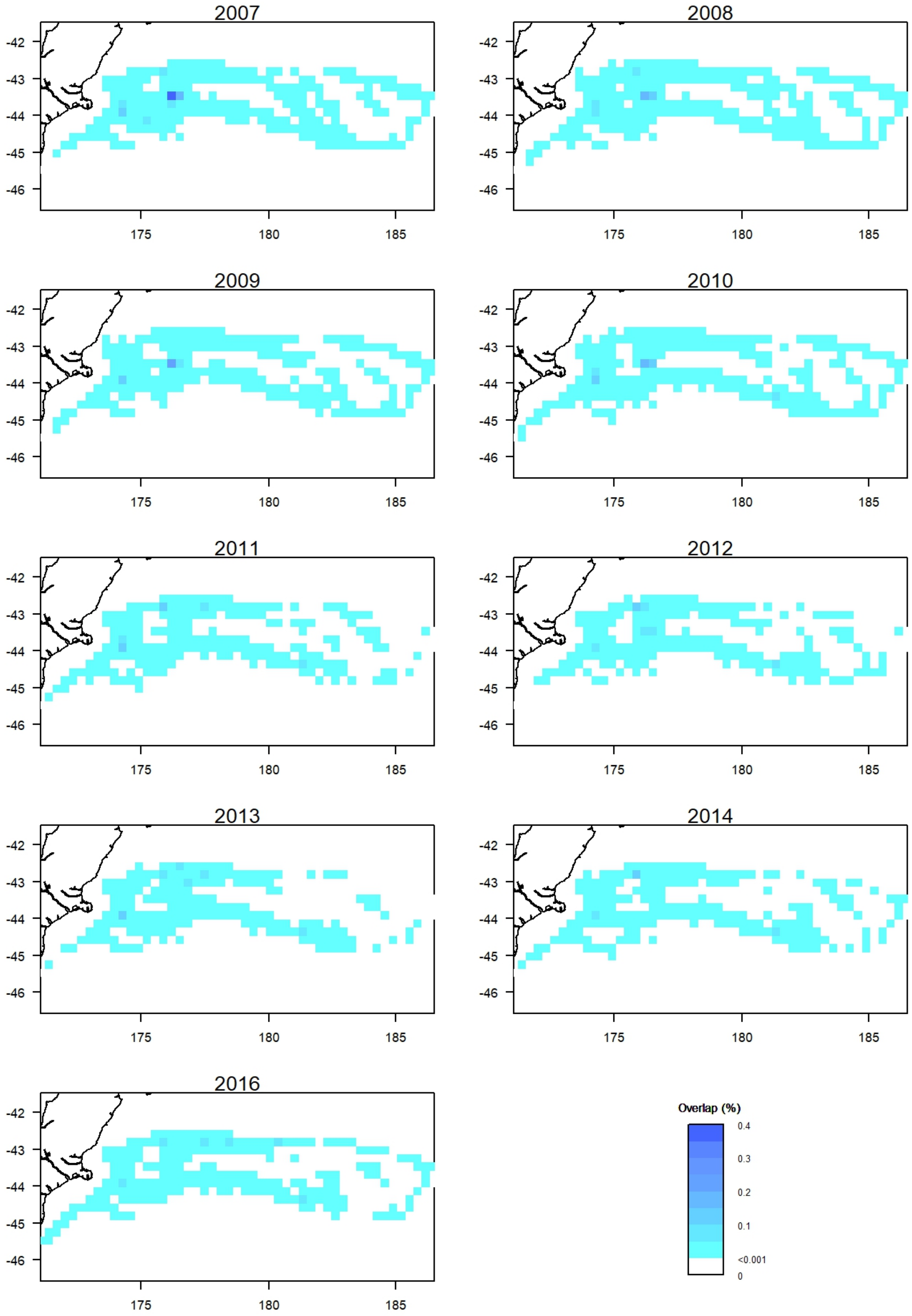


Figure 21: Example of fishing impact overlap in space and time for the combined fish (Figure 19) and scampi (Figure 20) fisheries, in percentage of total biomass impacted. The scale is identical in all plots and in all plots of Figure 19 and Figure 20.

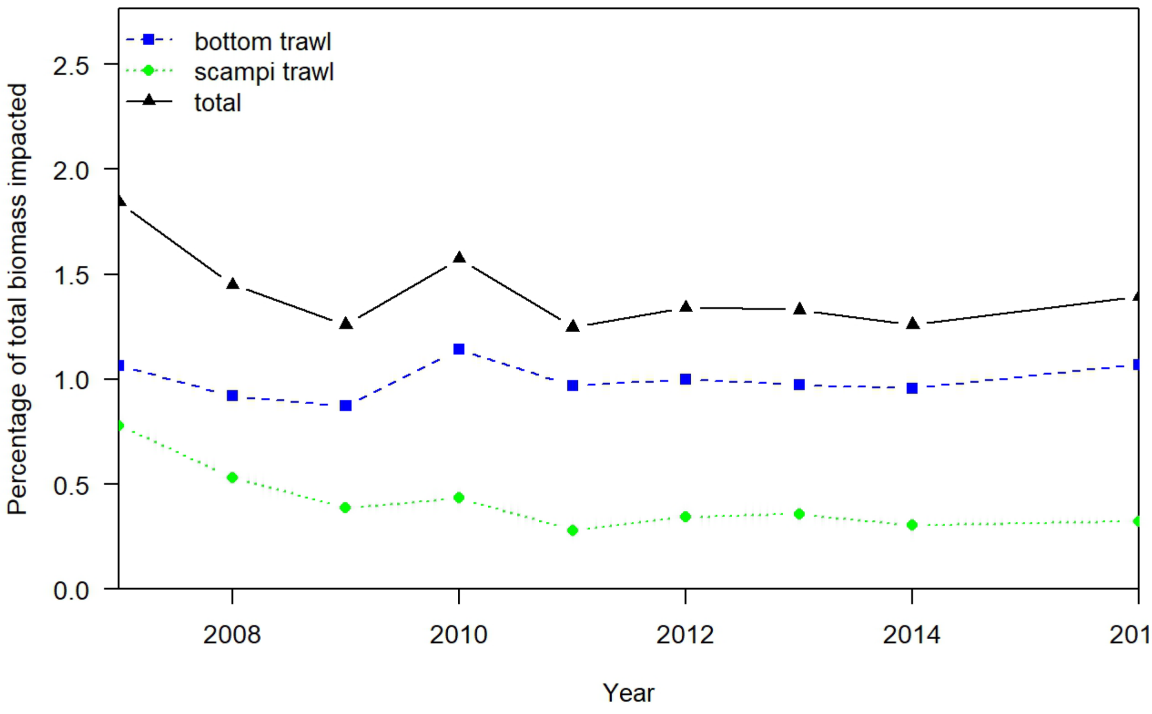


Figure 22: Example of fishing impact overlap index over time for the two fisheries, in percentage of total biomass impacted.

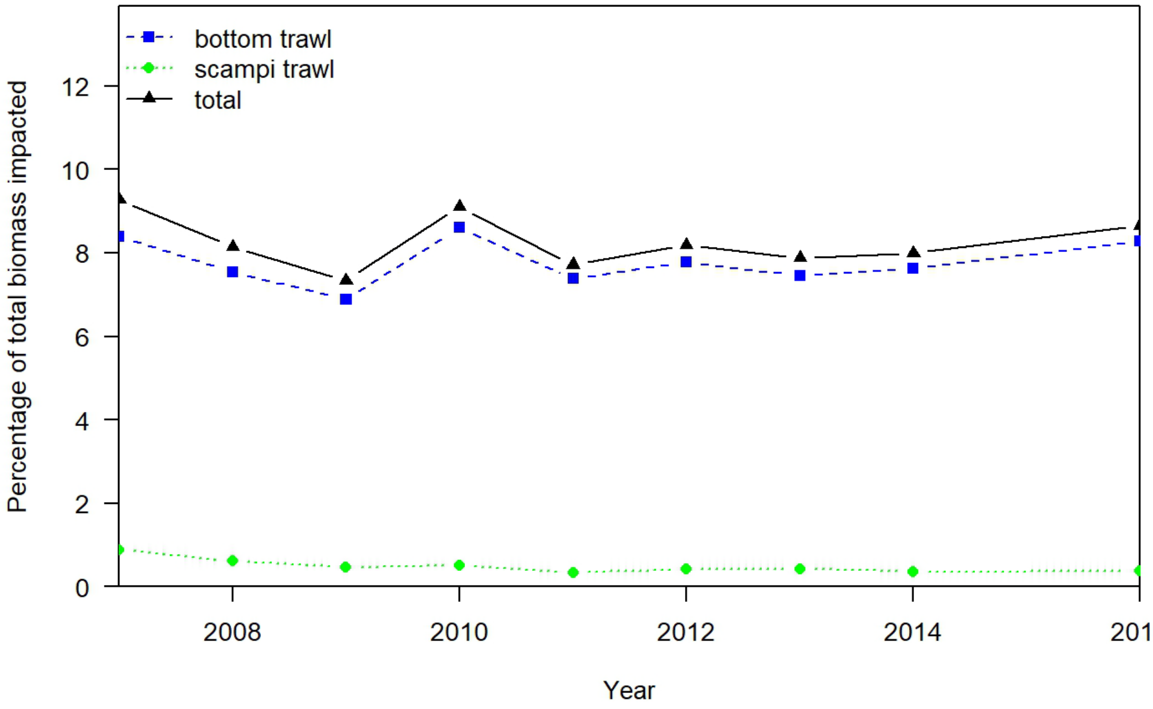


Figure 23: Example of trawl exposure index over time for the two fisheries, in percentage of total biomass exposed.

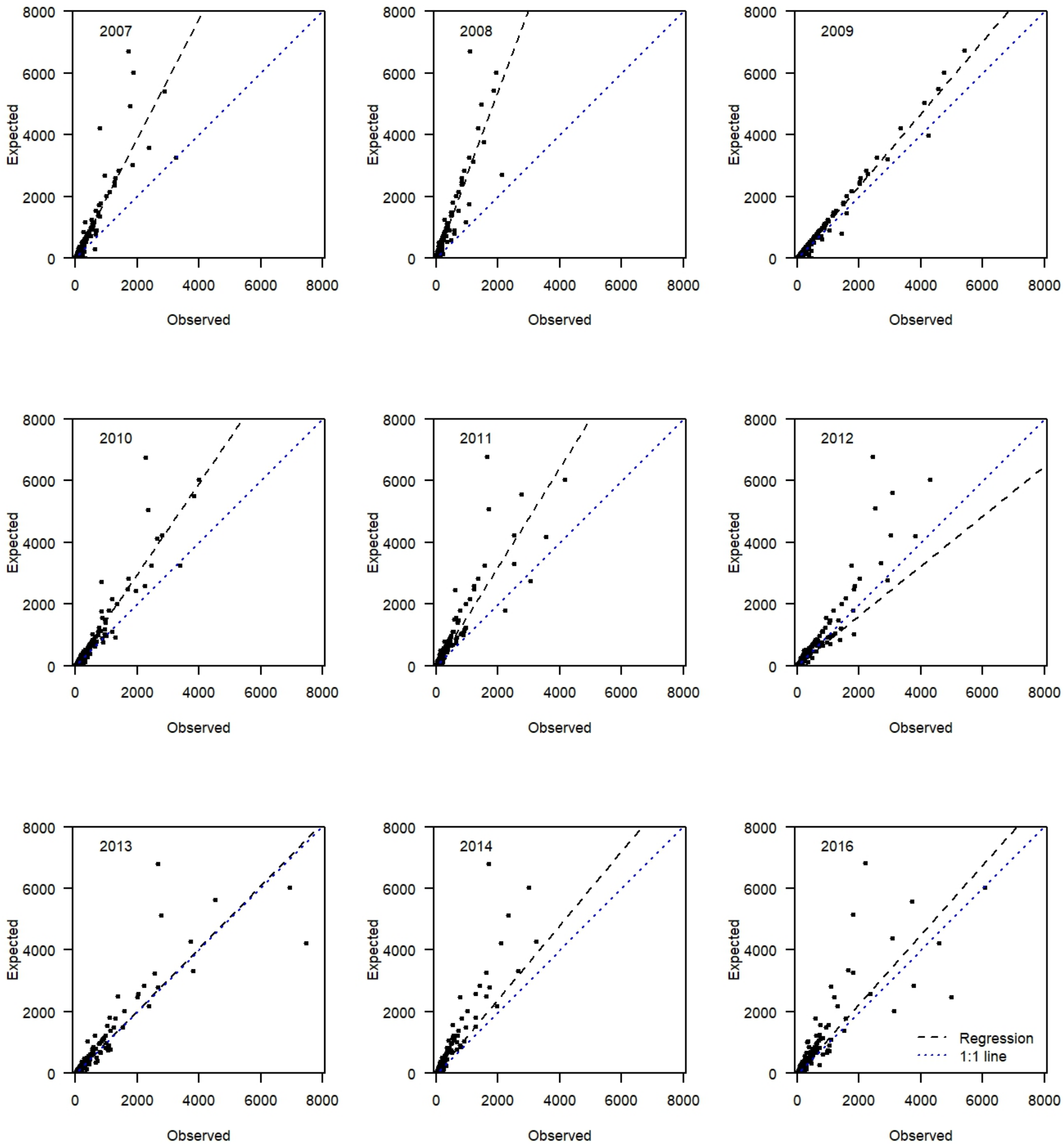


Figure 24: Fits to the biomass estimates in each year and cell where data is available, for the model where only initial recruitment was estimated.

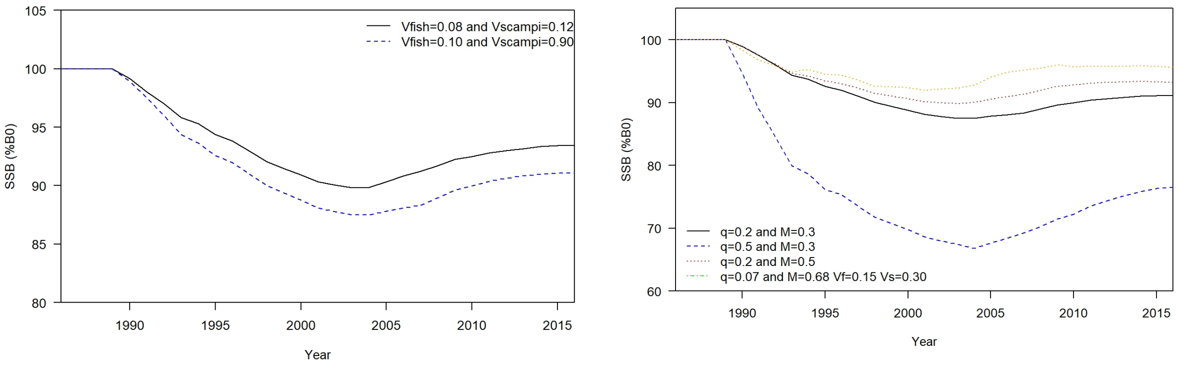


Figure 25: Effect of vulnerability for fish and scampi fisheries (*Vfish* and *Vscampi* respectively), trawl survey catchability (*q*) and natural mortality (*M*) on the biomass trajectory of holothurians on the Chatham Rise.

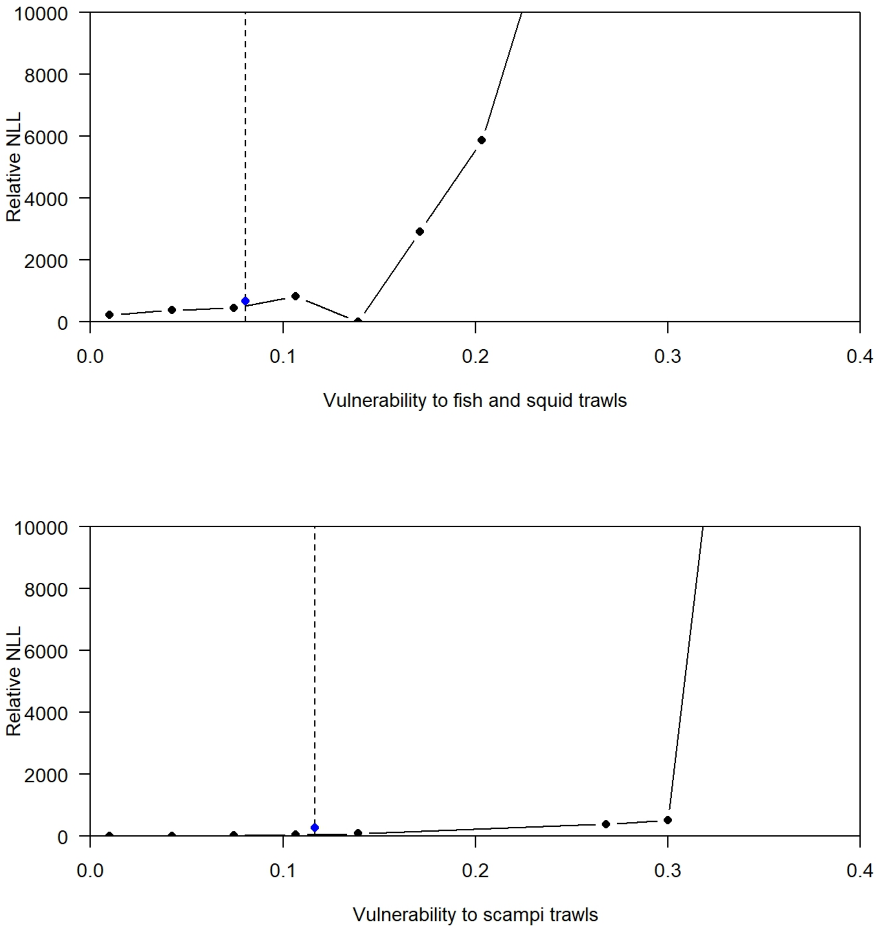


Figure 26: MPD profiles of the vulnerability parameters for holothurians for the two fisheries included (fish / squid – top, or scampi fishing - bottom). The relative negative log likelihood (NLL) is the NLL scaled to the lowest value obtained.

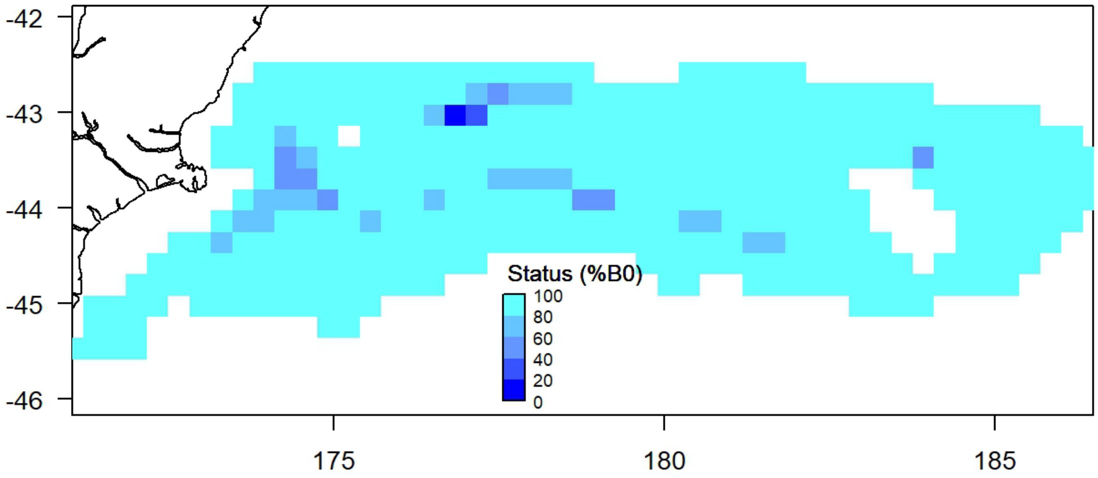


Figure 27: Current stock status of holothurians using model R6.2 with optimised parameters (q = 0.07, M = 0.68, V_{fish} = 0.15, V_{scampi} = 0.30), expressed as a percentage of B_0, by latitude and longitude on the Chatham Rise.