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Tini a Tangaroa

Determining the spatial distribution and connectivity of blue cod spawning stock in the Marlborough Sounds to guide area-based management

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T. Brough,
M.P. Beentjes,
E. Leunissen
C. Collins
M. Morrison

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Fisheries Science Editor

Ministry for Primary Industries
PO Box 2526
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Email: Fisheries-Science.Editor@mpi.govt.nz
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PLAIN LANGUAGE SUMMARY

Blue cod are a popular species of fish for recreational, commercial and customary fisheries in Aotearoa New Zealand. Blue cod stocks in many places have experienced significant declines compared to historical levels, particularly in the Marlborough Sounds.

Fisheries New Zealand is exploring measures to restore the blue cod population within the Marlborough Sounds, by identifying areas where fishing pressure could be reduced to increase abundance of spawning mature blue cod.

In this project, we use information from blue cod monitoring surveys, pooled with data that describe the types of habitat blue cod prefer, to predict the distribution of female biomass – a good index of spawning potential. Female biomass is predicted for two scales: across the full Marlborough Sounds area, including outer coastal areas; and for an inner sounds area including Pelorus and Queen Charlotte Sounds only. Areas with high female biomass occurred mostly on the outer coast around D'Urville Island and in outer Queen Charlotte Sound, however areas that had the right combination of habitat characteristics to support spawning were also predicted within the inner sounds. The impact of historical fishing on female biomass was unable to be realistically included in our analysis due to a lack of information on historical catch and so the areas we identify as important for spawning are based on present day relationships between female biomass and habitat characteristics.

Using information on local currents, we then determined the connectivity of sites of importance for spawning with juvenile habitats and explored how larvae from each site may be retained within the inner sounds. There was very low larval transport between spawning in coastal areas and the inner sounds, suggesting that spawning areas within each sound would be required to restore local stocks.

We use this information to identify and rank ten areas that hold good potential for the restoration of blue cod spawning within the inner Marlborough Sounds.

EXECUTIVE SUMMARY

Brough, T.[1]; Beentjes, M.P.[1]; Leunissen, E.[1]; Collins, C.[1]; Morrison, M.[1] (2025)
Determining the spatial distribution and connectivity of blue cod spawning stock in the Marlborough Sounds to guide area-based management.

***New Zealand Aquatic Environment and Biodiversity Report No. 369.* 74 p.**

Blue cod (*Parapercis colias*) are the basis of important recreational, commercial and customary fisheries in Aotearoa New Zealand, but have exhibited population decline in many areas. With high site fidelity and reliance on coastal habitats that face multiple stressors, blue cod are highly susceptible to localised depletion. In the Marlborough Sounds, blue cod have shown declines in abundance compared to historical levels, attributed to overharvesting, particularly in the recreational fishery. Fishing mortality in 2021 was more than three times the target reference point. As fishing pressure has significantly reduced the spawning potential for this population, particularly in the inner sounds, Fisheries New Zealand and wider stakeholder groups are interested in determining the most appropriate locations for restoration of spawning areas. This study aims to determine existing spawning habitats and those that have the most potential to support a healthy spawning population in the absence of fishing pressure.

A broad range of spatial data on blue cod, physical and biological habitat characteristics and environmental conditions were considered for inclusion in species distribution models (SDMs) to predict the distribution of female blue cod biomass (as a proxy of spawning potential). SDMs were used to predict the distribution of female biomass according to habitat/environmental characteristics at two scales: a wider Marlborough Sounds area; and an 'inner sounds' area that included Queen Charlotte (Tōtaranui) and Pelorus (Te Hoiere) Sounds only. Using spatial predictions from the SDMs, candidate areas of high importance for spawning were selected as 'release locations' for a particle tracking experiment to explore the connectivity between release locations and 'target locations' that represented areas of importance for juvenile blue cod.

Spatial predictions suggested that good habitat for spawning was largely found on the outer coast, particularly around D'Urville Island, however there were some hotspots for spawning in outer Queen Charlotte Sound. Spawning potential was low within inner Queen Charlotte and Pelorus Sounds, yet there were areas with some potential for spawning around Double Cove, Tennyson Inlet and Tory Channel, among others. Particle tracking revealed low connectivity between areas currently important for spawning on the outer coast and the inner sounds, with most particles being advected out of the study area into the wider Cook Strait. However, most inner sounds release locations had high to moderate particle retention, suggesting increased larval supply in these areas would likely contribute to local enhancement of blue cod stocks.

Based on a combination of areas with high spawning potential and areas with characteristics that may support spawning recovery, ten 'example' spatial scenarios were configured. The scenarios were ranked according to the percentage of inner-sounds spawning potential, larval retention and connectivity with juvenile habitats, and overlap with known habitats of significance and existing management measures. Top-ranked scenarios included sites around Blumine Island and Erie Bay in Queen Charlotte Sound, and Maud Island in Pelorus Sound. Lower ranked scenarios, that had lower spawning potential and connectivity, included Whekenui Bay near the eastern entrance to Tory Channel, and the junction between Tory Channel and Queen Charlotte. While the candidate scenarios are designed as a starting-point, and contain a range of subjective decision-points, the information generated by this study provides a good foundation for stakeholder engagement for the management of spawning locations for this important fishery.

[1] Earth Sciences New Zealand.

1. INTRODUCTION

Blue cod biology and ecology

Blue cod (*Parapercis colias*) is an inshore benthic reef fish species endemic to New Zealand. Blue cod has a wide depth range from a few metres to about 150 m and is found in a variety of habitats, including reef edges, shingle/gravel, biogenic reefs, or sandy bottoms close to rocky outcrops. Blue cod are especially prone to serial depletion as they have a restricted home range and display strong site fidelity (Rapson 1956, Mace & Johnston 1983, Mutch 1983, Cole et al. 2000, Carbines & McKenzie 2001, Govier 2001, Carbines & McKenzie 2004, Rodgers & Wing 2008). Further, they constitute a number of sub-populations along the coastline with limited mixing. However, sub-populations are not genetically distinct, with egg or larval dispersion coupled with the occasional larger scale movements sufficient to prevent genetic isolation (Gebbie 2014). Blue cod have a poorly understood social system but are known to be sequential protogynous hermaphrodites capable of changing sex from female to male (Mutch 1983, Carbines 2004, Beentjes 2021), a characteristic that is common among many reef fish families. Blue cod are a diandric species, where males either develop directly from the undifferentiated state without sex inversion (primary males) or begin life as a female and become male following sex inversion (secondary males). Fishing intensity can affect the dynamics of sex change and in more heavily fished areas, blue cod tend to have biased sex ratios favouring males, as is the case in Marlborough Sounds (Beentjes 2023). For example, parts of Pelorus Sound had a sex ratio of over 90% male in 2021 (Beentjes et al. 2022b). Not only are there many areas with few females, but they are also very small, which has implications for egg production.

Stock status of blue cod in Marlborough Sounds

Blue cod (*Parapercis colias*) have experienced a prolonged period of intense exploitation in and around Marlborough Sounds (Figure 1) that dates back to at least the early 20th century associated with the high recreational value and resource use of the sounds. In addition, recreational fishers from throughout New Zealand are attracted to the sounds because it provides a safe and sheltered destination for small boat operators (Hartill et al. 2017).

Early research from Marlborough Sounds in the late 1930s indicated that blue cod were larger than present-day populations, with a higher proportion of large (>330 mm TL), older fish (Rapson 1956), which are mostly absent today. We have no information on the abundance, and size of blue cod from virgin populations in Marlborough Sounds, but based on surveys of lightly fished populations elsewhere, the current population, particularly in the inner sounds, has small mean size (total length) and age, low abundance, and a skewed sex ratio favouring males, all strong indications of overfishing (Beentjes et al. 2022a, Beentjes et al. 2022b).

Attempts by Fisheries New Zealand to improve blue cod stock status (i.e., abundance, size, age and sex ratio) have been carried out since the early 1990s, via various input and output controls on recreational fishing such as hook limits, minimum legal size (MLS), daily bag limits (DBL), slot limits, and seasonal closures, as well as through temporary closed areas (Fisheries New Zealand 2025). Additionally, parts of the inner sounds are closed to commercial fishing of finfish. Despite these initiatives, the most recent (2021) Fisheries New Zealand Marlborough Sounds blue cod potting survey indicated that blue cod abundance was either declining or not improving, size was very small, age structure was severely truncated, and sex ratio remained strongly biased towards males (Beentjes et al. 2022b). These findings indicated that the current management measures were not effective in allowing the stock to rebuild, and that overfishing was continuing. Fishing mortality (F) was estimated at 0.48 yr^{-1} in 2021, which is more than three times the F_{MSY} (fishing mortality at maximum sustainable yield) proxy reference target (F) of 0.15 yr^{-1} (Beentjes et al. 2022b, Fisheries New Zealand 2025). It is also likely that there is considerable mortality from undersize hooked-fish returned to the water given that currently nearly all females caught, as well as a high proportion of males, are below the MLS of 33 cm total length.

This poor state of the fishery has persisted during a sustained period of static output controls (i.e., minimum legal size of 33 cm and daily bag limit of 2 fish, and seasonal closure) and is likely to be a

result of declining abundance, reduced or stunted size, and a strongly male-biased sex ratio, culminating in insufficient egg production to sustain the fishery (Beentjes et al. 2022b, Fisheries New Zealand 2025).

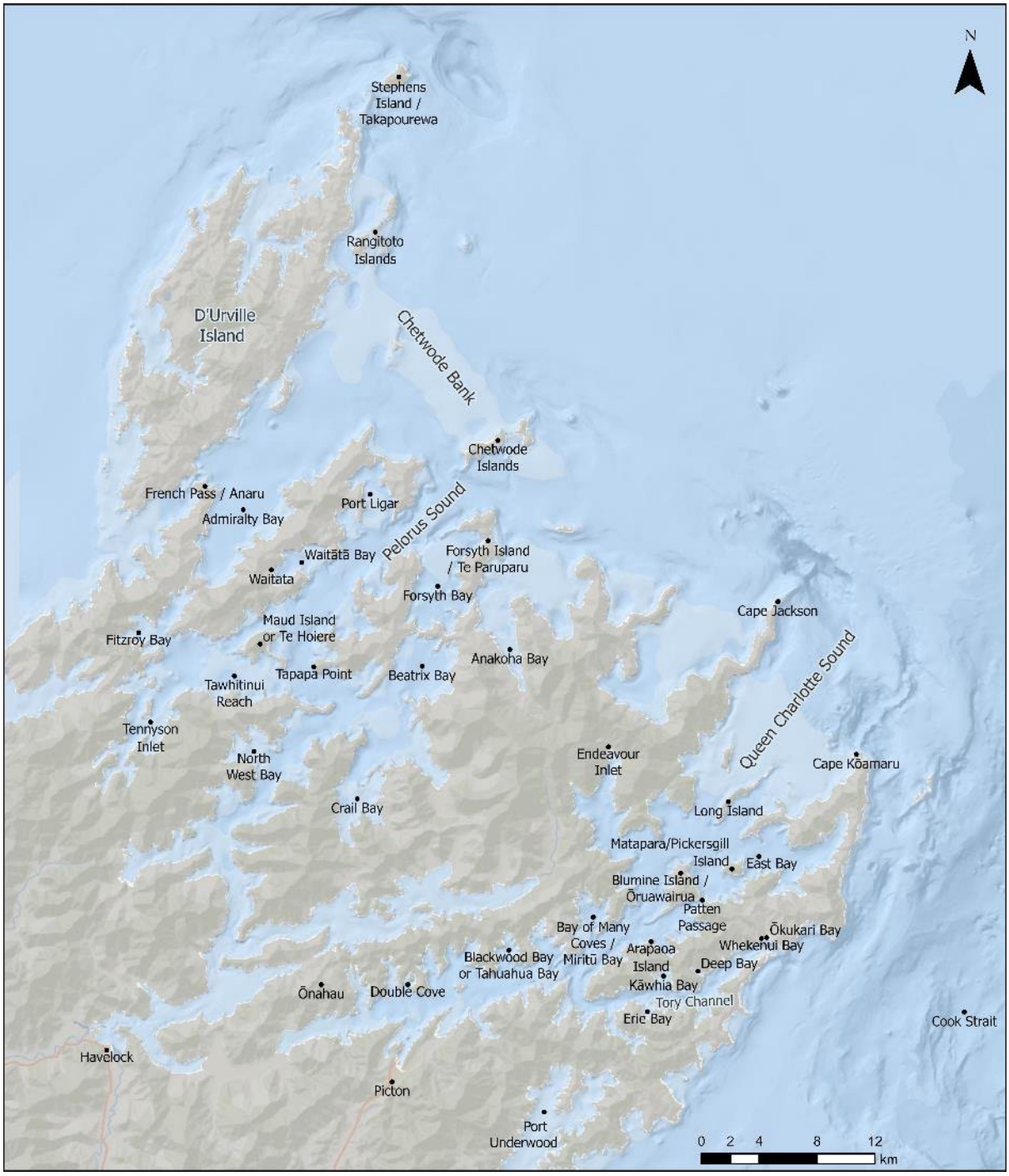

Figure 1: Study area - Marlborough Sounds.

Blue cod fishery

Blue cod is the third most common recreational species caught in New Zealand, mostly in the South Island, with a total catch of 223 t (413 000 fish) estimated from the 2022–23 panel survey (Heinemann et al. 2021, Fisheries New Zealand 2025). In the Marlborough Sounds (Figure 1), blue cod is the second most important recreational target species, closely behind snapper (Hartill et al. 2017). The recreational

take of blue cod within the BCO 7 Fisheries Management Area was estimated at 63 t from the 2017–18 national panel survey (Wynne-Jones et al. 2019) and 75 t from a 2016–17 aerial access survey (Hartill et al. 2017, Fisheries New Zealand 2025). Two-thirds (67%) of the aerial survey recreational harvest was from the outer Marlborough Sounds, and only 3.5% from the inner sounds, with 29% taken from Tasman and Golden Bays. The most recent panel survey in 2022–23 indicated that recreational harvest estimates of blue cod in BCO 7 had declined by more than a half, to 30 t (Heinemann et al. 2021, Fisheries New Zealand 2025), with declines evident in the Marlborough Sounds. The decline may indicate a drop in catch per unit effort, rather than effort.

The bulk of the catch from the BCO 7 commercial potting fishery comes from the outer Marlborough Sounds (80–90%) along rocky coastal areas, particularly north of D'Urville Island around Stephens Island (Figure 1), with the remainder from the west coast (Langley 2023). The commercial catch for BCO 7 as a whole has also gradually declined over the last 5 years from about 70 t to 39 t in 2022–23 (Fisheries New Zealand 2025), similar to the recreational take in the Marlborough Sounds, and only 3 to 4 vessels are actively fishing. The BCO 7 total allowable commercial catch (TACC) was reduced from 70 t to 58 t in the 2022–23 fishing year.

Marlborough Sounds blue cod fishery management controls

In the Marlborough Sounds, there have been frequent changes to both the recreational minimum/maximum legal size and to the daily bag limit (DBL) of blue cod, as well as area closures in the 'Marlborough Sounds Area' (Figure 2). These regulations are summarised below:

1. The Daily Bag Limit (DBL) progressively declined from 12 blue cod in 1985, to 2 blue cod since 2011.
2. The inner sounds (Queen Charlotte and Pelorus Sounds) were closed to target blue cod fishing from October 2008 to April 2011, a period of two and half years (Figure 2).
3. The minimum legal size (MLS) has varied from 28 cm to 33 cm total length, with a slot limit of 30–35 cm implemented from April 2011 to December 2015.
4. From December 2015, within 'Marlborough Sounds Area' and 'Challenger Area East', the MLS increased to 33 cm, DBL was 2 blue cod (or 2 from each area), with a maximum of two hooks per line permitted (Figure 2).
5. From 2015, the Marlborough Sounds blue cod fishery was closed from 1 September to 19 December each year, i.e., during the assumed spawning season in this region. In August 2025, the closed season was extended to 1 September to 10 January annually to address overfishing.
6. In July 2020, under the national blue cod strategy the area from Farewell Spit to Clarence River (out to 12 nautical miles), including Marlborough Sounds, was assigned a 'traffic light' colour of red, indicating that the blue cod stocks in this area were overfished. This is known as the 'Tasman Area' , which corresponds to the Challenger East Area shown in Figure 2.
7. In July 2020 the DBL was set at two blue cod per person within the Tasman Area (Marlborough Sounds Area and Challenger Area East) (Figure 2).

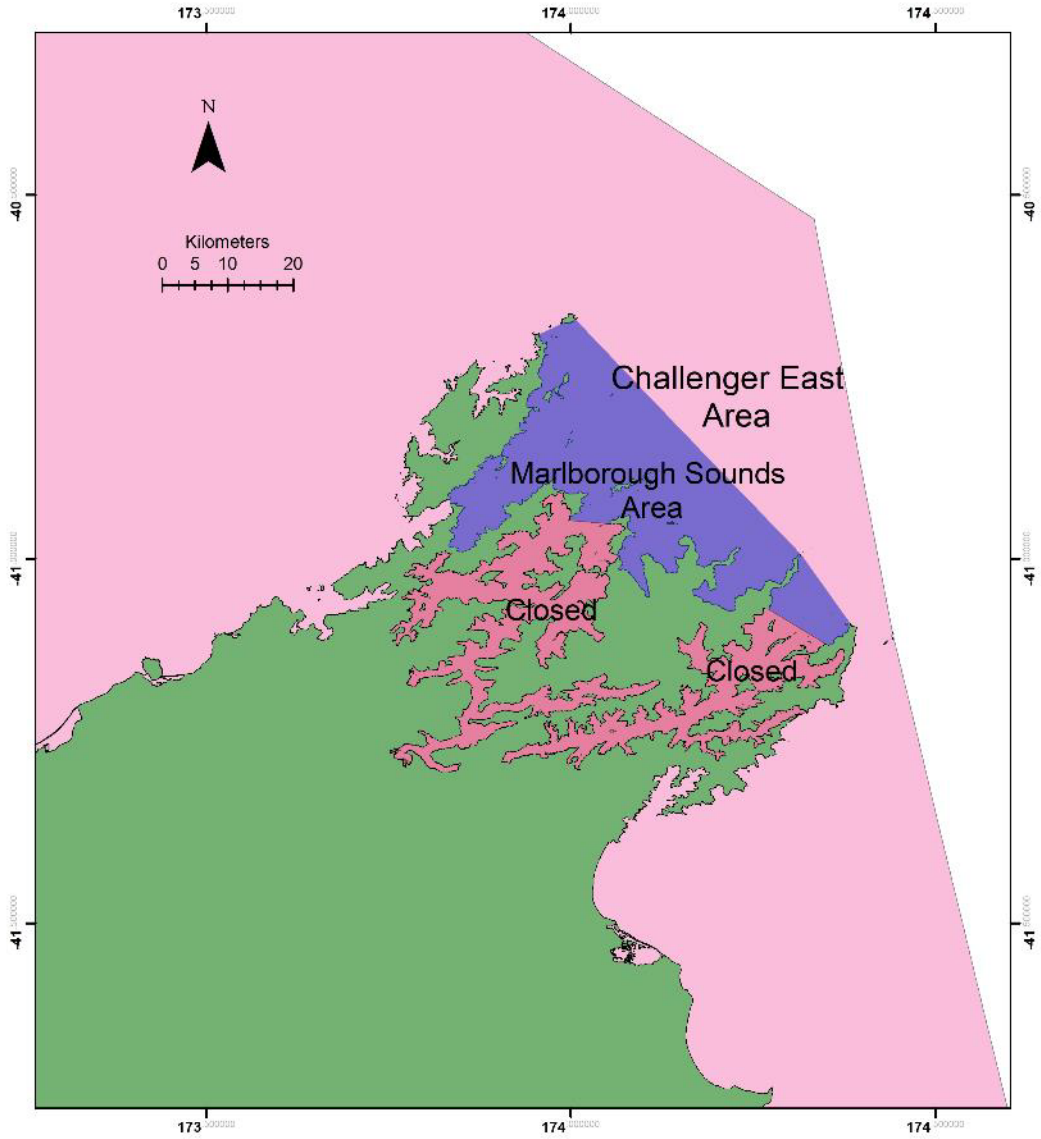

Figure 2: **The Marlborough Sounds showing fisheries management areas 'Marlborough Sounds Area' (dark blue and dark pink) and the 'Challenger East Area' (light pink). From 1 October 2008 to April 2011, the inner Queen Charlotte Sound and inner Pelorus Sound (part of the Marlborough Sounds Area) were closed to fishing (dark pink). This area now has a DBL of two per person.**

Evidence for improved stock status in areas closed to fishing

The current project is designed to inform the spatial management of blue cod within Marlborough Sounds, identifying areas where spawning biomass is currently high, and areas where spawning may recover based on an area's habitat characteristics. There are two clear examples of how a cessation to fishing within part of the Marlborough Sounds has resulted in improved health of the blue cod fishery. The first was the two-and-a-half-year closure of the inner Marlborough Sounds to blue cod recreational fishing from October 2008 to April 2011 (Figure 2). Following this closure, potting surveys indicated that blue cod became larger and more abundant within the inner sounds, indicating that fishing in the inner sounds had been having a substantial effect on the size and abundance of fish. The population returned to its pre-closure state soon after the inner sounds were re-opened to fishing (Beentjes et al. 2022b, Beentjes 2023). The second, and perhaps more relevant, example occurred with the

establishment in April 1993 of the Long Island-Kokomohua Marine Reserve near the entrance to Queen Charlotte Sound, by the Department of Conservation (Beentjes et al. 2022b, Beentjes 2023). The key findings from the random-site potting surveys within Long Island Marine Reserve in 2017 and 2021 were that compared to adjacent areas, blue cod within the marine reserve were 5 to 6-fold more abundant, 3 to 5 cm larger, and were in better condition. The larger number and size of fish inside these closures likely contribute to increased spawning capacity that will have benefits for the health of blue cod stocks in the wider area.

Both these examples indicate that specific area closures can have positive impacts on blue cod populations, and hence spawning potential, even within small areas such as Long Island Marine Reserve.

Aim of this project

Blue cod populations in the Marlborough Sounds appear to be unresponsive to the various input and output controls applied in the last 20 years, with the exception of temporary closed areas (Beentjes 2023), indicating that another approach is required to manage this fishery. Fishery exclusion areas (i.e., spatial management) to protect female spawners and enhance egg production has been suggested by Fisheries New Zealand stakeholder working groups as an option for the recovery of this degraded fishery.

The overall objective of Fisheries New Zealand research project ZBD2024-02 was to identify habitat in the Marlborough Sounds that support blue cod spawning and determine opportunities for restoration. The project aims to use a broad range of data to identify candidate areas within Queen Charlotte and Pelorus Sounds that could be closed to fishing, thereby enhancing the local recovery of blue cod, particularly in areas of current low or no abundance.

Specific project objectives:

Objective 1: Review, collate, and groom all available sources of blue cod abundance, sex ratio, fecundity, hydrographic and biogenic habitat data from the Marlborough Sounds for the analysis.

Objective 2: Analyse datasets to identify a network of potential locations throughout the Marlborough Sounds that provide opportunities for blue cod spawning recovery, considering areas of current low abundance, quality of adult habitat, associated potential egg production and distribution, proximity to juvenile habitat, and any other key factors.

Objective 3: Rank several spatial management approaches by potential to increase egg production across the Marlborough Sounds and provide advice on spatial management of blue cod spawning stock.

Together, the delivery of these objectives will enable Fisheries New Zealand and their stakeholders to make informed, evidence-based decisions on spatial management options to enhance blue cod spawning stock in the Marlborough Sounds and thus foster recovery of this important fishery.

2. METHODS

This study integrates several analyses to determine appropriate options for the protection of spawning habitat for blue cod in the Marlborough Sounds (Figure 3). The first step in the approach includes collation and review of all available data on: 1) blue cod relative abundance/biomass and life history characteristics; 2) data on the characteristics of blue cod habitat; 3) information on the relationship between female blue cod weight/length and reproductive output; and 4) hydrodynamic models that can be used to undertake particle tracking to explore potential larval retention and connectivity between spawning sites and known juvenile habitats. The second step of the approach utilises the combined data on blue cod and habitats/environmental conditions to develop species distribution models to predict the distribution of spawning potential throughout the Marlborough Sounds. This spatially explicit layer on spawning potential is used in step 3, where candidate sites for spatial management are distinguished based on their high spawning potential and desire for representative areas in both the outer sounds/coastal environments and within Queen Charlotte and Pelorus sounds. These candidate sites are

then used as release locations for particle tracking analysis (step 4) to explore connectivity between representative candidate locations and known juvenile habitats and to determine rates of larval retention. In step 5, we utilise the information generated in previous steps (distribution of spawning potential, known habitats of importance, connectivity) to determine a suite of spatial scenarios (i.e., potential areas closed to fishing) for the management of blue cod spawning habitats. See the sections below for full detail on each step.

Some areas in the coastal outer Marlborough Sounds hold good present-day spawning biomass while inner sounds habitats are known to be largely depleted (Beentjes et al. 2022b). However, a key aim of the study is to understand the potential for inner sounds habitats to recover spawning biomass, based on the occurrence of habitats where blue cod are absent but may support a spawning population. Thus, we undertook several of the key analyses detailed above at two spatial scales: 1) the wider Marlborough Sounds area that includes adjacent coastal habitat (hereafter 'wider sounds'); and 2) an inner sounds scale that is restricted to Queen Charlotte and Pelorus Sounds only, including Tory Channel (hereafter 'inner sounds') (Figure 4). Utilising the two scales allows for the identification of potential spawning areas of importance for the wider Marlborough Sounds blue cod population as well as identifying locations that may hold potential for recovery of spawning within the inner sounds (Figure 4).

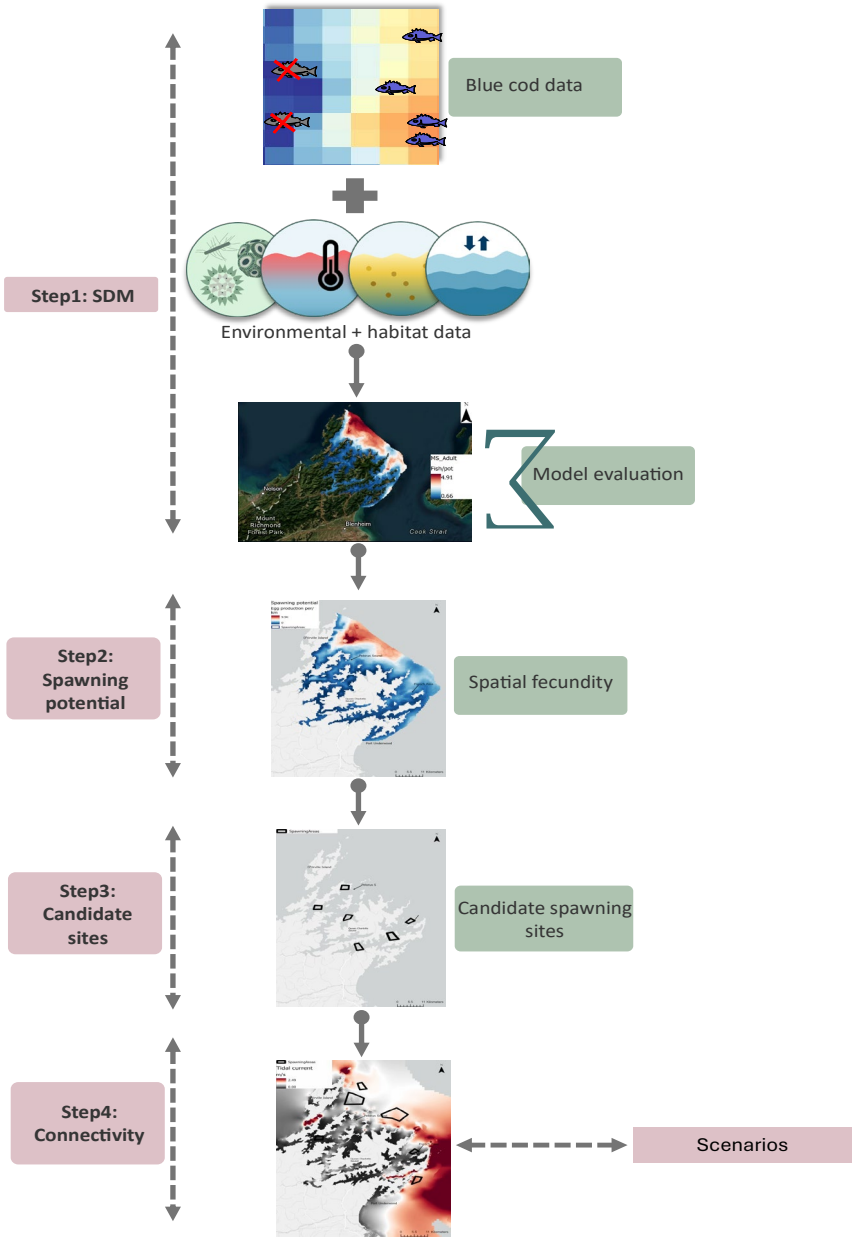

Figure 3: **Schematic showing the key steps in the approach used in this study to determine potential spatial scenarios for the protection/restoration of blue cod spawning habitat in the Marlborough Sounds. SDM, species distribution models.**

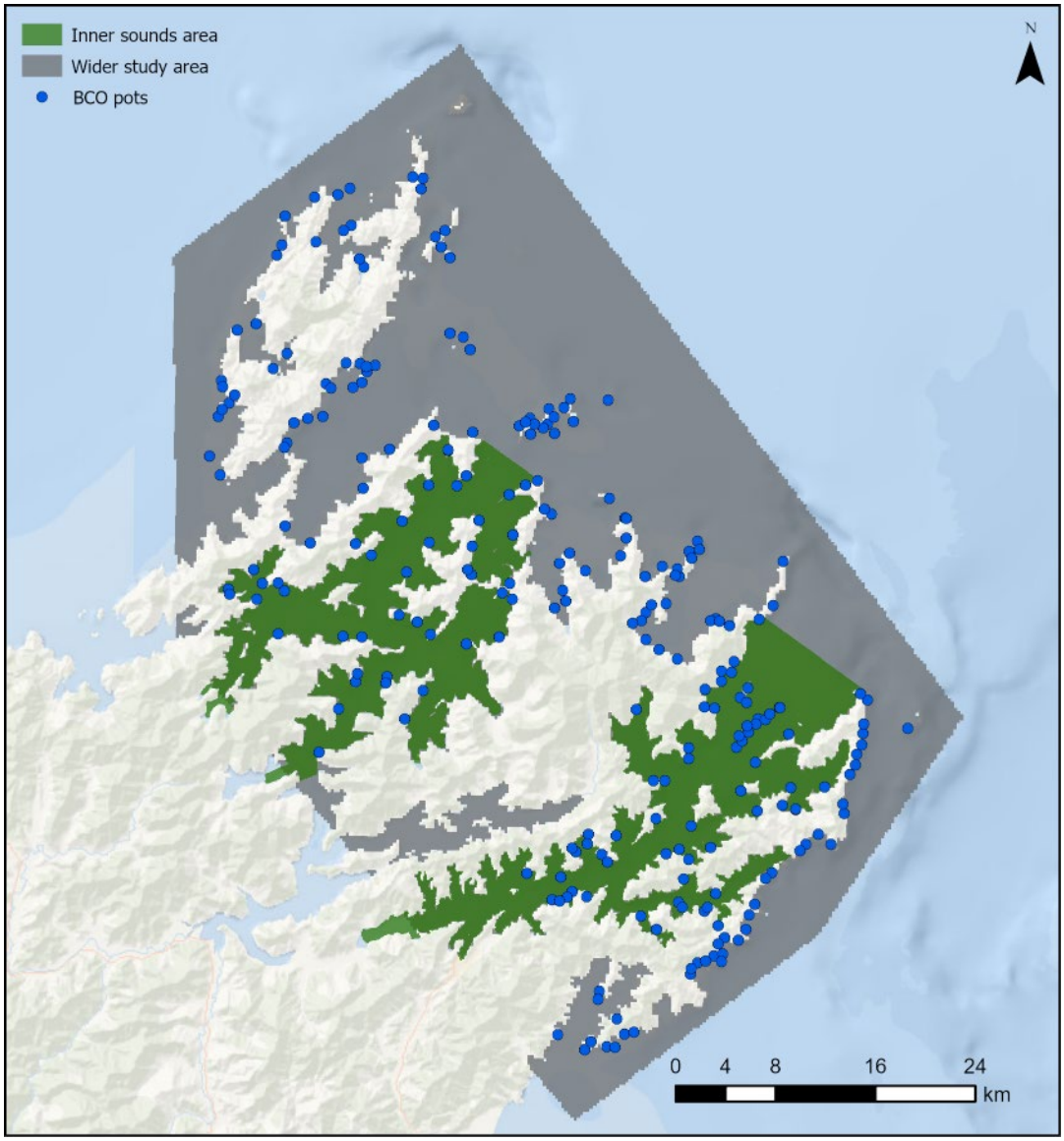

Figure 4: **The potting sites for the 2013, 2017 and 2021 surveys (blue dots). Wider study area (BCO 7 + western D'Urville, grey) encompasses all the blue cod potting. The inner sounds area (green) is restricted to the area for which high-resolution multibeam data was available.**

2.1 Data collation and grooming

Blue cod potting survey data

South Island recreational blue cod fisheries are monitored by Fisheries New Zealand using potting surveys (Fisheries New Zealand 2025). These surveys occur in areas that are most important for the recreational fishery, although there is substantial overlap between the commercial and recreational fishing grounds for most surveys. Surveys are generally carried out every four years to monitor local relative abundance, size, age, and sex structure of geographically separate blue cod populations. The surveys provide a measure of the response of populations to changes in fishing pressure and management intervention, such as changes to the daily bag limit, minimum legal size, and area closures.

The Marlborough Sounds potting surveys began in the mid-1990s and originally used a fixed-site design. However, a review by an international expert panel in 2009 (Stephenson et al. 2024) recommended that a random-site design should be used on these surveys. Subsequently, surveys transitioned to a fully random-site design in 2021 (Beentjes et al. 2022b), with interim sampling of both fixed and random sites in 2013 and 2017 to allow comparison of catch rates, length and age composition, and sex ratios (Beentjes et al. 2017, Beentjes et al. 2018). Raw data from the 2013, 2017, and 2021

potting surveys on blue cod female and juvenile spatial abundance estimates, are used in the species distribution modelling in this project (Figure 5), to provide up-to-date data on the distribution of spawning potential.

All three surveys used a two-phase stratified design (Francis 1984). Simulations using Earth Sciences New Zealand[2] (ESNZ)'s Optimal Station Allocation Program (Francis 2006) and previous survey catches informed allocation of sites among strata with the aim of achieving a coefficient of variation of less than 20% around catch rates. Nine pots (= one set), built to specifications of pot plan 2 (Beentjes 2019), were set at each site on the surveys. All pots were baited with pāua (*Haliotis iris*) viscera and left to fish (soak) for one hour. In the Marlborough Sounds, blue cod habitat is largely restricted to a band of reef and rubble adjacent to the coastline. For fixed-site surveys, pots were set along the coastline, no further than 0.5 km from the site position, but separated by at least 100 m, and pot placement was 'directed'. For the random-site surveys, the coastline was divided into 1.01 km blocks and a latitude and longitude at the centre of each block was assigned and sites within strata were randomly selected from all possible random sites. Pots were set along the coastline 100 m apart, in a randomly selected depth over the extent of the habitat, as it extends out from the shoreline, and pot placement was 'systematic'.

After pots were retrieved the blue cod catch was weighed to the nearest 10 g using Marel motion compensating scales, and total length (TL) rounded down to the nearest centimetre, individual weight (g), and sex were recorded for all blue cod. Sex was determined by macroscopic examination of the gonads (Carbines 2004). The Long Island Marine Reserve was surveyed in 2017 and 2021 using identical methods except that blue cod were not sexed and were returned alive after measuring for length and weight.

For this study, potting data were groomed to create descriptive plots by grouping the data per set, per survey, and mapping total blue cod biomass, total mature female biomass, and sex-ratio per set. A set is defined as the total number of pots (i.e., 9) deployed at a particular site. For descriptive purposes, averaged biomass and sex ratio was calculated across all pots in a set.

Potting surveys do not accurately record the occurrence and distribution of juveniles due to size-selectivity bias of the method (Brough et al. 2023). Thus, in this study we pooled data on the distribution of juvenile blue cod from the MBIE Juvenile Fish Habitat Bottlenecks programme (CO1X1618). This project sampled throughout the Marlborough Sounds region using predominantly towed video, supplemented with some beam trawling. Towed video stations provided count data on the number of juveniles (0+ and 1+ years), and beam trawl data provided information on the relative density of juveniles. These data were mapped and areas of likely importance for juveniles distinguished by manually viewing clusters of high counts/density of juveniles using both methods. The designation of likely juvenile habitat was used to investigate connectivity between potential spawning areas and juvenile habitat, which is an important consideration for the success of any management scenarios.

[2] Previously National Institute of Water and Atmospheric Research (NIWA)

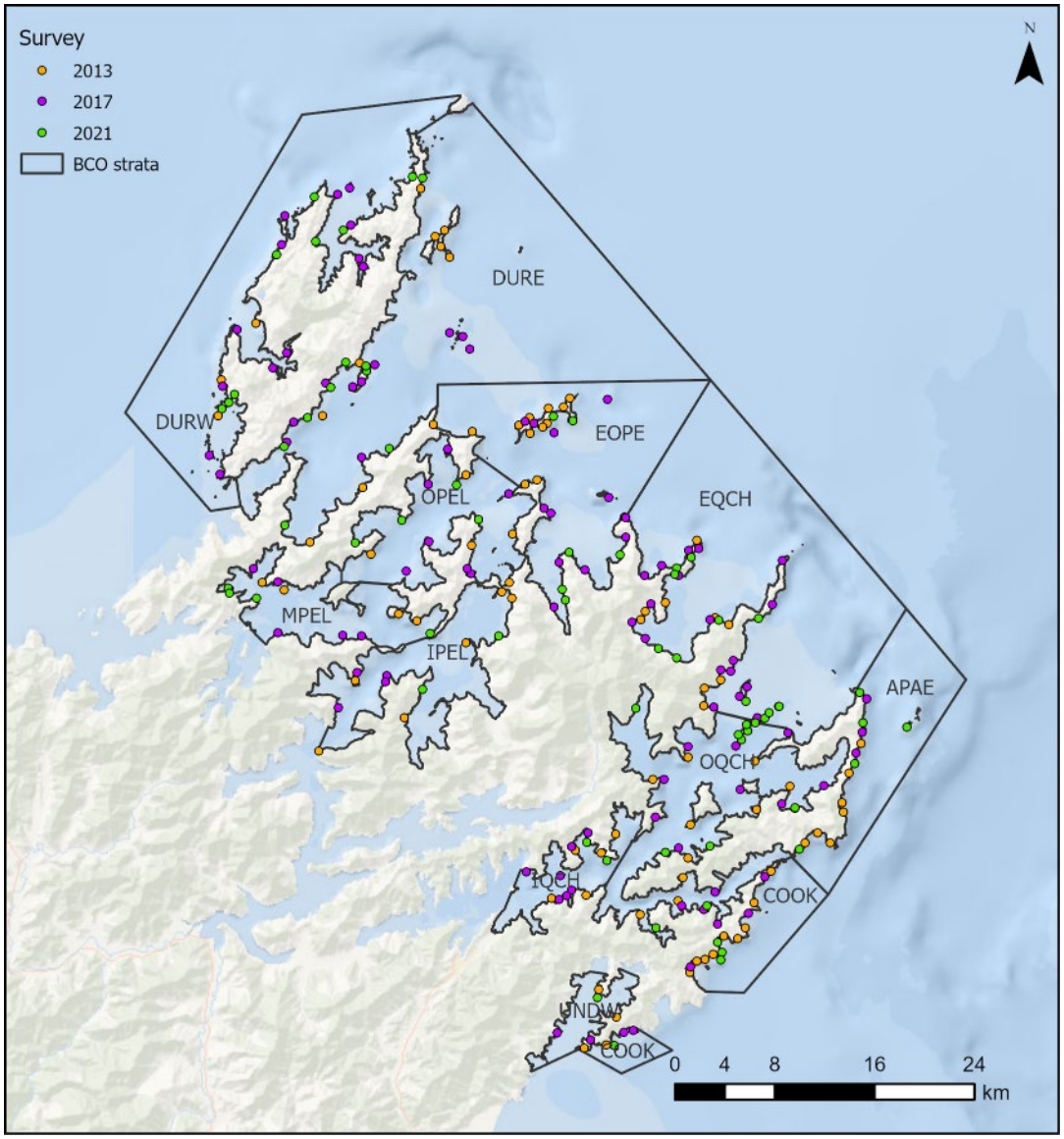

Figure 5: **Blue cod potting surveys in 2013, 2017 and 2021 (the three most recent) and survey strata in the Marlborough Sounds. Dots represent sites around which 9 pots were set along the coast.**

Habitat data

Several seafloor mapping projects have been undertaken within and around the Marlborough Sounds using multibeam echosounders (Neil et al. 2018; IXblue 2020)[3]. Multibeam surveys provide high quality data on the physical characteristics of sea floor habitats at very fine spatial resolution (e.g., 1 – 2 m). While bathymetric data (i.e., depth of the sea floor) is the most used variable for hydrographic surveys, derivatives from bathymetry (e.g., slope, rugosity, bathymetric position index, aspect) also hold significant value for characterising benthic habitats for ecological investigations (Brown et al. 2011; Ierodiaconou et al. 2011; Porskamp et al. 2022). Further, backscatter data can provide a useful index of substrate type (based on the strength of the returned acoustic signal) which can be a key factor influencing benthic species distributions. For this study, we pooled all available data from multibeam echosounder surveys in the Marlborough Sounds, including those undertaken for Marlborough District Council (MDC) in Queen Charlotte and Pelorus Sounds (Neil et al. 2018, IXblue 2020), surveys undertaken for the MBIE juvenile bottlenecks programme, and areas mapped during the 2013 blue cod potting survey (Beentjes et al. 2017) to characterise blue cod habitat. Bathymetric data and bathymetric derivatives (Table 1) from each study were deemed high quality and were retained for analysis. While

[3] Seabed Habitat Mapping - Marlborough District Council

backscatter data from each study were also high quality, there was a lack of calibration during some surveys which means that backscatter values between systems (i.e., between surveys) are not directly comparable. Thus, backscatter was not used in this study.

Additionally, the footprint of the available multibeam data covers only a portion of the wider sounds area and available potting data (Figure ***6***). To enable a full prediction of spawning potential, data derived from multibeam surveys were therefore not used for the wider sounds area analysis and was restricted to the inner sounds area only (where coverage was largely complete, which also excludes inner Pelorus Sound). Variables on seafloor characteristics for the wider sounds area were pooled from national scale databases at a coarser resolution of 250 × 250 m (Table 1).

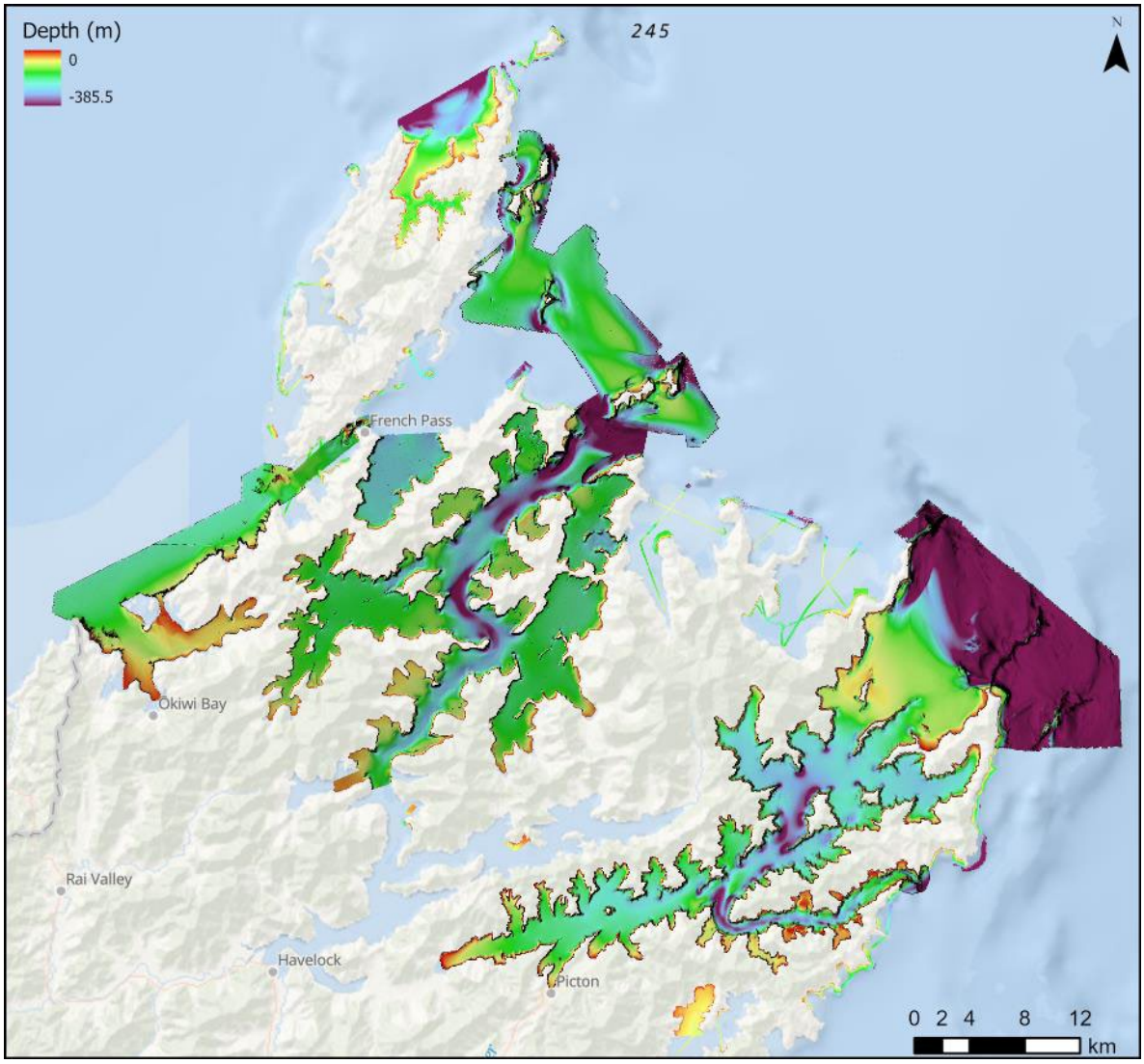

Figure 6: Extent of high-resolution (1–2 m grid) multibeam coverage in the Marlborough Sounds.

Blue cod have known associations with biogenic habitats, particularly those derived from benthic invertebrates (Morrison et al. 2014; Brough et al. 2023, Wade et al. 2025), with some studies showing associations with macroalgae (Brough et al. 2018; Wade et al. 2025). In this study, we obtained spatial data on the presence of large brown macroalgae (i.e., kelps) for the full Marlborough Sounds area from recent work that uses remote sensing technology to map the multispectral signature of kelp beds at the sea surface (Tait et al. 2025). Kelp presence was extracted from the database compiled by Tait et al. (2025) as a time-integrated (from 2016 to 2021) raster layer. If kelp signatures were detected within each (20 by 20 m) raster cell at any time between 2016 and 2021, cells were coded as 'kelp-present' (1) and cells without a kelp signature were coded as 'kelp absent' (0) (Figure ***7***). It should be noted,

however, that these kelp data more accurately reflect species that produce a surface canopy (e.g., *Macrocystis pyrifera)* and thus likely to not provide robust data on other kelps that are more abundant in the Marlborough Sounds (e.g., *Ecklonia radiata)* which may be important for blue cod. Additionally, while kelp presence was noted throughout the sounds, there were few areas where kelp was abundant.

The data available on biogenic habitat included the MBIE Juvenile Bottlenecks and MDC Ecologically Significant Marine sites (ESMs) datasets. Both datasets were collected using towed video and thus provide point locations of biogenic habitat, and in many cases have sufficient coverage to fully delineate habitats (e.g., on Chetwode Bank). However areas with such high coverage are not well represented throughout the Marlborough Sounds (Figure *7*) and thus coverage of these datasets was therefore not sufficient to include in the modelling, however, the information on biogenic habitats is useful to include qualitatively when considering the placement of potential closed areas. Similarly, layers for the distribution of filter feeding bivalves (Ribó et al. 2021; Anderson et al. 2021), bryozoans and Galeolaria (Anderson et al. 2020a) generated using spatial models provided robust information, but only for the Queen Charlotte/Totaranui area (Figure 7), and thus were not included in this study.

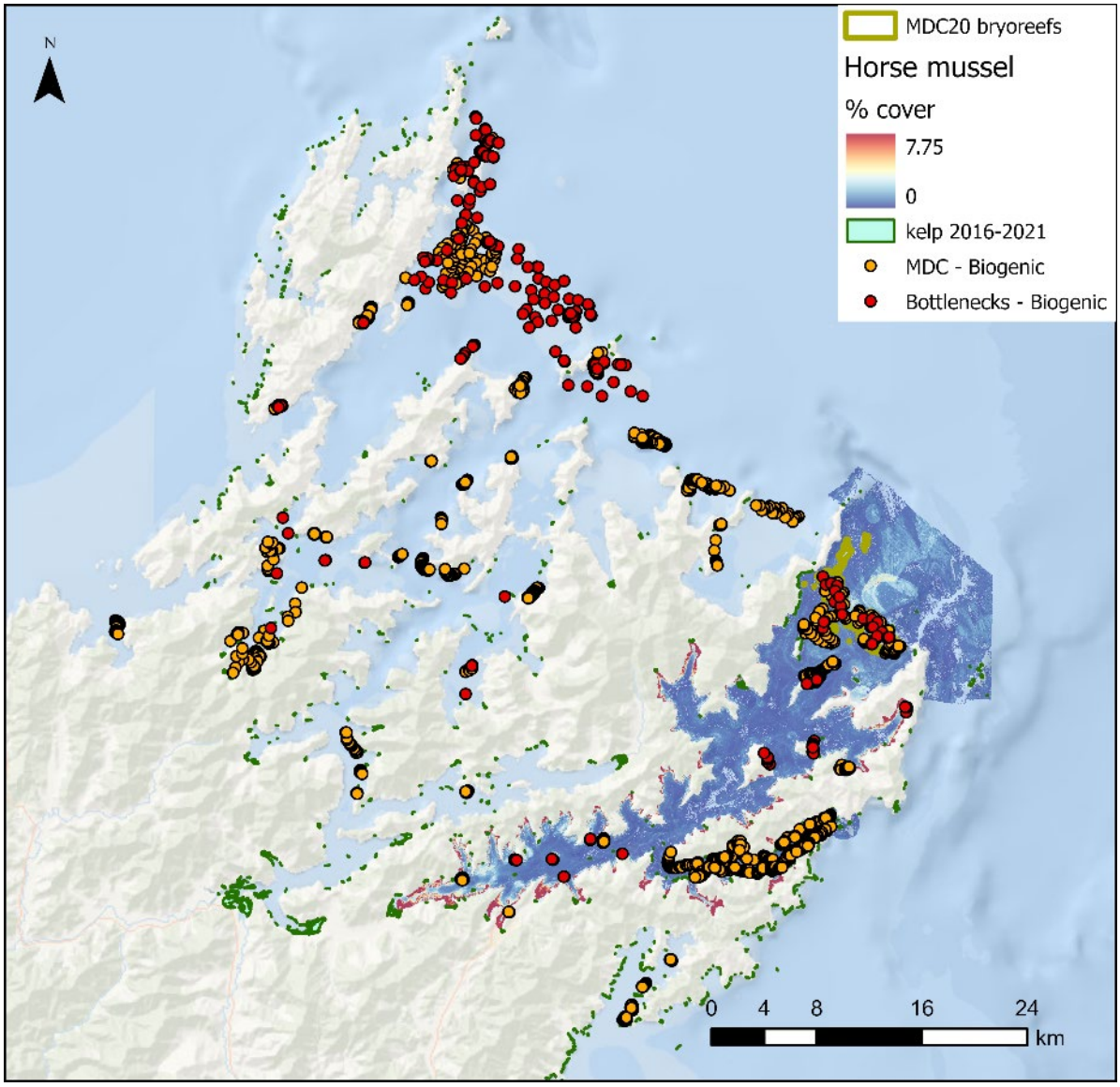

Figure 7: **Available biogenic habitat data on the occurrence of biogenic habitat forming taxa in the Marlborough Sounds, including predictions from spatial models for benthic taxa in Queen Charlotte Sound (e.g., Anderson et al. 2021). Kelp polygons also include some signature of subtidal seagrass indicated in the upper reaches of the sounds.**

Table 1: The compilation of environmental datasets used to represent the environmental characteristics of blue cod habitats. Many of the environmental layers used for this work were compiled as national scale datasets for other projects (Lundquist et al. 2020b, Stephenson et al. 2022). Layer names, descriptions, and units are given as well as reference and source information for each layer.

Layer name	Full name	Temporal range	Description	Units	Source
ADET	Detrital absorption	2002 – 2021	Total detrital absorption coefficient at 443 nm, including due to coloured dissolved organic matter (CDOM) and particulate detrital absorption	m^{-1}	SCENZ (Pinkerton et al. 2022)
Aspect	Aspect	Static	Aspect measures surface direction. It ranges from 0 to 359.9 degrees, measured clockwise from north, and −1 for locations of no slope. Derived from high resolution multibeam data available for inner sounds domain	°	NIWA, unpublished (Juvenile Bottlenecks, BCO survey), MDC
Bathy	Bathymetry	Static	Depth of the seafloor. Derived from high resolution multibeam data available for inner sounds domain	m	National scale dataset NIWA, unpublished (Juvenile Bottlenecks, BCO survey), MDC
BBP	Particulate backscatter	2002 – 2021 (monthly)	Backscatter of particulates at 555 nm (derived from satellite remote sensing)	m^{-1}	SCENZ (Pinkerton et al. 2022)
BedDist	Benthic sediment disturbance	2017 – 2018	One-year mean value of friction velocity from wave action	ms^{-1}	National scale dataset (Swart 1974); updated in 2019
BPI_broad	BPI_broad	Static	Bathymetric position index (BPI) is a measure of where a referenced location is relative to the locations surrounding it. Terrain metrics were calculated using an inner annulus of 25 m and a radius of 125 m. Derived from high resolution multibeam data available for inner sounds domain	m	NIWA, unpublished (Juvenile Bottlenecks, BCO survey), MDC

Layer name	Full name	Temporal range	Description	Units	Source
BPI_fine	BPI_fine	Static	Bathymetric position index (BPI) is a measure of where a referenced location is relative to the locations surrounding it. Terrain metrics were calculated using an inner annulus of 5 m and a radius of 25 m. Derived from high resolution multibeam data available for inner sounds domain	m	NIWA, unpublished (Juvenile Bottlenecks, BCO survey), MDC
Carbonate	Percent carbonate	Static	Percent carbonate layer developed from >30 000 sediment core data	%	National scale dataset (Bostock et al. 2019)
CHL	Chlorophyll-a concentration	2002 – 2021 (monthly)	A proxy for the biomass of phytoplankton present in the surface ocean (to ~30 m depth)	mg m^{-3}	SCENZ (Pinkerton et al. 2022)
ChlAGrad	Chlorophyll-a concentration spatial gradient	2002 – 2019	Smoothed magnitude of the spatial gradient of annual mean Chl a, derived from Chl a described above	mg m^{-3} km^{-1}	National scale dataset NIWA unpublished, updated in 2020
DynOc	Dynamic oceanography	1993 – 1999	Mean of the 1993 – 1999 period sea surface above geoid	m	National scale dataset NIWA, unpublished
EBED	Seabed incident irradiance	2002 – 2021 (monthly)	Broadband (400–700 nm) incident irradiance (E m^{-2} d^{-1}) at the seabed, averaged over a whole year	E m^{-2} d^{-1}	SCENZ (Pinkerton et al. 2022)
Gravel	Percent gravel	Static	The percent gravel layers for the region were developed from >30 000 raw sediment sample data compiled in dbseabed (Jenkins et al. 1997), which were then imported into ArcGIS and interpolated using Inverse Distance Weighting (Bostock, pers. comm.)	%	Bostock et al. 2019
Kelp	Kelp occurrence	Time integrated (from 2016 to 2021)	Occurrence of kelp between 2016 and 2019. Any cell that has recorded kelp presence over this time is designated kelp 'present'.	Presence/ absence	Tait et al. 2025
KPAR	Diffuse downwelling attenuation	2002 – 2019	Vertical attenuation of diffuse, downwelling broadband irradiance (Photosynthetically	m^{-1}	National scale dataset NIWA unpublished,

Layer name	Full name	Temporal range	Description	Units	Source
			Available Radiation, PAR, 400–700 nm)		updated in 2020
Mud	Percent mud	Static	The percent mud layers for the region were developed from >30 000 raw sediment sample data compiled in dbseabed (Jenkins et al. 1997), which were then imported into ArcGIS and interpolated using Inverse Distance Weighting (Bostock, pers. comm.)	%	Bostock et al. 2018
PAR	Photosynthetically active radiation	2002 – 2021 (monthly)	Daily-integrated, broadband, incident irradiance at the sea-surface based on day length, solar elevation and measurements of cloud cover from ocean colour satellites (Frouin et al. 2002)	E m^{-2} d^{-1}	SCENZ (Pinkerton et al. 2022)
Rugosity	Rugosity	Static	Roughness of the seafloor calculated as the variation in three-dimensional orientation of grid cells within a 3 m neighbourhood. Derived from high resolution multibeam data available for inner Sounds domain	m	NIWA, unpublished (Juvenile Bottlenecks, BCO survey), MDC
Sand	Percent sand	Static	The percent sand layers for the region were developed from >30 000 raw sediment sample data compiled in dbseabed (Jenkins et al. 1997), which were then imported into ArcGIS and interpolated using Inverse Distance Weighting (Bostock, pers. comm.)	%	Bostock et al. 2018
Slope	Slope	Static	Bathymetric slope was calculated from water depth and is the degree change from one depth value to the next. Derived from high resolution multibeam data available for inner sounds domain	°	NIWA, unpublished (Juvenile Bottlenecks, BCO survey), MDC
SST	Sea surface temperature	2002 – 2021 (monthly)	Blended from OI-SST (Reynolds et al. 2002) ocean product and MODISAqua SST coastal product. Long term (2002 – 2021) average values at 250 m resolution	°C	SCENZ (Pinkerton et al. 2022)

Layer name	Full name	Temporal range	Description	Units	Source
SSTGrad	Sea surface temperature gradient	1981 – 2018 (ocean); 2002–2018 (coastal)	Smoothed magnitude of the spatial gradient of annual mean SST. This indicates locations in which frontal mixing of different water bodies is occurring (Leathwick et al. 2006)	°C km^{-1}	National scale dataset NIWA unpublished, updated in 2020
TC	Tidal Current speed	2009 – 2020	Maximum depth-averaged (New Zealand bathymetry) flows from tidal currents calculated from a tidal model for New Zealand waters (Walters et al. 2001)	ms^{-1}	National scale dataset NIWA unpublished, updated in 2020
TempRes	Temperature residuals	2017 – 2018	Residuals from a GLM relating temperature to depth using natural splines – highlights areas where average temperature is higher or lower than would be expected for any given depth	°C	National scale dataset (Leathwick et al. 2006)
VGPM	Net primary production by the vertically generalised production model	2002 – 2019	Daily production of organic matter by the growth of phytoplankton in the surface mixed layer, net of phytoplankton respiration	mgC m^{-2} d^{-1}	National scale dataset NIWA unpublished, updated in 2020

Predictor variables

Explanatory predictor variables for modelling the distribution of spawning potential included data on habitat characteristics discussed above, data on environmental conditions, and information on the distribution of fishing effort from recreational and commercial fisheries for blue cod.

The environmental data used in this project were compiled from three data types:

1. A repository of spatially explicit environmental datasets recently compiled for spatial analyses of biodiversity patterns at the national scale (Stephenson et al. 2022, Stephenson et al. 2023). The repository provides a broad range of information on the physical seafloor environment (e.g., depth, slope, rugosity), oceanographic properties and processes (temperature, light, tidal and boundary current velocity, swell exposure) and primary productivity (e.g., chlorophyll-a gradient, vertically integrated productivity). The database includes both static variables (i.e., variables not expected to vary over time, e.g., depth, slope) and oceanographic data averaged for the period 2002–2019, all gridded at resolution of 250 × 250 m, but with a range of native resolutions (Table 1).
2. Dynamic variables were sourced from NIWA's Seas, Coasts, Estuaries – New Zealand (SCENZ) database that houses satellite-derived environmental data (Pinkerton et al. 2022) at a resolution of 500 × 500 m. SCENZ variables include sea surface temperature, chlorophyll-a concentration, light at the seabed (EBED) and three measures associated with coastal water quality/turbidity (BBP, TSS, ADET) (Table 1). SCENZ variables were accessed at monthly resolution, matching the month of each blue cod survey (October of each survey year). The

model output predictions were made using an average across the annual averages from 2013 to 2021.

3. The high-resolution multibeam data collected for MDC, the MBIE Juvenile Bottlenecks Programme and the 2013 blue potting cod survey. These datasets only cover the inner sounds and small patches around the outer sounds but are at a much higher resolution of 2 × 2 m. These layers were re-sampled to 10 × 10 m for the analysis to reduce computational system load. The multibeam data includes bathymetry but also derived variables such as seafloor aspect, slope, bathymetric position index (BPI) and rugosity.

Spatially explicit data on the distribution of recreational fishing pressure for blue cod was extracted from the 2016–17 aerial access survey (Hartill et al. 2017, Fisheries New Zealand 2025) of recreational fishing in the Marlborough Sounds. Data were provided as point locations for recreational fishing vessels with an attributed estimate for blue cod harvest (in kg) (Figure 8). A spatial layer for the relative distribution of fishing pressure was generated by applying a fixed kernel density estimator (Worton 1989), to these point locations using the reference bandwidth as a smoothing parameter. For commercial fishing, the location and green weight of all commercial fishing pot sets in the Marlborough Sounds was extracted from the geospatial position reporting (GPR) database by the Research Data Management team at Fisheries New Zealand and this was gridded at the same 250 m grid resolution used for modelling (Figure 8). Commercial fishing was available from the 2019 to present fishing year and provides an estimate of the distribution of commercial fishing pressure that may influence the distribution of blue cod in the Marlborough Sounds. Commercial fishing data cannot be plotted at the same resolution used for analysis due to commercial sensitivities and thus Figure 8 shows an outline of the spatial distribution of these data only.

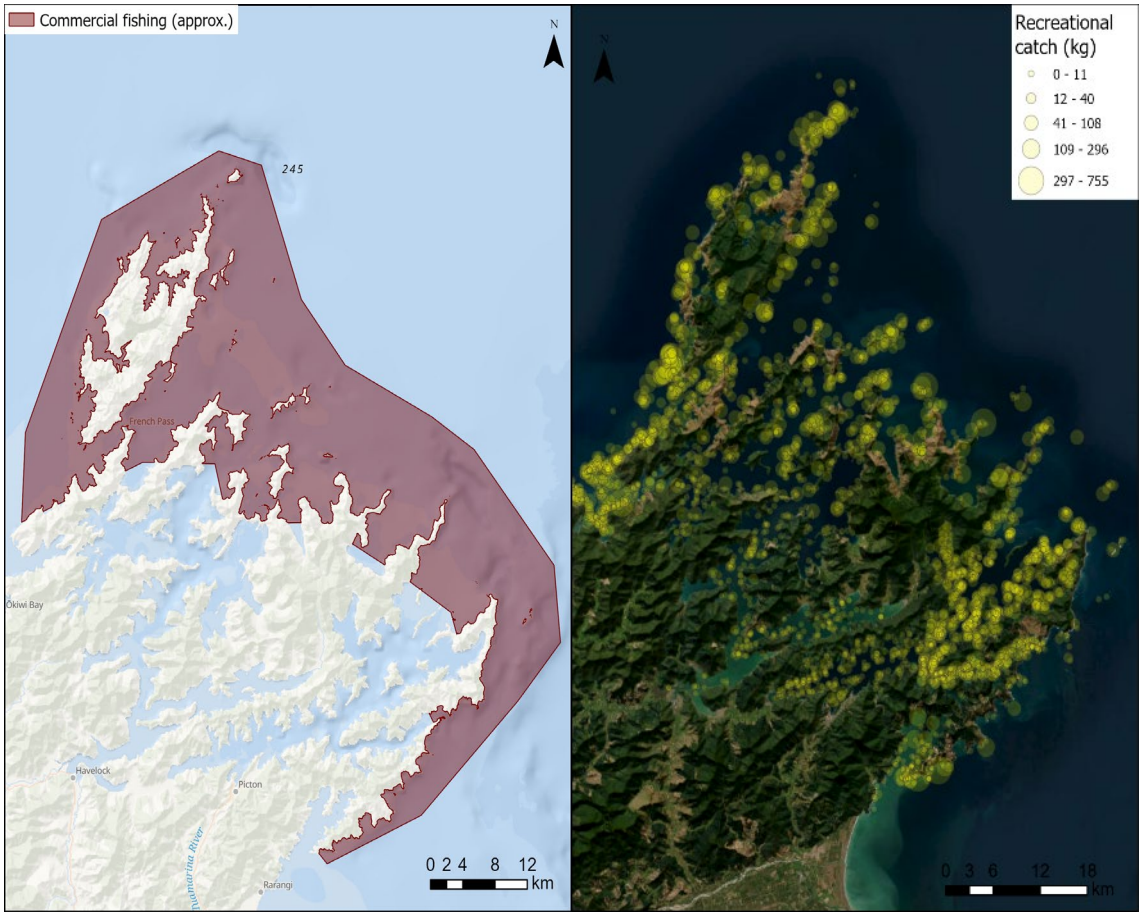

Figure 8: **Raw data on the distribution of estimated blue cod catch (in kg) from commercial fisheries (left) and recreational fisheries (right) within the Marlborough Sounds area. Commercial data was sourced from the GPR database and gridded at 250 m resolution. Recreational data was sourced from the 2016-2017 aerial access survey of the Marlborough Sounds (Hartill et al. 2017). Note commercial data cannot be displayed at the resolution used for analysis due to commercial sensitivities and thus this figure shows an outline of the distribution of the raw data only.**

2.2 Distribution of blue cod and key habitats

There were clear patterns in the raw data on the distribution of blue cod and indices of blue cod stock status across the Marlborough Sounds when pooling data across the last three potting surveys (Figure 9; Figure 10). Pooled by pot set, the total biomass of blue cod was substantially higher in coastal areas adjacent to the sounds, particularly around D'Urville Island (Figure 9). Other areas with high overall biomass included the Chetwode Islands and the Long Island-Kokomohua Marine Reserve, with the latter being the only area within the inner sounds with high biomass. All other areas in both Pelorus and Queen Charlotte Sounds had very low total biomass of blue cod. The distribution of sex ratio across the Marlborough Sounds followed a similar pattern, with the areas with a more balanced sex ratio typically occurring around D'Urville Island. Sex ratio was skewed to a very high proportion of males on the east coast between Port Underwood and Cape Koamaru, but also included coastal areas from the Chetwode Islands to Cape Jackson. Alternatively, inner Queen Charlotte Sound and around Fitzroy Bay exhibited a comparatively high proportion of females. However, this should be viewed in context with the very low biomass in these areas; the fact is that there are very few fish of either sex in these locations. Female biomass (Figure 10), showed trends similar to total biomass, with the only areas of high female biomass occurring in the west of D'Urville Island and within Long Island-Kokomohua Marine Reserve.

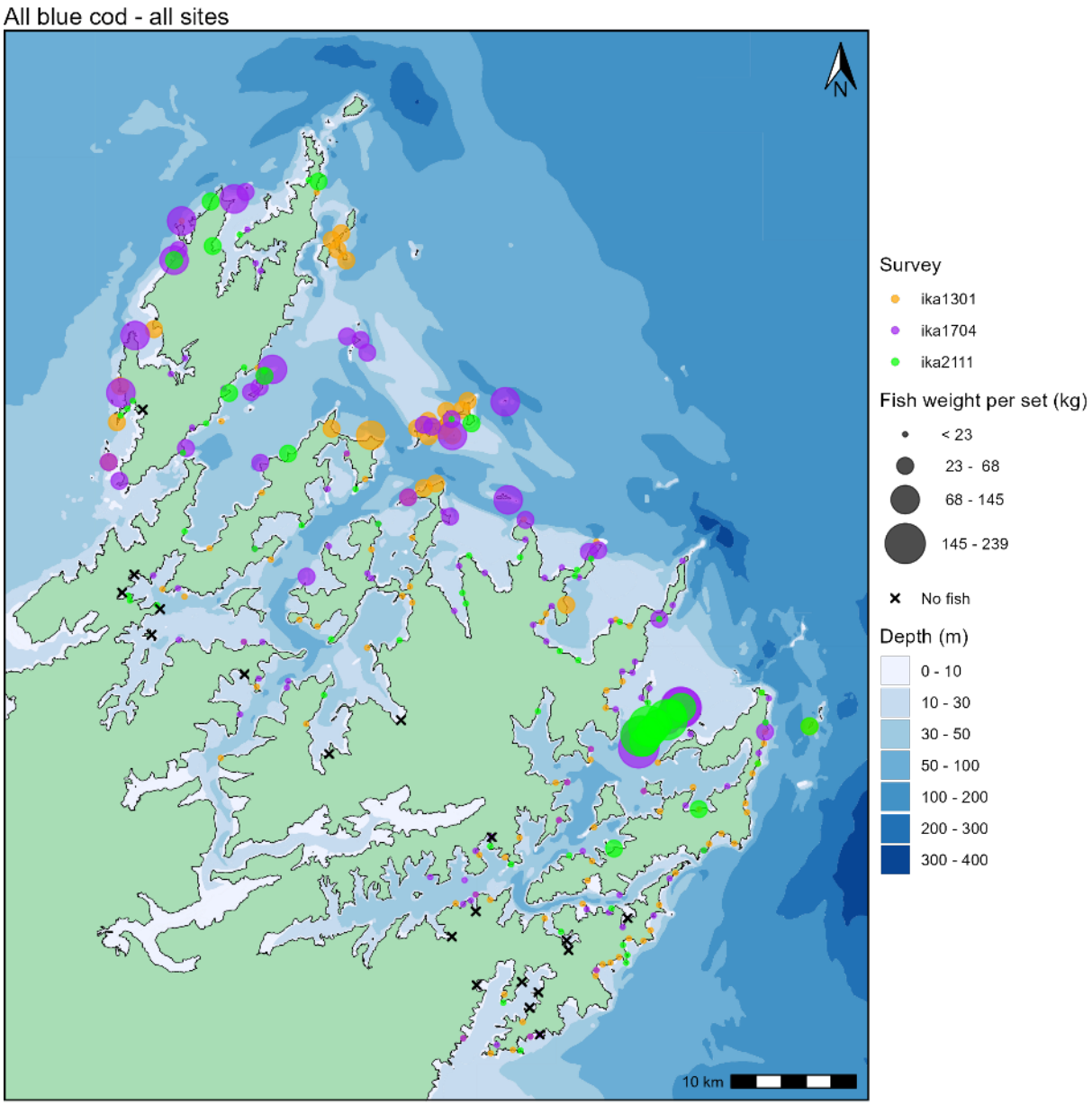

Figure 9: Blue cod weight (kg) per pot set. Data on the total blue cod weight per pot set from three potting surveys of the Marlborough Sounds (IKA1301, IKA1704, IKA2111) undertaken in 2013, 2017 and 2021 respectively.

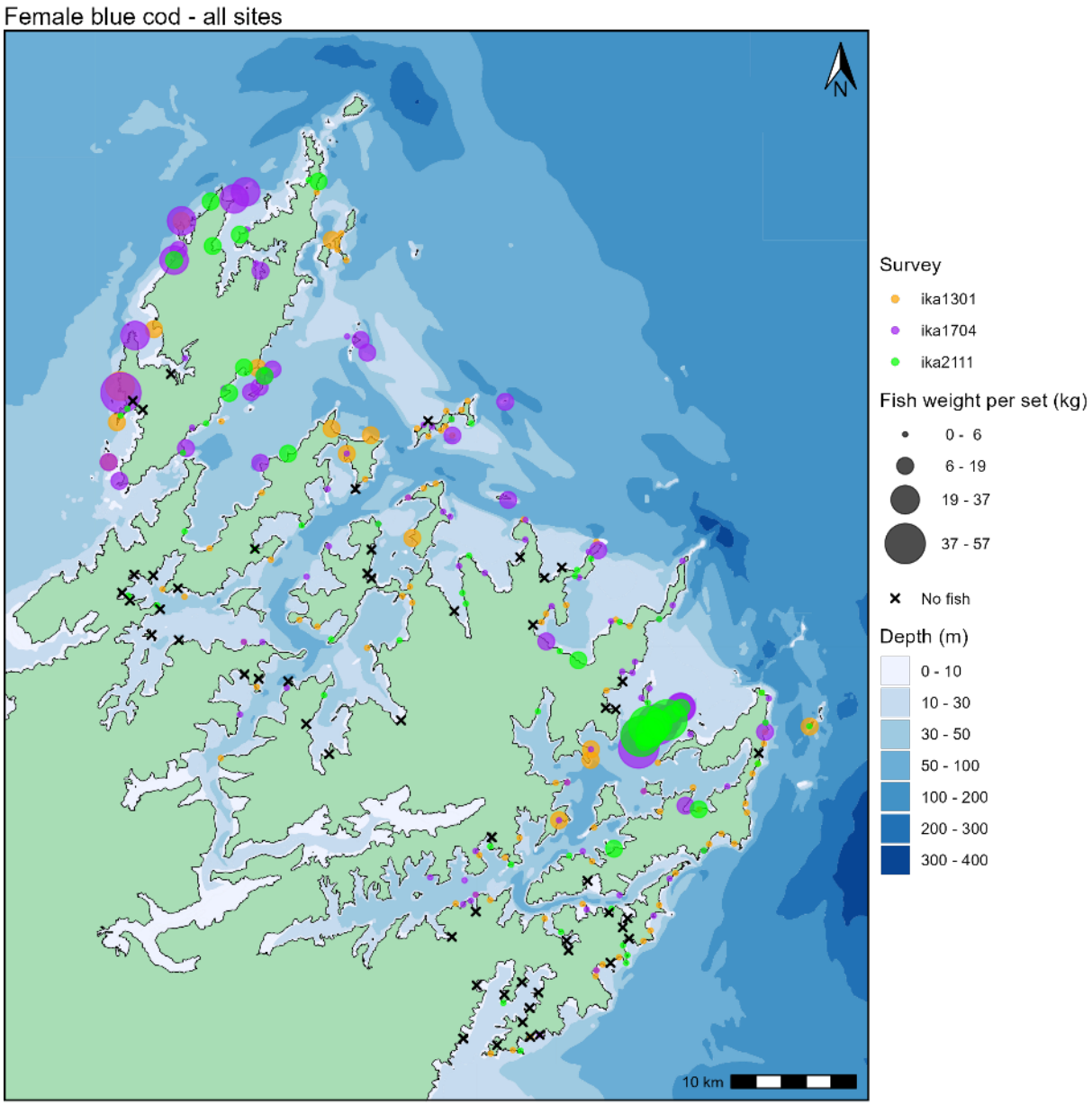

Figure 10: Female blue cod weight (kg) per set. Data on the total biomass (kg) of female blue cod weight per pot set from three potting surveys of the Marlborough Sounds (IKA1301, IKA1704, IKA2111) undertaken in 2013, 2017 and 2021 respectively

According to data from the Research Programme 'Juvenile fish habitat bottlenecks', juvenile blue cod (0+ and 1+ year olds) were essentially absent from the inner half of both Queen Charlotte and Pelorus Sounds (Figure 11). In the outer half of Pelorus Sound, limited sites with low juvenile cod abundance were found where headlands and open shores fronted onto the main channel axis, with associated higher tidal currents and the availability of cleaner reef surfaces (reefs being fine scale mosaics of low rock and coarse sand pockets/terraces, sloping down into the main channel). Soft sediment biogenic habitats of value to juvenile cod (e.g., horse mussel beds, dead dog cockle drifts, calcified bryozoan patched/fields) were missing from Pelorus Sound (considered historically lost). The outer half of Queen Charlotte Sound (QCS) was in better shape environmentally (albeit still greatly reduced from its historical state), with higher juvenile blue cod densities found associated with habitats of: a) dead dog cockle shell drifts (e.g., southern side of Long Island, Patten Channel, Pickersgill Channel; b) bryozoan *Celleporaria agglutinans* patch reefs with associated epifauna/epiflora, present as larger patch reefs (1–3 m width, 20–50 cm height) in two large but low-density adjacent fields in outer QCS (an area known

as the Duck Pond), and as smaller biogenic clumps along the reef edges of Tory Channel; c) low density horse mussel beds in East Bay on coarse sand/shell; and d) emergent tubeworm patch field associated with the eastern reef edges of Blumine and Pickersgill islands (Figure ***12***).

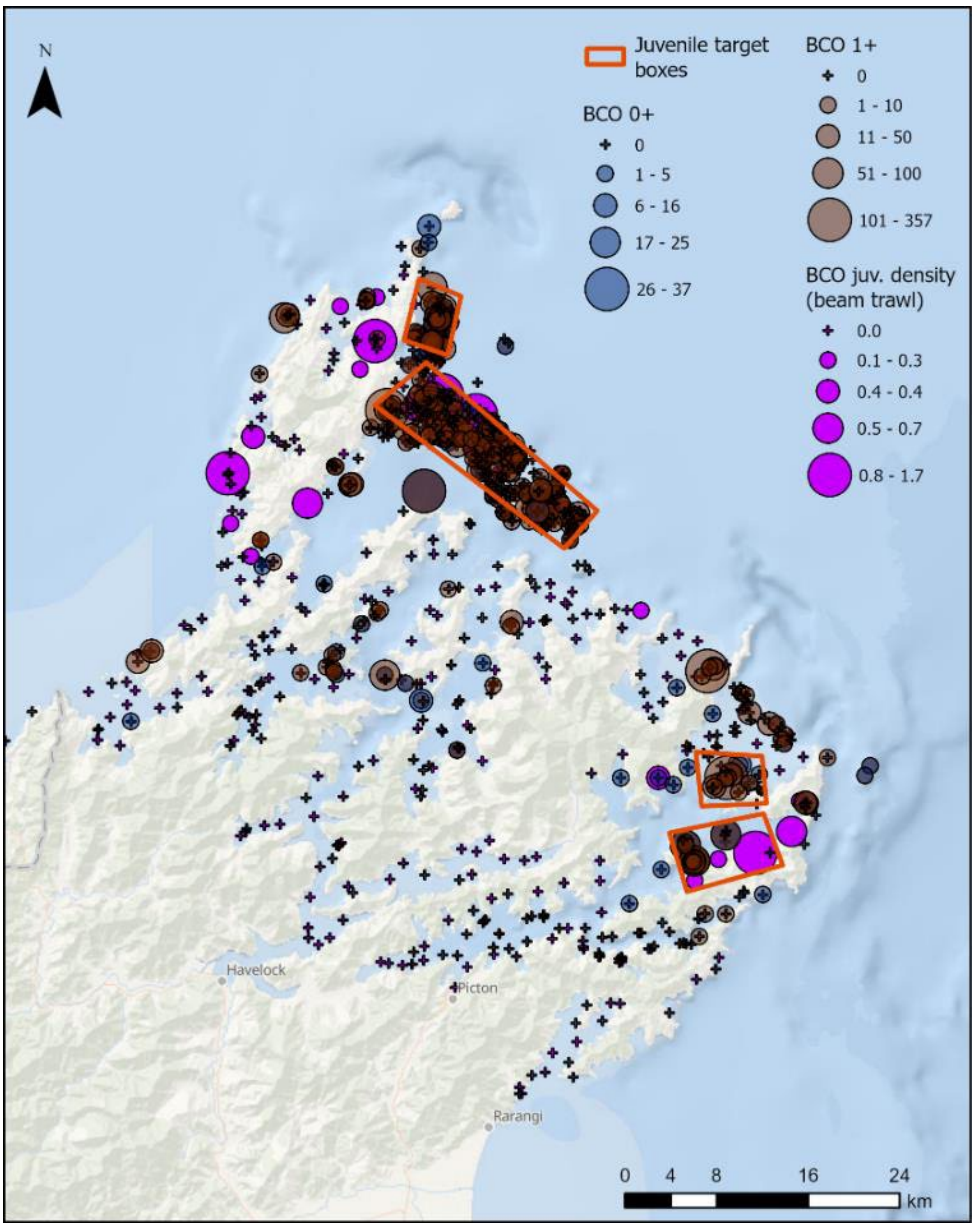

Figure 11: Distribution of juvenile blue cod that were used to define the target polygons in particle tracking (Section 2.4) (orange boxes). These data are from the NIWA[4] MBIE Research Programme 'Juvenile fish habitat bottlenecks [CO1X1618]'. Included are survey data from 2017 (towed video and fine mesh research beam trawl), 2019 (towed video select sites), 2020 (towed video, inner Sounds), and 2021 (towed video, range of sites across region, strong focus on Chetwode Bank. The 2019–2021 data series is provisional, with more stations to add, with a draft AEBR being prepared (Morrison et al., unpubl. data, in prep.) There are some differences in the metrics used to summarise juvenile abundance between surveys in 2017 and later surveys, however all data give useful indications on areas of high abundance of juvenile fish.

[4] Now Earth Sciences New Zealand (ESNZ)

On the coast and adjacent islands, areas of higher juvenile blue cod densities were associated with: a) reef edges (often with associated biogenic rubble ribbons); and b) dead dog cockle shell drifts, which were usually found relatively near to shorelines in this region (Figure ***12***). The presence of Chetwode Bank (here defined as from the Rangitoto Islands through to the Chetwode Islands, including the Trio Islands – to a variable water depth of 40 to 60 m) provided additional high value juvenile blue cod habitats, including areas of: a) denser horse mussels in a range of configurations (patches to large beds); b) bryozoan fields of several distinctive kinds (contributing dominant species); and c) mixed biogenic habitats, with varying contributions of habitat formers, including calcified bryozoans, horse mussels, hydroids/hydroid trees, sponges, and ascidians, on both sand and shell-dominated seafloor sediments (Figure ***12***).

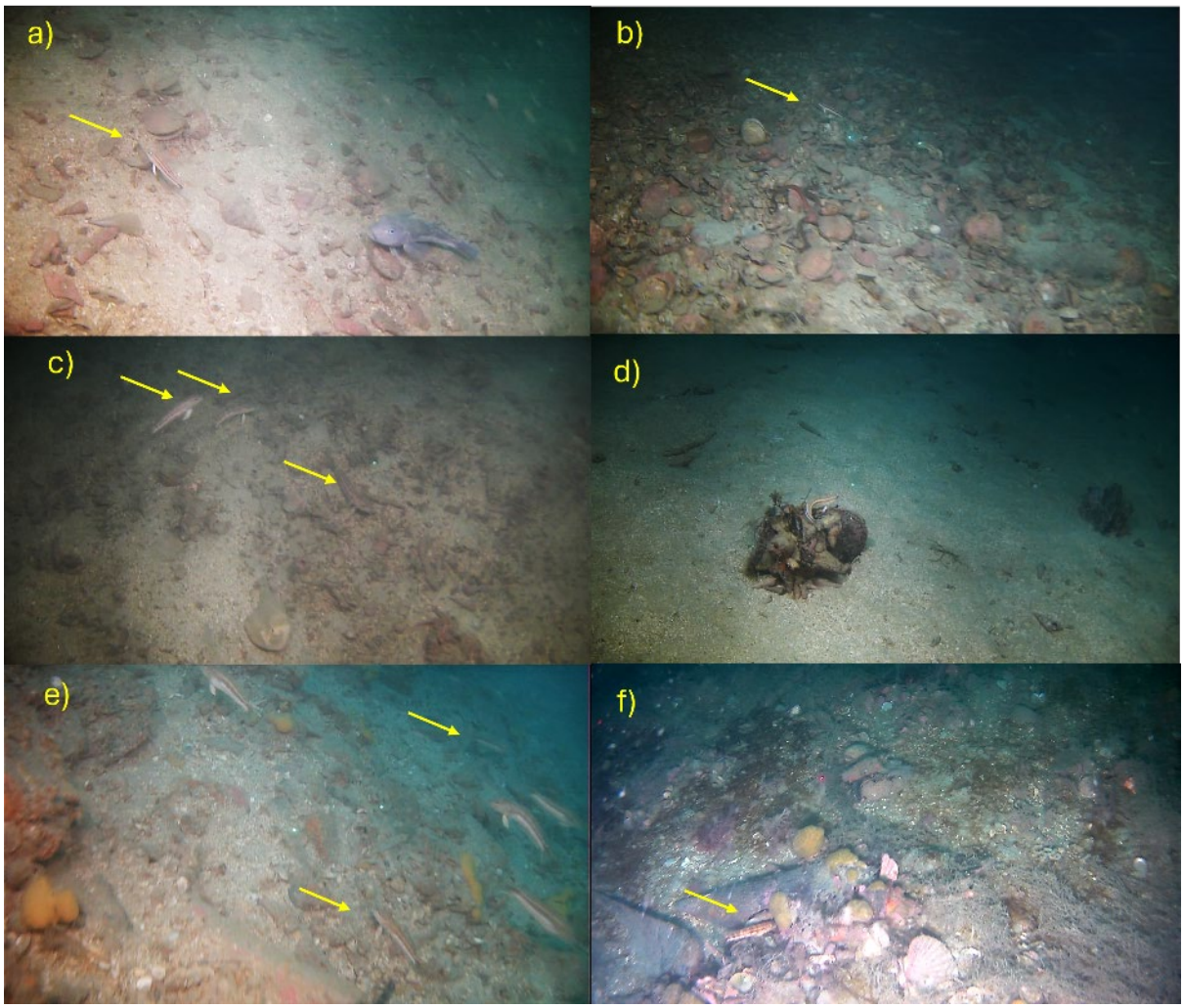

Figure 12: Juvenile (0+/1+) blue cod nursery habitats in the Marlborough Sounds proper. Queen Charlotte Sound, Patten Passage, a) 0+ blue cod along with adult on mixed dog cockle/shell and shell grit, b) 0+ newly settled 0+ blue cod (black and white striped) on dead dog cockle shells; Blumine Island east side, c) 0+/1+ blue cod on mixed shell/shell grit; Upper East Bay, d) 0+ blue cod on horse mussel and ascidians clump; Pelorus Sound, Tapapa Point (east of Maud Island), e) 0+/1+ blue cod on mixed rock and coarse sediment slope, Maud Island; f) 0+ blue cod on dead horse mussel shell and whole shell debris. Yellow/orange blobs in e–f are the ascidian Cystodytes dellachiajei, the most common ascidian seen by towed video in the Marlborough Sounds. Laser scale is 175 mm. (Source: NIWA Juvenile fish habitat bottlenecks programme, CO1X1618).

2.3 Modelling the distribution of spawning potential

Species distribution models (SDMs) were used to predict the distribution of spawning potential for blue cod across two scales – the 'wider' model domain, and the 'inner sounds' domain (Figure 4). Using groomed data from the potting surveys, pooled over the last three surveys, we constructed SDMs that fit the relationship between the total weight of female blue cod (i.e., cumulative biomass) at each potting location and the habitat characteristics/environmental conditions at that site. For each data point, we also included estimates of present-day harvest in recreational and commercial fisheries to attempt to compensate for the influence of fishing on distribution (see discussion). Modelling used female biomass as a proxy for fecundity, based on the relationship between female size and egg production (Kolodzey 2021), and following feedback from the Fisheries New Zealand Aquatic Environment Working Group (AEWG). Initial model development explored modelling fecundity directly by transforming female biomass to batch fecundity using equations developed by Kolodzey (2021), however these relationships were deemed highly uncertain and thus female biomass was retained as the final response variable. SDMs were fit for the wider sounds and inner sounds domains separately. For the inner sounds, we used a broad range of local-scale data on benthic habitats (e.g., multibeam derived variables, kelp occurrence) pooled with data from NIWA's database of national scale environmental layers (Table 1) to explore holistic contributors to good quality habitat for blue cod. As noted above, multibeam derived variables do not cover the full extent of the wider sounds domain, thus, were not included for analyses at that scale. With the exception of data on kelp presence, data on biogenic habitats were similarly patchy (Figure 7), covering only a small portion of the extent of both model domains and thus was not included in the SDMs (see Section 2.4 for the use of these data). SDMs also included two categorical variables to account for any variation attributed to survey design (i.e., fixed or random site selection) or survey occasion (i.e., 2013, 2017, 2021).

A 'hurdle model' SDM framework was used for predicting the distribution of female blue cod biomass. A hurdle model is a two-part SDM approach that combines predictions from a presence-absence (PA) formulation with predictions of biomass on a continuous scale (so-called 'abundance models') (Maunder & Punt 2004, Fletcher et al. 2005). The PA component of the hurdle models used each record of a female blue cod in an individual pot set as a 'presence' data point (= 1), while absences were pots with no female fish recorded (= 0), which was supplemented with a randomly generated 'background' dataset (10 000 points randomly distributed throughout the wider sounds domain). The potting surveys are designed to target areas of known blue cod habitat and have high overlap with recreational and commercial fishing (Section 2.1) which was visually confirmed using spatially explicit data on blue cod catch from both fisheries (see Section 2.1). However it should be noted that there are some areas with high reported catches that are not currently included in the potting survey area (e.g., Kenepuru Sound). Including randomly generated background data is a standard approach for presence-only SDMs (Barbet-Massin et al. 2012) and ensures that the environmental signature of areas that are not considered blue cod habitat are included within the modelling framework. The abundance component of the hurdle model used a log transformed measure of the female blue cod biomass per pot as a response variable. Spatial predictions and partial dependence plots were back-transformed for visualisation purposes.

All input environmental, habitat and fishing predictor variables were checked for collinearity using standard procedures (Dormann et al. 2013), and variables with lower importance scores within any correlated pairs were discarded. The residuals of the SDMs were checked for spatial autocorrelation that may undermine the robustness of our predictions (Elith & Leathwick 2009). Boosted regression tree (BRT) and random forest (RF) algorithms were used for both the PA and abundance components of the hurdle model (Breiman 2001, Elith & Leathwick 2017). BRTs were iteratively fit using an initial learning rate of 0.01, tree complexity of 2 and step size of 25, with each iteration halving the learning rate until a model with at least 1500 trees could be fit. RFs were fit with 1000 trees at each tuning step, a step factor of 1.5 and an 'out of bag' error improvement threshold of 0.00001. PA and abundance models were modelled with a binomial and gaussian error distribution respectively for both the BRTs and RFs. Models were tuned with a bootstrapping procedure using a random selection of 70% of the available training data, with the remaining 34% being retained as a withheld evaluation dataset for each iteration. For PA models, BRT and RF models were evaluated using area under the curve (AUC) and true skills statistic (TSS) metrics while abundance models used R^2 and Spearman's correlation

coefficient, using the withheld dataset at each iteration. The bootstrapping procedure was carried out 100 times with independently selected training (70%) and evaluation data (30%) for each iteration.

The relative importance of each predictor variable to the models used to predict spawning potential was calculated for the RF and BRT models at each bootstrap iteration. The importance of each environmental variable p in a RF model, R_p^2, is given by (Ellis et al. 2012):

$$R_p^2 = \frac{R^2 I_p}{\sum_{p'} I_{p'}}$$

where I_p is the accuracy importance of each variable in a forest, and R_p^2 is the proportion of variance explained by the forest. The goodness of fit, R_p^2, is partitioned among the variables in proportion to their accuracy importance, I_p. The accuracy importance (I_p) is standardised by the densities across the raw importance from each split in each tree (for each variable p) and normalized such that they sum to R_p^2 (Ellis et al. 2012). For BRTs, the predictor variable importance is based on the number of times the variable is selected for splitting, weighted by the split's squared improvement to the model, and averaged over all trees (Friedman & Meulman 2003). Using the *partial* function in pdp R package (Greenwell 2024), partial dependence plots were also generated for each model iteration showing the relationship between habitat suitability (for the PA models) or biomass (for the abundance models) and the environmental/habitat variables retained in each model formulation.

Spatial predictions of habitat suitability index (HSI) and biomass, for the PA and abundance components respectively, were generated from the BRT and RF models for each bootstrap iteration using a 10 m (inner sounds) and 250 m (wider sounds) grid of environmental variables averaged over the time of the potting survey data (i.e., 2013 – 2021). Final ensemble predictions that combined BRT and RF outputs were then generated by taking weighted averages of the predicted HSI and biomass from each model type, using methods described by Stephenson et al. (2021b) and Anderson et al. (2020b). The procedure uses a two-part weighting, with contributions from the overall model performance (AUC or Spearman's correlation) of each model type (BRT / RF) and the uncertainty (SD) in each cell from spatial predictions from each model type.

$$W_{1BRT} = \frac{MPS_{BRT}}{MPS_{BRT}+MPS_{RF}} \text{ and } W_{1RF} = \frac{MPS_{RF}}{MPS_{BRT}+MPS_{RF}}$$

$$W_{2BRT} = 1 - \frac{SD_{BRT}}{SD_{BRT}+SD_{RF}} \text{ and } W_{2RF} = 1 - \frac{SD_{RF}}{SD_{BRT}+SD_{RF}}$$

$$W_{BRT} = \frac{W_{1BRT}+W_{2BRT}}{2} \text{ and } W_{RF} = \frac{W_{1RF}+W_{2RF}}{2}$$

$$X_{ENS} = X_{BRT} * W_{BRT} + X_{RF} * W_{RF}$$

$$SD_{ENS} = SD_{BRT} * W_{BRT} + SD_{RF} * W_{RF}$$

where MPS_{BRT} and MPS_{RF} are the model performance statistics; X_{BRT} and X_{RF} are the model predictions; SD_{BRT} and SD_{RF} are the bootstrapped SDs; and X_{ENS} and SD_{ENS} are the weighted ensemble predictions and weighted SDs, respectively, from which maps of predicted distribution and model uncertainty were produced.

A final hurdle model prediction was then generated by combining the ensemble predictions for the PA and abundance components of the framework, such that the predicted biomass of females is contingent on the probability of female presence (Maunder & Punt. 2004).

$$E[X] = P(Y > 0) \times E[Y \mid Y > 0]$$

Where E[X] is expected biomass, P(Y > 0) = predicted probability of presence and E[Y | Y > 0] is the expected abundance conditional on presence. The final spatial predictions from the hurdle model should be interpreted as a relative, dimensionless measure of female biomass given the presence of female blue cod. In other words, if female blue cod are present in a given area, what would be their likely biomass given the habitat, environmental and fishing characteristics of each cell.

Similar to the ensemble spatial predictions, the weighted mean (by model evaluation statistics) of the other key model outputs was also generated across the 100 bootstrap iterations including variable importance scores and partial dependence plots along with the averaged BRT and RF model evaluation statistics.

The same modelling procedure was undertaken separately for the wider and inner sounds modelling domains, with the key difference being the input data; the full quantity of blue cod potting data was used for the wider sounds, with the inner sounds using only potting data that overlay multibeam survey coverage (which included a small number of outer sounds locations). Additionally, the spatial grid for the wider sound's prediction covered the full study area and was more coarse (250 × 250 m), while the inner sounds grid covered areas with continuous multibeam coverage (i.e., largely Queen Charlotte and Pelorus Sounds) at a high resolution (10 × 10 m) (Figure 4).

2.4 Connectivity analysis – particle tracking

Lagrangian particle tracking was used to determine the potential connectivity between blue cod spawning areas and juvenile habitats and the retention of larvae (i.e., particles) within the inner sounds. Lagrangian particle tracking, or dispersal modelling, is a numerical technique that simulates the movement of virtual particles – such as larvae or pollutants – within a realistic ocean or hydrodynamic model. In this way, the particle tracking model calculates particle trajectories based on ocean currents provided by the underlying ocean model.

Lagrangian particle tracking is widely used to investigate the transport and dispersion of marine pollutants, including plastic debris (e.g., Collins & Hermes 2019) and oil spills (Ono et al. 2013). It is also a commonly applied method for modelling larval transport and connectivity (e.g., Michie et al. 2024; Marinone et al. 2008), with broad applications in population genetics (e.g., van der Reis et al. 2022), spatial fisheries management (e.g., Melaku Canu et al. 2021), and the planning and design of marine protected areas (e.g., Carlson et al. 2016).

It should be noted that while particle tracking is regularly used to model larval transport, the approach carries a range of caveats that act to simplify the processes by which larvae disperse. These include, 1) the challenges in incorporating the full range of physical processes that influence particle dispersal in dynamic coastal environments, 2) limited information on life history, spawning (e.g., environmental cues for egg release and settlement) or other biological processes (e.g., predation) or an inability to include these factors within particle tracking models. 3) the use of proxy information on larvae buoyancy characteristics sourced from other fish species due to an absence of this type of information for blue cod. Together, these caveats increase the uncertainty around understanding how blue cod larvae are transported throughout the Marlborough Sounds, however the approach still provides valuable information on the connectivity of habitats that is an important consideration for designating spatial management.

Hydrodynamic models

Currently, no single ocean model provides sufficient resolution to accurately capture the complex dynamics of both the greater Cook Strait and the Marlborough Sounds. To address this, currents for the particle tracking were sourced from three of NIWA's existing high-resolution regional ocean models:

Cook Strait 1 km grid, Pelorus Sound 200 m grid, and Queen Charlotte Sound 200 m grid. All three models are implementations of the Regional Ocean Modelling System (ROMS; Shchepetkin & McWilliams 2005), an open source, 3-dimensional hydrodynamic model widely used by the scientific community for a diverse range of applications including coastal dynamics (e.g., Chao et al. 2018; Collins & Macdonald 2025) and Lagrangian particle tracking (e.g., Michie et al. 2024; Silva et al. 2019).

Cook Strait 1 km model

The largest model domain used for the Lagrangian particle tracking, Cook Strait (1 km grid), was designed to encompass the greater Cook Strait including the South Taranaki Bight and the Cook Strait Narrows at a horizontal resolution of 1 km (Figure 13a). The model bathymetry was constructed from several different sources. The General Bathymetric Chart of the Oceans (GEBCO; https://www.gebco.net/data-products/historical-data-sets#gebco_one) one-minute resolution dataset was used for depths greater than 500 m. This dataset was combined with 250 m grid resolution bathymetric data from NIWA (https://niwa.co.nz/environmental-information/download-bathymetry-data) and land elevation data at 200 m resolution from Land Information New Zealand (LINZ; https://www.linz.govt.nz/). At the surface, the model is forced by wind, heat and freshwater fluxes as well as riverine freshwater inflow. Surface heat and freshwater fluxes were derived from 6-hourly NCEP/NCAR reanalysis data (Kalnay et al. 1996), which provides global analyses of atmospheric fields at a 2.5° resolution. Surface wind stress was derived from 3-hourly winds obtained from the 12 km New Zealand Limited Area Model (NZLAM; Lane et al. 2009). All the rivers draining into the Cook Strait domain (120 rivers) were represented as point sources of freshwater. The rivers draining into the model domain were identified from the New Zealand River Environment Classification (Biggs et al. 1990, Snelder et al. 2010) and a constant annual-mean value of riverine freshwater input was used for each river.

The open boundaries of the model domain were forced by a combination of tides and subtidal ocean conditions. The subtidal lateral boundary conditions were obtained from a global ocean analysis and prediction system based on the Hybrid Coordinate Ocean Model (HYCOM; Chassignet et al. 2009). The HYCOM product used here provides daily snapshots of the 3-dimensional state of the global ocean on a 1/12° grid. The tides imposed at the boundaries of the model domain were specified in terms of amplitude and phase of 13 tidal constituents derived from the NIWA Exclusive Economic Zone (EEZ) tidal model (Walters et al. 2001).

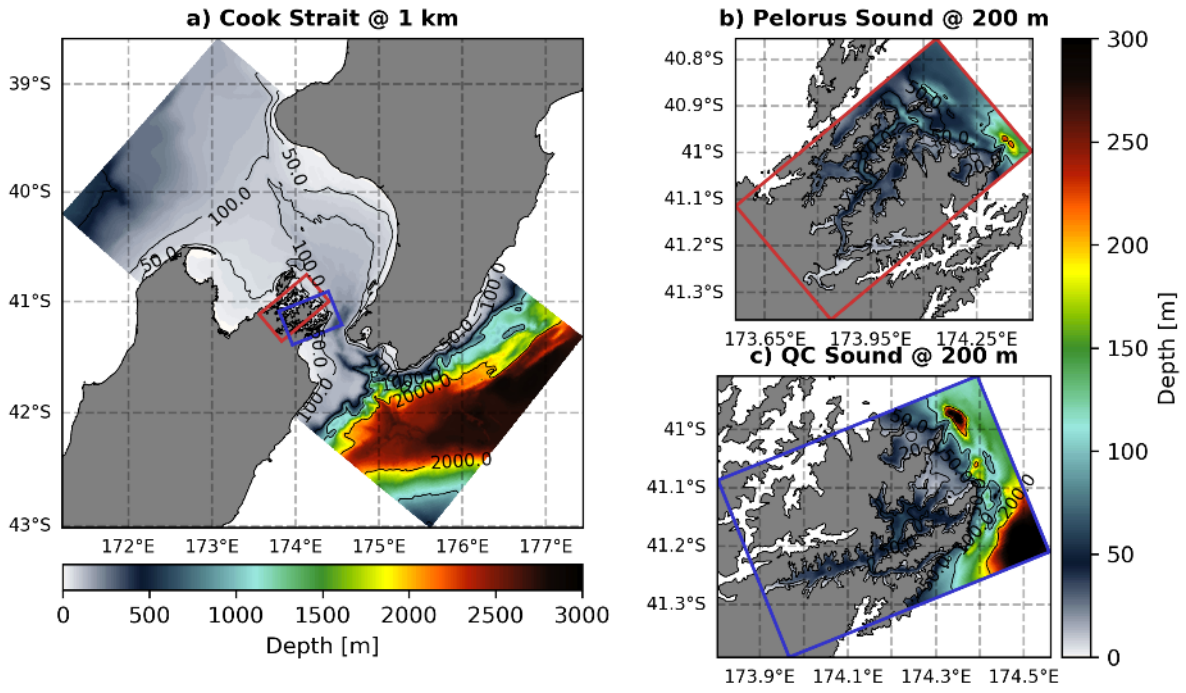

Figure 13: Domains of the three hydrodynamic models used for the Lagrangian particle tracking: a) Cook Strait 1 km; b) Pelorus Sound 200 m; and c) Queen Charlotte Sound 200 m.

Pelorus Sound 200 m and Queen Charlotte Sound 200 m

The high-resolution Pelorus Sound model domain (Pelorus Sound 200 m) was designed to resolve the dynamics in Pelorus Sound and stretches from Admiralty Bay in the west to Kenepuru Sound in the east at a horizontal resolution of 200 m (Figure 13b). The Queen Charlotte Sound model domain (Queen Charlotte Sound 200m) has a similar horizontal resolution and was designed to resolve the dynamics in Queen Charlotte Sound (Figure 13c).

The model bathymetry for both domains was generated using the same data sources as those used for the Cook Strait 1 km model, supplemented with data from a 25 m resolution digital terrain model of the Marlborough Sounds. Atmospheric forcing for the Pelorus and Queen Charlotte sounds model domains was also derived from the same sources as those used for the Cook Strait 1 km domain. However, open boundary conditions for both high resolution domains were derived from the Cook Strait 1 km model.

Sea surface temperatures from the Cook Strait 1 km model have previously been validated against satellite-derived observations (Chiswell et al. 2017). The comparison showed that the model accurately captured the annual cycle of sea surface temperature, with cooler conditions during winter (June–August) and warmer temperatures in summer (December–February). It also realistically reproduced key spatial patterns, including the northwest-to-southeast temperature gradient and advection of cooler water from the Cook Strait narrows into the broader Cook Strait region. The good agreement between modelled and observed sea surface temperatures suggests that the model resolves the dynamics of Cook Strait reasonably well. Hadfield et al. (2014) evaluated the Pelorus Sound 200 m model against a range of historical observational datasets and found that it reproduced the key hydrodynamic features of Pelorus Sound with reasonable accuracy. They found good agreement between modelled currents (tidal and sub-tidal) and observed currents, as well as strong consistency between modelled and observed temperature and salinity profiles. Similarly, Broekhuizen et al. (2015) assessed the Queen Charlotte Sound 200 m model against observational datasets and found strong agreement between modelled and observed temperature and salinity fields. The model also reproduced the well-defined estuarine circulation of Queen Charlotte Sound with reasonable accuracy.

Particle tracking

Particle trajectories were simulated using velocity fields from the hydrodynamic models described above, in combination with the open-source package OpenDrift (Dagestad et al. 2018; https://opendrift.hithub.io/). OpenDrift is an offline Lagrangian particle modelling framework that can be used to predict the dispersal of particles in the ocean using advection, diffusion, and user-prescribed particle behaviour. It also has the capability to merge velocity fields from different hydrodynamic models with different horizontal resolutions, enabling particle movement to be driven by the combined flow fields.

Lagrangian particle trajectories were simulated using the fourth-order Runge-Kutte advection scheme. To account for sub-grid scale hydrodynamic processes not resolved by the hydrodynamic models, a Brownian motion (or random walk) component was included. A horizontal diffusivity coefficient of 0.1176 m^2/s was applied to represent lateral sub-grid scale diffusion, while a vertical diffusion coefficient of 0.01 m^2/s was used to simulate vertical mixing due to turbulence. These coefficients are consistent with those used in Michie et al. (2024). Particles remained active for the entire simulation period unless they were advected out of the model domain or encountered the coast, in which case they were considered stranded.

Two different trajectory scenarios were considered: passive and buoyancy-modified. In the passive scenario, larval transport was entirely driven by ocean currents, with no active movement. In the buoyancy-modified scenario, particles 'hatched' after five days, at which point a prescribed vertical velocity of 0.0013 m/s was applied to simulate larval swimming behaviour. Additionally, these particles were assigned a density based on a salinity of 31.25 psu and the ambient water temperature, making them positively buoyant and enabling them to ascend in the water column. Both the vertical velocity and prescribed density were based on characteristics of Northeast Arctic (NEA) cod (*Gadus morhua*) eggs, which have low density and ascend rapidly towards the surface (Sundby 1983). Active vertical swimming and the positioning of larvae within the water column can influence dispersal trajectories. Nevertheless, the majority of Lagrangian particle tracking studies (e.g. Dauden-Bengoa et al. 2024; Marinone et al. 2008) represent fish eggs and larvae as purely passive particles, primarily due to the paucity of species-specific data on vertical behaviour and buoyancy. In the absence of species-specific information on the buoyancy characteristics of blue cod eggs and larvae, parameters from Northeast Arctic (NEA) cod, one of the few species for which such information exists, were used as a proxy. Information on egg buoyancy is available for very few species internationally, with most other species being other gadids (cod) that have very similar buoyancy properties to NEA cod or pelagic species (Sundby & Kristiansen 2015). While there are key differences between NEA cod and blue cod, the information on buoyancy characteristics is believed to be the best available information. The buoyancy-modified scenario highlights the sensitivity of blue cod larval dispersal to vertical velocity and buoyancy, underscoring the need for species-specific data to enhance model realism and reduced uncertainty.

The release locations were chosen based on areas with the highest predicted female biomass from the SDMs, within different sub-regions of the Marlborough Sounds (to ensure a holistic understanding of particle motion throughout the study area). For both scenarios (passive and buoyancy-modified), particles were released from a total of 13 polygons (Figure 14) to determine the dispersal patterns and connectivity between spawning locations and juvenile target polygons (TP1–TP4). The 13 release locations were divided into two broader areas: wider Marlborough Sounds and inner Marlborough Sounds in line with the model domains used for the SDMs. The wider Marlborough Sounds consists of five polygons around D'Urville Island - two along the west coast and the remainder along the east coast of the island (RP1 – RP5, Figure 14a) – and one in the outer Queen Charlotte Sound (RP6, Figure 14a). The inner Marlborough Sounds consists of seven polygons (Figure 14b) designed to represent the following areas within Queen Charlotte and Pelorus Sound (see Section 2.5 for rationale for selection of these areas):

- Double Cove (brown polygon, Figure 14b)

- Bay of Many Coves (blue polygon, Figure 14b)
- Erie Bay (yellow polygon, Figure 14b)
- Whekenui Bay (green polygon, Figure 14b)
- Inner Pelorus (red polygon, Figure 14b)
- Maud Island (purple polygon, Figure 14b)
- Blumine Island (peach polygon, Figure 14b)

Each day over a 123-day spawning period (1 July – 31 October), 1000 particles were released from the seafloor within each of the release polygons, resulting in a total of 123 000 particles per polygon. Across all 13 release polygons, this amounted to a total of 1 599 000 particles released. The model recorded the position (longitude, latitude, and depth) of each particle at 12-hour intervals, and all particles were tracked for a minimum duration of 50 days.

Post-simulation analyses

All analyses were conducted separately for the two particle tracking scenarios and for the wider and inner Marlborough Sounds release polygons. The release polygons are widely distributed throughout the Marlborough Sounds, and while spawning biomass is much higher in certain locations (Figure 14), some spawning does occur throughout the study area (as indicated by survey data). (Figure 10).

Historically, the larval development stage of blue cod was considered to be between 5 and 10 days. However, tank experiments carried out by Plant and Food Research (Cook 2017) suggest that eggs remain pelagic for approximately five days after spawning, followed by a pelagic larval stage lasting around another five days. After hatching, the larvae are predicted to be free-swimming for a period of 7 to 49 days. Given this information we summarized the results of the two particle tracking scenarios for three pelagic larval durations; (PLDs) - 10, 25, and 50 days. These durations were selected based on the life history of blue cod egg and larval development determined by Cook (2017), and the use of three PLDs helps to assess any sensitivities associated with any uncertainties between PLDs derived from tank experiments and those that may occur naturally.

The analysis consisted of estimating particle densities and calculating the connectivity between release and target polygons for the three PLDs. Spatially resolved (2D) particle density estimates were calculated on a 1 km × 1 km grid for each PLD by aggregating particles from all release locations. Densities were computed as the proportion of particles within each grid cell relative to the total number of particles released - 738 000 for the wider Marlborough Sounds and 861 000 for the inner Marlborough Sounds. The connectivity between release and target polygons was calculated as the proportion of particles from each release polygon (N = 123 000) that entered a given target polygon by the end of each PLD.

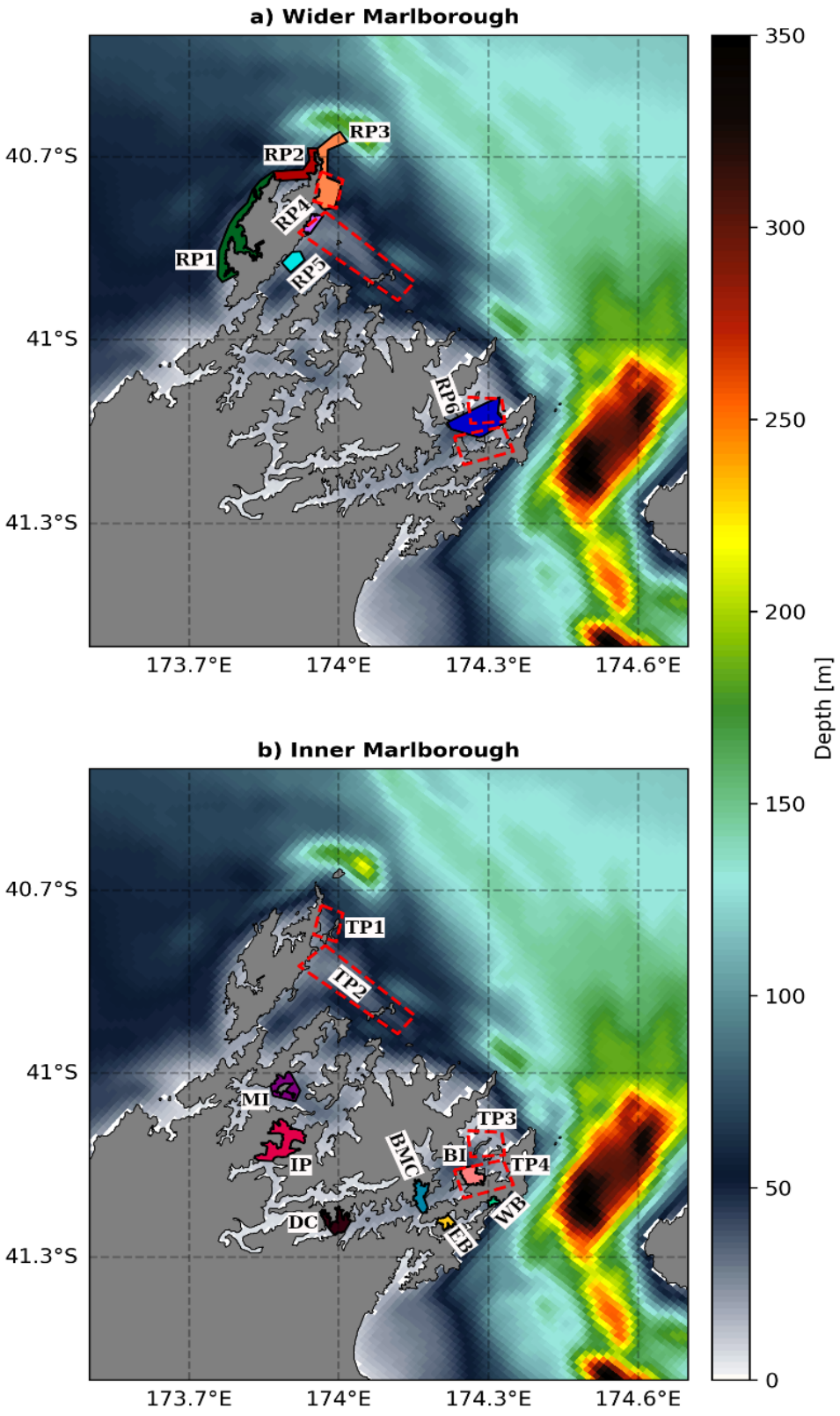

Figure 14: Release polygons for the a) wider Marlborough Sounds and b) inner Marlborough Sounds used for the Lagrangian particle tracking. Named inner sounds release locations are Maud Island (MI), Inner Pelorus (IP), Double Cove (DC), Bay of Many Coves (BMC), Blumine Island (BI), Erie Bay (EB) and Whekenui Bay (WB). Red dashed polygons indicate the target polygons (TP1 – TP4).

2.5 Spatial management scenarios

Using the outputs from the previous steps, we developed a suite of spatial management areas (hereafter scenarios) in the Marlborough Sounds area that have potential for the protection and restoration of blue cod spawning stocks in the degraded, inner sounds habitat. The release locations used for particle tracking, being based on areas with high predicted spawning biomass from the SDM, formed the basis of these scenarios. However, Fisheries New Zealand expressed particular interest in sites located within the inner sounds domain with potential to enhance local spawning capacity and the local fishery, and thus sites used for scenarios are located only within Queen Charlotte and Pelorus Sounds. Based on conversations with Fisheries New Zealand, scenarios were developed considering:

- The predicted distribution of female biomass (as a proxy for spawning potential) from the final hurdle model prediction for the inner sounds domain developed under Section 2.2. This spatial layer is based on a combination of habitat and environmental characteristics that contribute to higher modelled levels of spawning biomass.

- The distribution of other important habitats for blue cod, including the occurrence of biogenic habitats (both from benthic invertebrates and kelp), or significant reef-edge habitat. For the latter, these data were unable to be included in models due to inadequate coverage, however they may still make important contributions to selecting spatial management scenarios.

- The results of the particle tracking analysis that indicates the connectivity of several broadly distributed 'candidate' areas and known juvenile habitats as well as the retention of particles (i.e., larvae) within the inner sounds. The candidate areas are used as representations of the connectivity to different areas within the inner sounds and so may inform other, nearby management scenarios.

- The best spread of sites across the Queen Charlotte and Pelorus Sounds areas, that takes into account existing areas closed to fishing (i.e., Maud Island, Double Cove, Long Island Marine Reserve).

The shape and size of each candidate scenario has been informed by the team's knowledge of existing successful spatial management approaches for blue cod (e.g., Long Island Marine Reserve, Maud Island), and by pooling information on the design principles for successful spatial management (e.g., Brough et al. 2021 and references therein). For example, a significant body of literature recommends considering the average home range of the focal species when determining the size of spatial management areas and consideration of the shape should take into account enhanced effectiveness when the area to boundary ratio of a management area is minimised (reducing edge-effects) (Brough et al. 2021 and references therein). Blue cod tagged by Cole et al. (2000) in Long Island Marine Reserve moved just 72 m on average from tagging sites, considerably less than the 463 m distance from the islands to the outer marine reserve boundary, indicating that most movements are confined to within the reserve. The overt differences in abundance, presence, size and condition inside the marine reserve compared to outside, suggests that the width of the marine boundary is adequate to provide protection to blue cod, despite some movement across the boundary into fished areas, and vice versa (Beentjes 2023). Hence for blue cod it appears that the areas to protect don't always need to be geographically large, and points towards establishing more smaller, than fewer large reserves. Long Island Marine Reserve is around an island however, and to some extent limits movement of individuals across the fringes as would likely happen in stretches of coastline that are protected from fishing.

With these considerations in mind, the project team delineated a range of spatial management zones for Fisheries New Zealand to consider as informative examples if developing any proposals with stakeholders. Zones were delineated in ArcGIS Pro version 3.3.0 with polygons. Using each polygon, we summarised the following information that can be used to rank each scenario: 1) total area; 2) proportion of inner sounds female biomass contained; 3) occurrence of potential habitats of significance

(e.g., biogenic habitats); 4) connectivity with juvenile habitats; 5) larval retention within the inner sounds; 6) area to boundary ratio. This information was tabulated to guide Fisheries New Zealand on the potential pros and cons for each scenario. However, it is noted that these scenarios are intended as 'examples' only to inform any future management process that Fisheries New Zealand may wish to undertake, rather than management recommendations.

3. RESULTS

3.1 Spawning potential

Wider sounds domain

Both the presence-absence and biomass components of the hurdle model for predicting the distribution of spawning potential in the wider sounds' domain performed well according to standard performance metrics (Table 2). For the presence-absence component, AUC scores using withheld data were above 0.9 and TSS scores were above 0.6, indicating 'excellent' model performance (Allouche et al. 2006). For the biomass component, Spearman's correlation coefficient was above 0.5 for both the BRT and RF models indicating robust model predictions (Waldock et al. 2022). The standard deviation around the mean performance metrics (averaged across 100 bootstrap iterations) was low for all metrics indicating consistent high predictive performance (i.e., good model stability).

Table 2: Mean model evaluation statistics for the presence-absence models (True Skill Statistic - TSS, and Area Under the Curve - AUC), and for the biomass models (R^2 and Spearman's Correlation Coefficient - Corr) for the models of female blue cod in the wider Marlborough Sounds.

	RF (SD)	BRT (SD)
Presence-absence		
TSS	0.81 (0.02)	0.69 (0.02)
AUC	0.97 (0.01)	0.91 (0.01)
Biomass		
R^2	0.32 (0.03)	0.36 (0.04)
Corr	0.56 (0.02)	0.60 (0.03)

A distinct suite of predictor variables was deemed important for the PA and biomass components of the hurdle model for the wider sounds domain (Table 3). For the PA component, 10 variables contributed to the final model, with the most important being variables related to physical seafloor characteristics: slope (33.4% contribution) and bathymetry (12.1% contribution), light irradiance at the seafloor (EBED, 12.1% contribution), and temperature-depth anomaly (TempRes, 8.1% contribution). There were moderate contributions (>5 %) from swell exposure at the seafloor (BedDist), recreational fishing extraction pressure (rec_fishing_kde), and tidal current velocity (TC). For the biomass component, the most important variables were turbidity (BBP, 18%), BedDist (12.9%), and vertically integrated productivity (VGPM, 14.1%), with less influence from variables describing seafloor characteristics, except slope (6.9%) and percent sand (8%). The biomass component had moderate contributions from horizontal gradient in chlorophyll-a, photosynthetically active radiation (PAR), sea surface temperature (SST), TC and TempRes (Table 3). The categorical variables for survey and sampling design (site.type) had negligible influence for either model component.

Table 3: Environmental variable importance – wider Marlborough Sounds. Relative importance scores (RIS) for the predictor variables for the presence-absence (PA) and biomass (Biom.) models. Variable names and abbreviations are listed in Table 1. Green shading is used to distinguish the variable with the highest contribution (dark green) and the lowest contribution (white), with colour between the highest and lowest contributions being established based on linear interpolation based on the relative position of a variable between the highest and lowest contributor. Blank cells indicate that the variable was not used in the model due to collinearity with other variables or was removed by the model due to very low importance

	RIS (%)	
Variable	PA	Biom.
Bathy	12.1	
BBP		18.0
BedDist	6.6	12.9
BPI_fine	4.6	
ChlAGrad		5.9
Com.fishing		
EBED	13.3	
PAR		7.8
rec_fishing_kde	5.5	
Sand		8.0
site.type		0.6
Slope	33.4	6.9
SST		7.3
SSTGrad	4.9	4.6
survey	0.9	0.8
TC	6.1	5.0
TempRes	8.4	8.0
VGPM	4.3	14.1

Partial dependence plots on the relationship between environmental gradients and spawning habitat suitability (from the PA models), revealed clear relationships with some variables, however the relationships were more moderate than for the biomass model (Figure 15). For the PA component, habitat suitability peaked at low values of bathymetry (around 10 m depth) and plateaued again between 50 and 100 metres. Habitat suitability for bathymetric position index-fine (BPI-fine) was higher at both high and low values indicating a preference for non-planar sea floor habitat. There was a positive spatial relationship between recreational fishing extraction and habitat suitability, and low slope values had lower habitat suitability. The other variables had marginal partial, univariate effects on habitat suitability.

For the biomass component of the wider sounds hurdle model, there was a strong relationship between turbidity (BBP) and predicted biomass – biomass declined with increasing turbidity (Figure 16). There was also a strong relationship with BedDist (swell exposure), where biomass was higher at greater exposure. High light irradiance was positively correlated with biomass, and the percent sand substrate had a strong positive association with biomass. Slope had an inverse relationship with biomass with higher predicted values at low values. High tidal current speed was positively correlated with female biomass and areas that have warmer temperatures than expected for a given depth (TempRes) also had higher predicted values. Female biomass was predicted to be lower at lower values of integrated productivity. The remaining variables, including the categorical factors for survey and site type, had minimal influence on predicted female biomass.

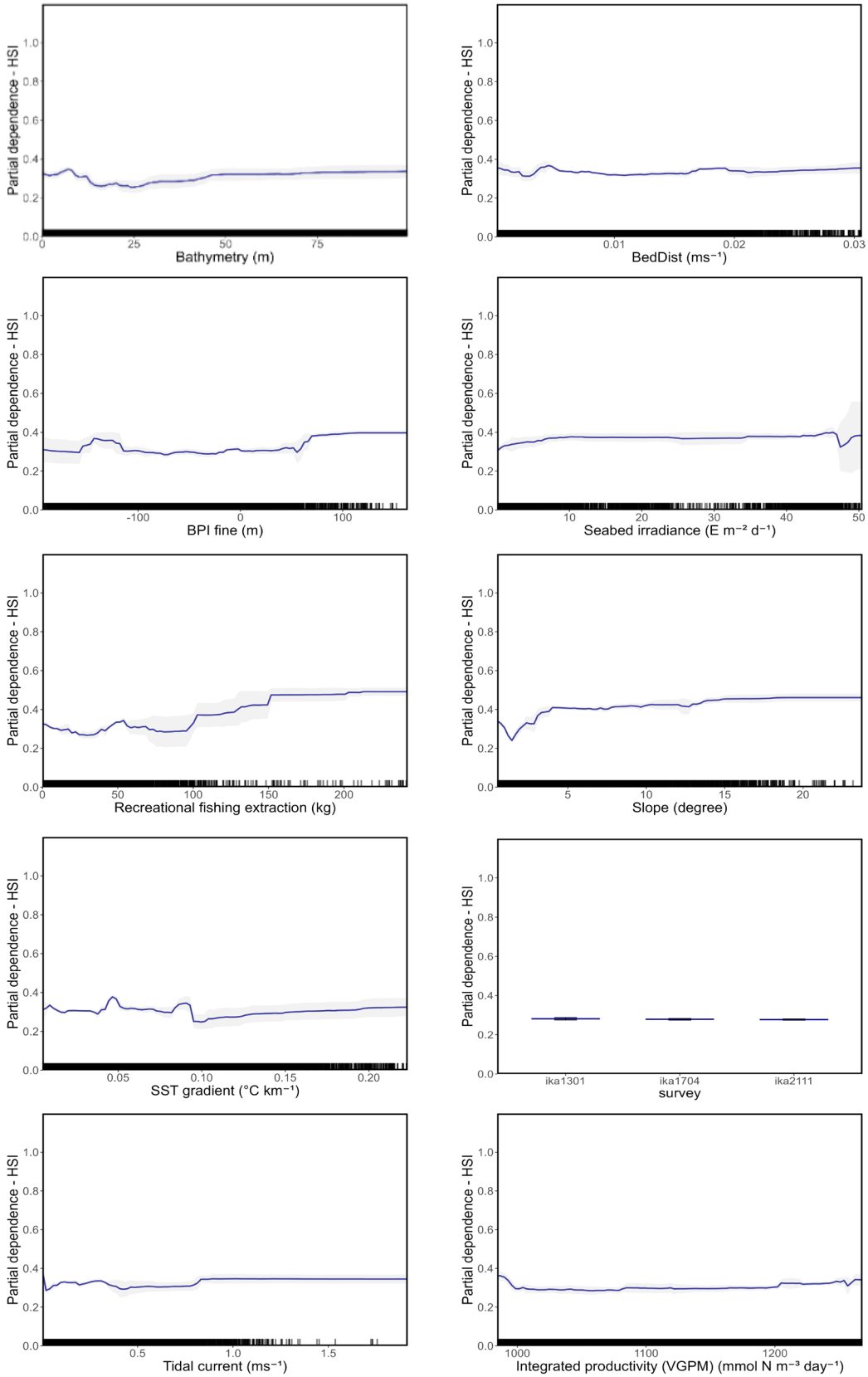

Figure 15: Partial dependence plots for the presence-absence model for the wider Marlborough Sounds.. Panels show the relationships between the presence/absence of female blue cod and the final predictor variables retained by the presence-absence component of the hurdle model. The y-axis is the partial dependence of habitat suitability index (HSI) across the gradient of each predictor variable when the values of all other variables are set to mean values – isolating the univariate influence of each variable on habitat suitability.

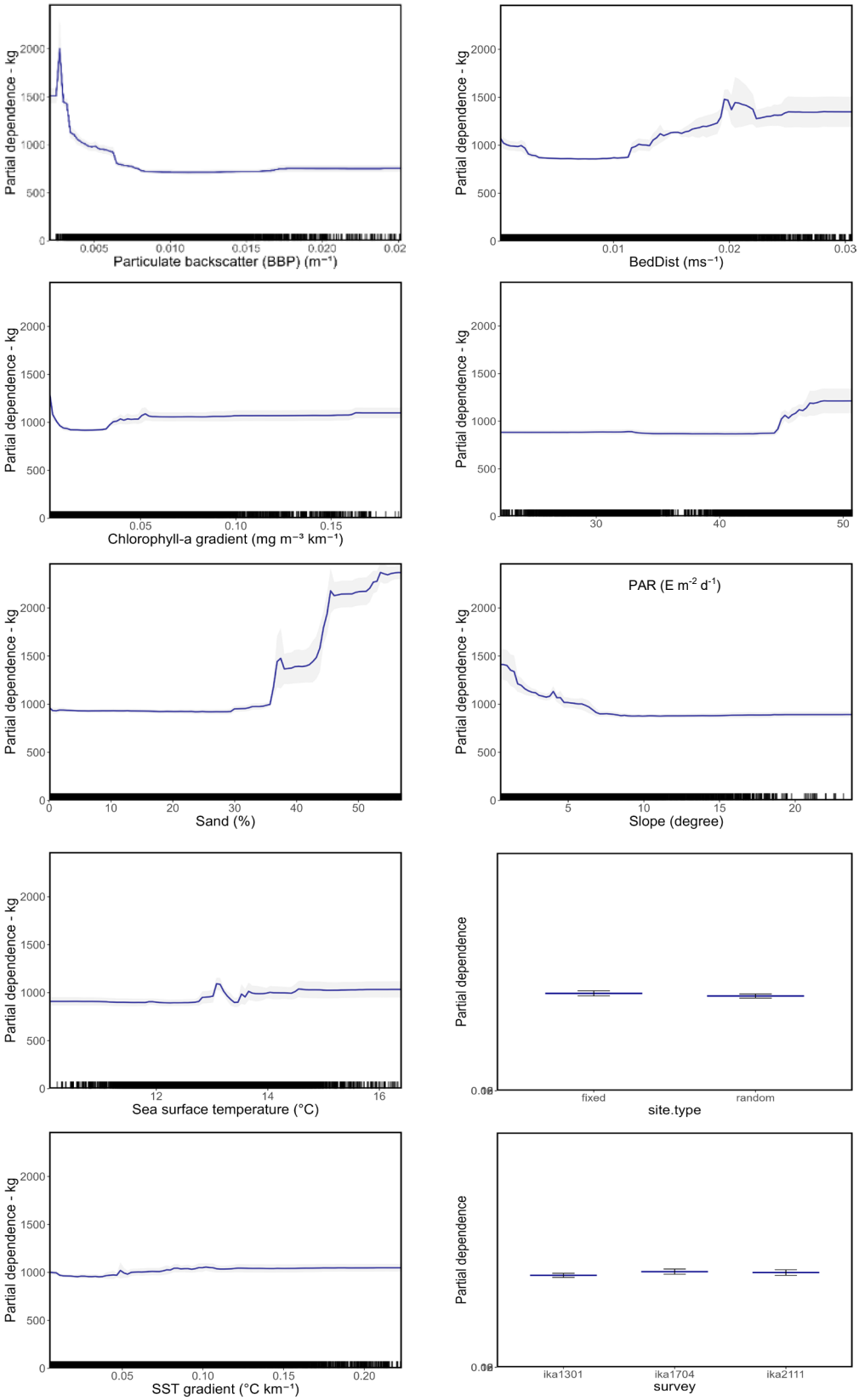

Figure 16: Partial dependence plots for the abundance model for the wider Marlborough Sounds. Figure continued on next page. Panels show the relationships between the biomass of female blue cod and the final predictor variables retained by the abundance component of the hurdle model. The y-axis is the partial dependence of female biomass across the gradient of each predictor variable when the values of all other variables are set to mean values – isolating the univariate influence of each variable on female biomass.

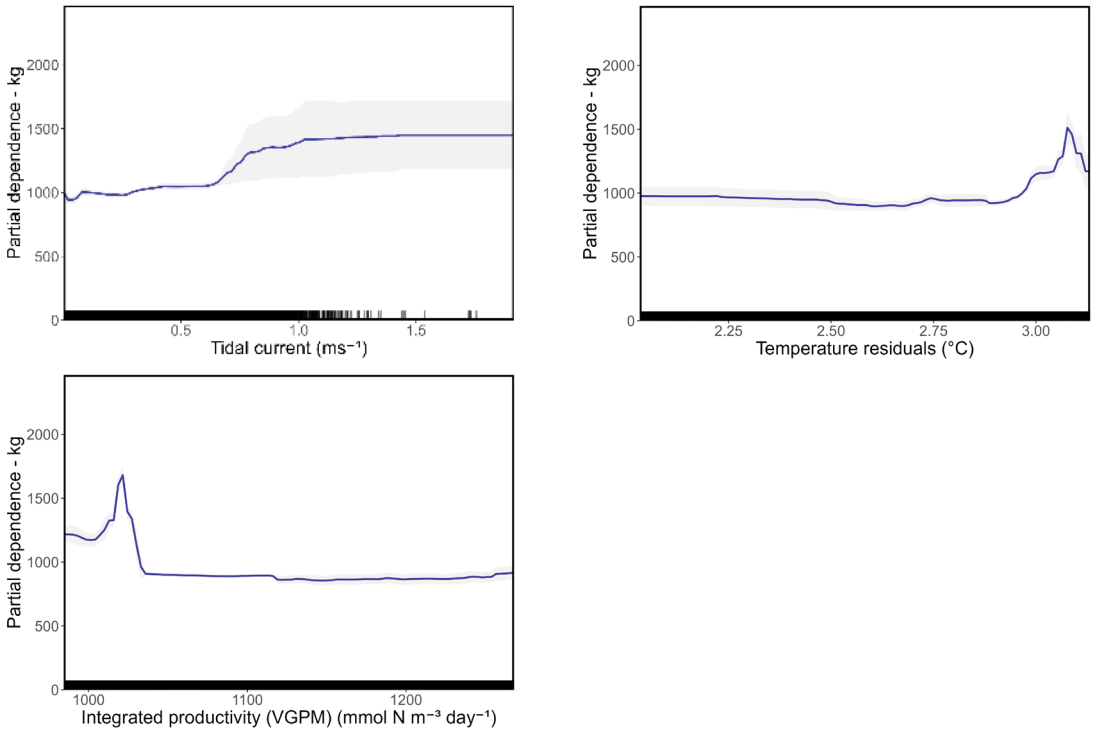

Figure 16: continued.

The distribution of female biomass (as a proxy for spawning potential) predicted from the final hurdle model for the wider sounds model domain, revealed distinct 'hotspots' for spawning biomass (
Figure ***17***). Coastal areas around D'Urville Island had high predicted biomass, particularly within and south of Greville Harbour, Nile Head and Cape Stephens. Smaller areas of high predicted biomass also occurred on the eastern side of D'Urville Island between Rangitoto Island and D'Urville Peninsula. Biomass was predicted to be uniformly low within Pelorus Sound and inner Queen Charlotte Sound apart from some moderate levels predicted within Double Cove and Ōnahau Bay (
Figure ***17***). Outer Queen Charlotte Sound contained another 'hotspot' in predicted biomass – particularly around Long Island and adjacent coastline including East Bay and headlands adjacent to Resolution Bay and Endeavour Inlet. The uncertainty (standard deviation) around the mean spatial predictions is low for most of the wider sounds model domain, with moderate uncertainty coinciding with areas of high predicted abundance.

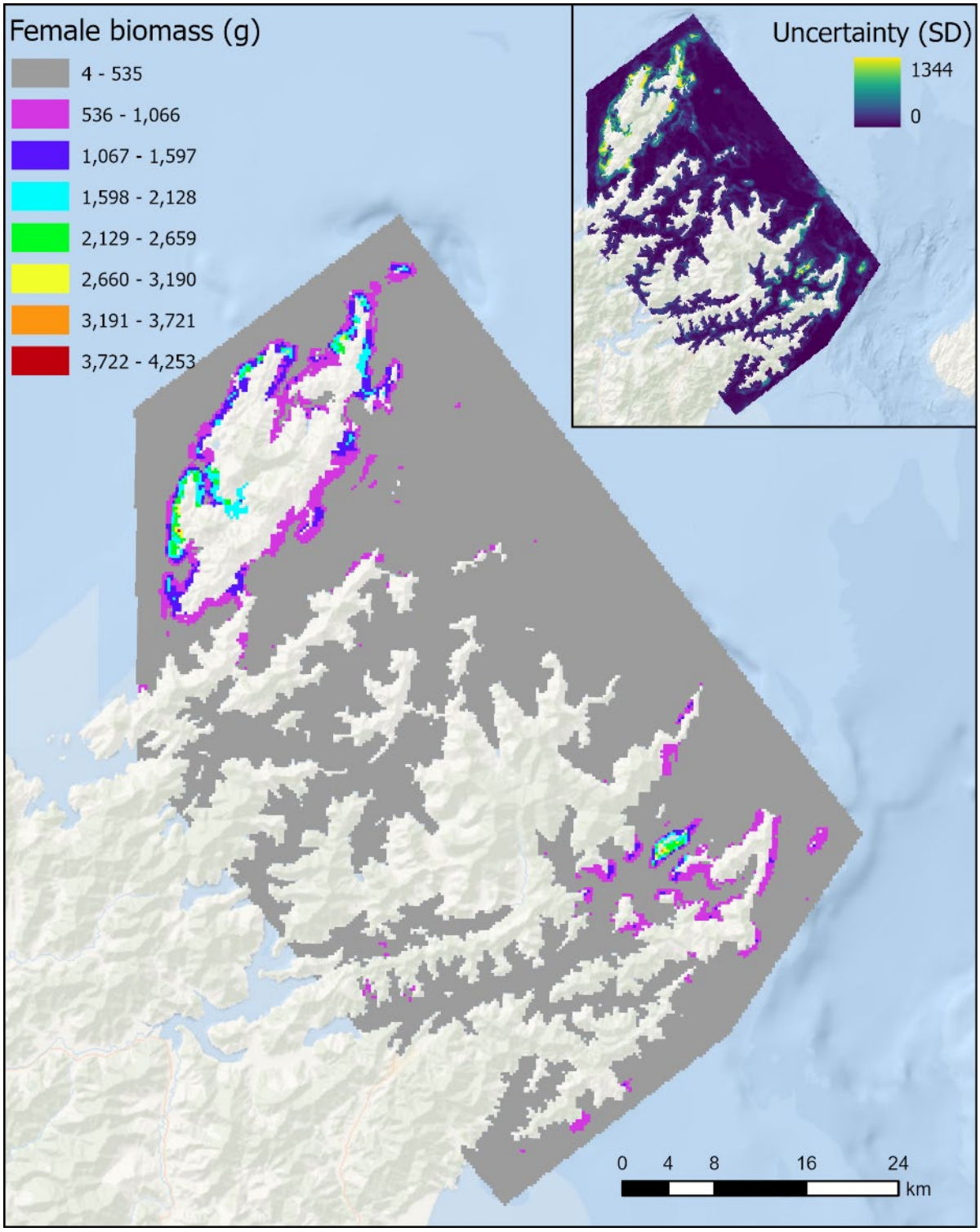

Figure 17: Predicted female blue cod biomass (g) per cell in the wider sounds area from the final hurdle model, combining predictions from the presence/absence and biomass components. Spatial predictions show the relative biomass of female blue cod across the wider sounds domain with grey colouring indicating areas of low female biomass and oranges/reds showing the locations with the highest predicted biomass. Inset: Uncertainty (SD) of the predicted biomass.

Inner sounds domain

Both the presence-absence and biomass components of the hurdle model for predicting the distribution of spawning potential in the inner sounds domain performed well according to standard performance metrics (Table 4). For the presence-absence component, AUC scores using withheld data were 0.96 for both the BRT and RF and TSS scores were 0.83 and 0.84 respectively, indicating 'excellent' model performance (Allouche et al. 2006). For the biomass component, Spearman's correlation coefficient was above 0.5 for both the BRT and RF models indicating robust model predictions (Waldock et al. 2022). The standard deviation around the mean performance metrics (averaged across 100 bootstrap iterations) was low for all metrics indicating consistent high predictive performance.

Table 4: Mean model evaluation statistics for the presence-absence models (True Skill Statistic - TSS, and Area Under the Curve - AUC), and for the biomass models (R^2 and Spearman's Correlation Coefficient - Corr) for the models of female blue cod in the inner Marlborough Sounds

	RF (SD)	BRT (SD)
Presence-absence		
TSS	0.84 (0.02)	0.83 (0.02)
AUC	0.96 (0.01)	0.96 (0.01)
Biomass		
R^2	0.30 (0.04)	0.36 (0.06)
Corr	0.55 (0.04)	0.60 (0.05)

There were substantial differences in the variables retained between the PA and biomass components off the hurdle model for the inner sounds domain (Table 5). Seven variables were retained in the PA component, and of these, most were derived from multibeam echosounder data on the characteristics of the sea floor. The most important variables for the PA model included bathymetry (40.3%), slope (23.7%), bathymetric position index – broad (BPI_Broad, 13.1%) and rugosity (11.2%). For the abundance component, the key variables were typically related to more dynamic oceanographic conditions with the most important variables being turbidity (BBP, 26.2%), integrated productivity (11.8%) and swell exposure at the seafloor (BedDist, 10.6%). There were moderate contributions (i.e., greater than 5%) from detrital absorption, sand content, sea surface temperature, tidal current velocity and temperature-depth anomaly (TempRes). The categorical variables for survey and sampling design (site.type) had negligible influence for either model component.

Table 5: Environmental variable importance – inner Marlborough Sounds. Relative importance scores (RIS) for the predictor variables for the presence-absence (PA) and abundance (Abun.) models. Variable names and abbreviations are listed in Table 1. Green shading is used to distinguish the variable with the highest contribution (dark green) and the lowest contribution (white), with colour between the highest and lowest contributions being established based on linear interpolation based on the relative position of a variable between the highest and lowest contributor. Blank cells indicate that the variable was not used in the model due to collinearity with other variables or was removed by the model due to very low importance.

	RIS (%)	
Variable	PA	Abun.
ADET		6.6
Bathy	40.3	
BBP		26.2
BedDist		10.6
BPI_broad	13.1	6.7
BPI_fine	2.1	
ChlAGrad		5.0
Com.fishing		
EBED	8.6	
Gravel		3.3
rec_fishing_kde		
Rugosity	11.2	
Sand		6.2
site.type		0.1
Slope	23.7	
SST		6.7
SSTGrad		5.0
survey	1.0	0.7
TC		5.7
TempRes		5.5
VGPM		11.8

There was limited variability in the habitat suitability index of female blue cod across the gradient in the environmental variables selected by the PA model. The BRT and RF models used to predict distribution by default include interactive effects among predictor variables and thus the high performance of the models (Table 4) and lack of clear univariate effects indicates that there are likely to be several multivariate effects that determine the habitat suitability that are not evident in univariate partial dependence plots (Figure 18). Thus, interactive (i.e., multivariate) effects of the environmental predictors on blue cod habitat suitability are likely to be the core drivers of presence/absence of females. The exception to this is bathymetry, which shows higher habitat suitability at low values between 0 and 10 metres depth. Additionally, both light irradiance at the sea floor (EBED) and seabed slope had a slight positive relationship with female habitat suitability.

For the biomass component of the inner sounds hurdle model, there were clear univariate relationships between some environmental variables and predicted biomass (Figure 19). There was substantially higher biomass predicted at low levels of turbidity (BBP) and higher predicted biomass at lower levels of the detrital absorption (ADET), which indicates a preference for clear water with less suspended material in the water column. Similar to the wider sounds model, there was higher biomass predicted at higher swell exposure (BedDist), higher sand concentration and in uneven seafloor habitats (e.g., reefs). Additionally, predicted biomass was higher at low levels of productivity (VGPM) and in areas with higher temperature than expected at the seafloor for a given depth (TempRes). The remaining variables,

including the categorical factors for survey and site type, had minimal influence on predicted female biomass, at least in terms of univariate effects.

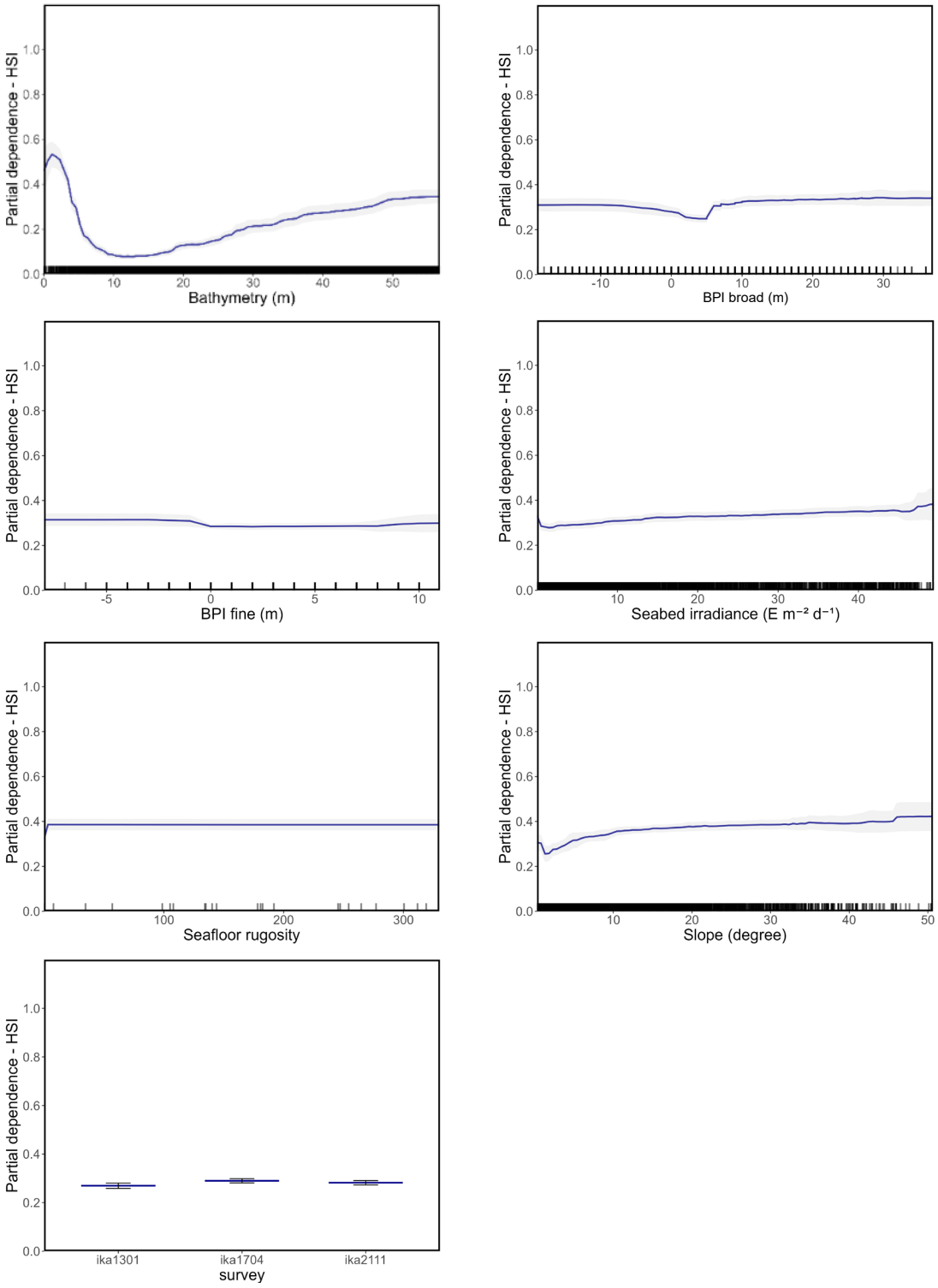

Figure 18: Partial dependence plots for the presence-absence component of the hurdle model for the inner Marlborough sounds area. Panels show the relationships between the biomass of female blue cod and the final predictor variables retained by the abundance component of the hurdle model. The y-axis is the partial dependence of female biomass across the gradient of each predictor variable when the values of all other variables are set to mean values – isolating the univariate influence of each variable on female biomass.

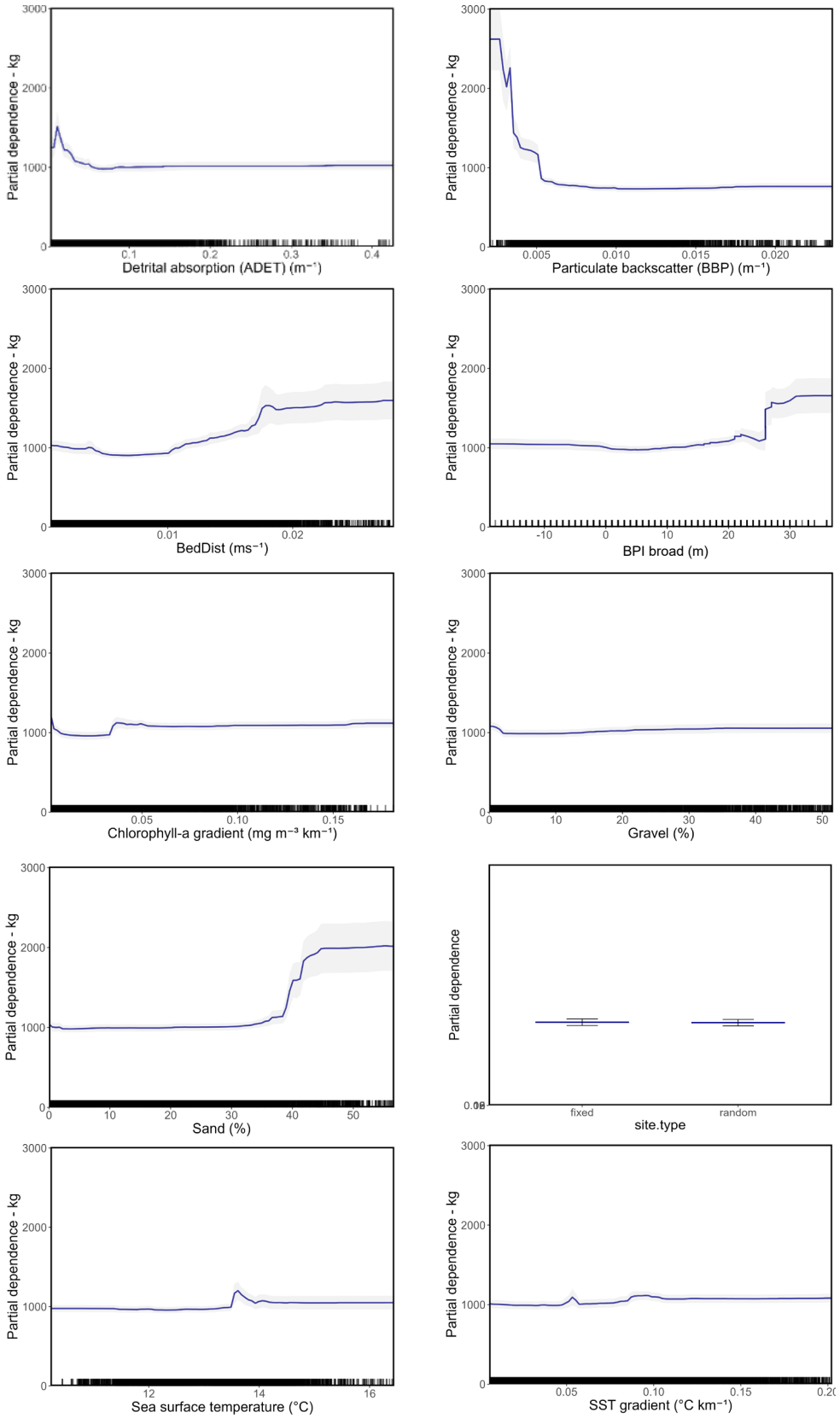

Figure 19: Partial dependence plots for the abundance component of the hurdle model for the inner Marlborough sounds area. Panels show the relationships between the biomass of female blue cod and the final predictor variables retained by the abundance component of the hurdle model. The y-axis is the partial dependence of female biomass across the gradient of each predictor variable when the values of all other variables are set to mean values – isolating the univariate influence of each variable on female biomass. Figure continued on next page.

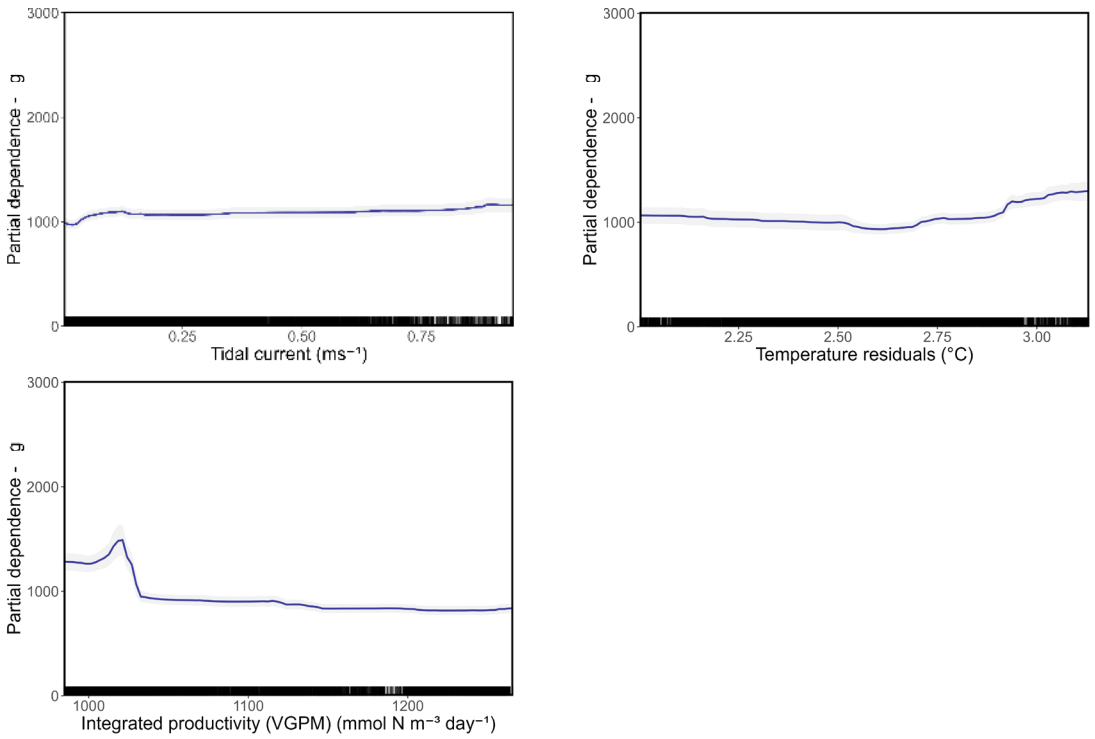

Figure 19: continued.

The distribution of female biomass (as a proxy for spawning potential) predicted from the final hurdle model for the inner sounds provided more high resolution predictions for Queen Charlote and Pelorus Sound than the wider sounds domain (Figure ***20***). Biomass was predicted to occur in a thin coastal margin throughout both sounds, representing likely reef and reef-edge habitat. Generally, the areas with the highest predicted biomass in each sound was similar to the wider sounds predictions, with outer Queen Charlotte Sound having the highest predicted biomass. Areas around Long Island, Blumine Island and within East Bay had high predicted biomass, along with headlands around Endeavour Inlet and Resolution Bay (Figure ***20***). Most of the remaining coastal habitat in outer Queen Charlotte had low to moderate predicted biomass. Within inner Queen Charlotte, areas with moderate female biomass were predicted to occur only within Double Cove and Ōnahau Bay. Tory Channel also had some areas of moderate biomass predicted around Erie Bay and Kawhia Bay and along the coast between Deep Bay and Okukari Bay. In Pelorus Sound, female biomass was generally low, with the few areas of moderate biomass including Tennyson Inlet, within and south of North-West Bay, Maud Island, Waitata Bay to Port Ligar and either side of the Isthmus between Beatrix and Forsyth Bay. The uncertainty (standard deviation) around the mean spatial predictions was low for most of the inner sounds domain, with some slightly elevated uncertainty in the outer reaches of Queen Charlotte Sound.

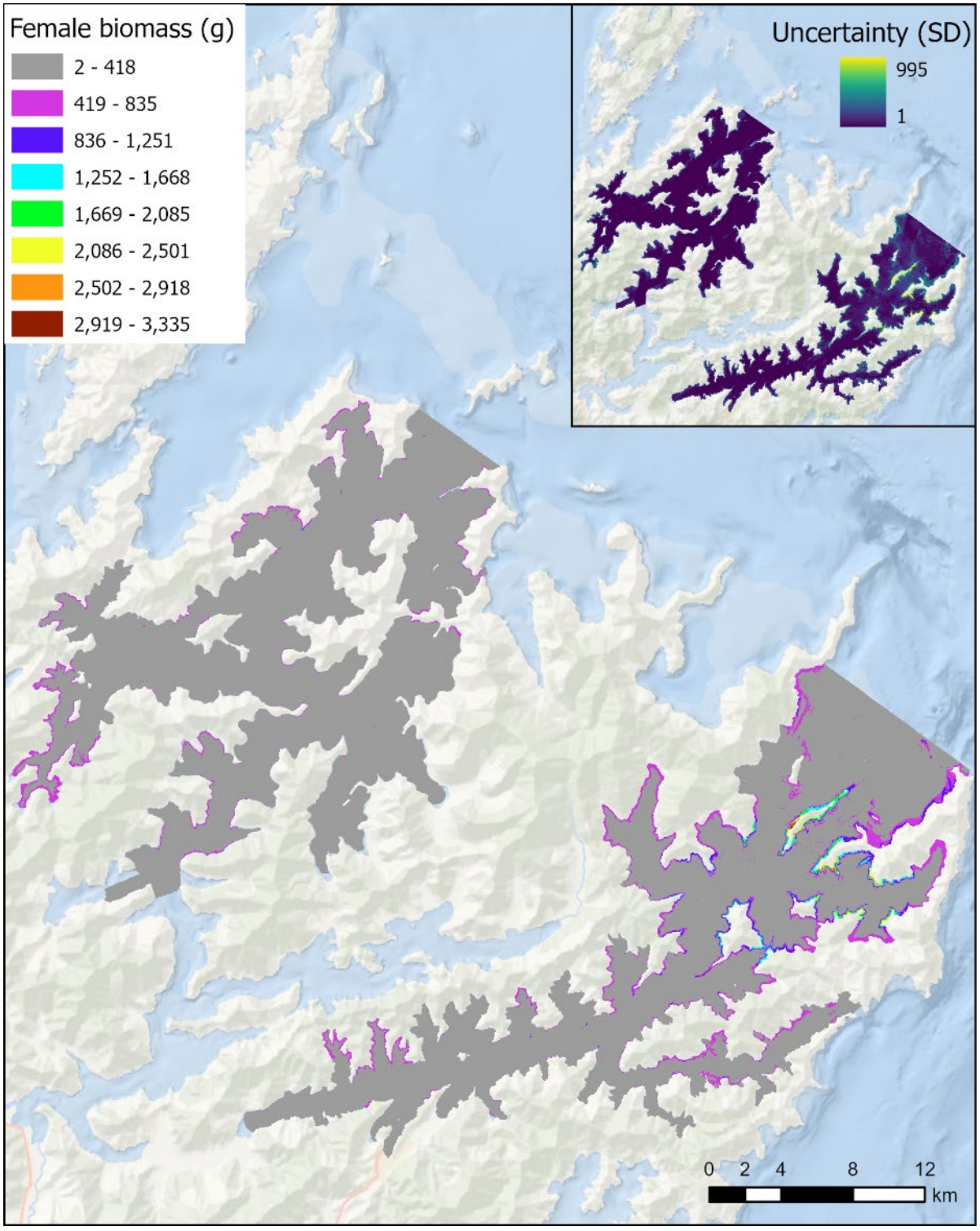

Figure 20: Predicted female blue cod biomass (g) per cell in the inner sounds area from the final hurdle model, combining predictions from the presence/absence and biomass components. Spatial predictions show the relative biomass of female blue cod across the inner sounds domain with grey colouring indicating areas of low female biomass and oranges/reds showing the locations with the highest predicted biomass. Inset: Uncertainty (SD) of the predicted biomass.

3.2 Particle tracking

Wider Marlborough sounds

A total of 738 000 simulated particles were released over the six wider Marlborough Sounds polygons and tracked for one year under both particle tracking scenarios. The low particle densities (<0.02%) observed for releases from the wider Marlborough Sounds polygons under the passive scenario suggest rapid advection of particles outside of Marlborough Sounds and into wider Cook Strait (Figure 21). The buoyancy-modified scenario in which particles are assigned a salinity density and a random walk vertical velocity, shows an even more rapid advection of particles out of Cook Strait (Figure 22).

Under the passive scenario, higher concentrations of particles are observed to the east and north of D'Urville Island and outside of Pelorus Sound after 10 days (Figure 21a). Particles released from the three largest polygons around D'Urville Island (RP1, RP2 and PR3; Figure 14a) are advected into the wider Marlborough Sounds region, contributing significantly to the elevated concentrations in these areas. Localised areas of high particle concentrations (>0.02%) appear along the coastline of D'Urville Island, outer Pelorus Sound, and outer Queen Charlotte Sound (Figure 21a), primarily due to the stranding of particles along the coast. The elevated concentrations along the outer Queen Charlotte Sound coastline originate mainly from particles released in the nearby polygon (RP6), while those along the outer Pelorus Sound coastline derive mainly from particles released from the polygons along the east coast of D'Urville Island (RP3, RP4 and RP5).

In the passive scenario, particle concentrations in the wider Marlborough Sounds region are substantially reduced by day 25 (Figure 21b), with higher concentrations persisting offshore beyond the 100 m isobath (indicated in Figure 21). By day 50, concentrations outside of Marlborough Sounds decline further to below <0.002%, reflecting continued advection of particles out through Cook Strait (Figure 21c). In contrast, areas of high concentration along the coastline remain largely unchanged over time, due to the coastline interaction of the model configuration.

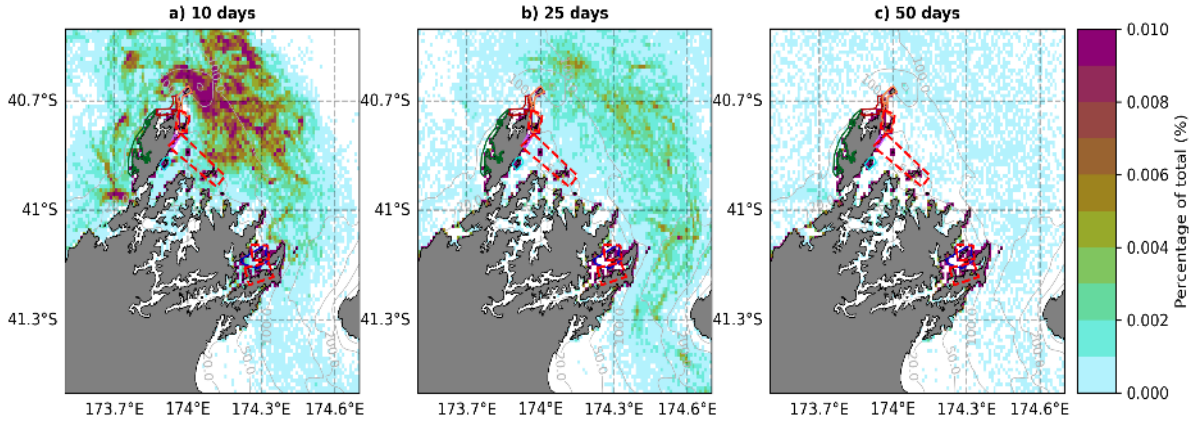

Figure 21: Particle densities of the six Wider Marlborough Sounds release polygons (shown in Figure 14) combined under the passive scenario. Particle densities were calculated on a 1 × 1 km grid and are based on the spatial distribution of particles after a) 10 days, b) 25 days and c) 50 days. Warmer colours indicate a higher probability of a particle being located in a particular grid cell, whereas cooler colours signify lower probabilities. Red dashed polygons indicate the target polygons. The 100 m and 1000 m isobaths are shown in grey.

The pattern of particle densities under the buoyancy-modified scenario largely mirrors that of the passive scenario; however, overall concentrations tend to be lower (Figure 22). Additionally, the more rapid decline in particle concentrations over time suggests faster advection of particles out of Cook Strait compared to the passive scenario. This accelerated transport can be attributed to the positive buoyancy and additional vertical velocity prescribed to particles in the buoyancy-modified scenario, which causes particles to rise more quickly through the water column exposing them to faster currents in surface layers compared to their passive counterparts.

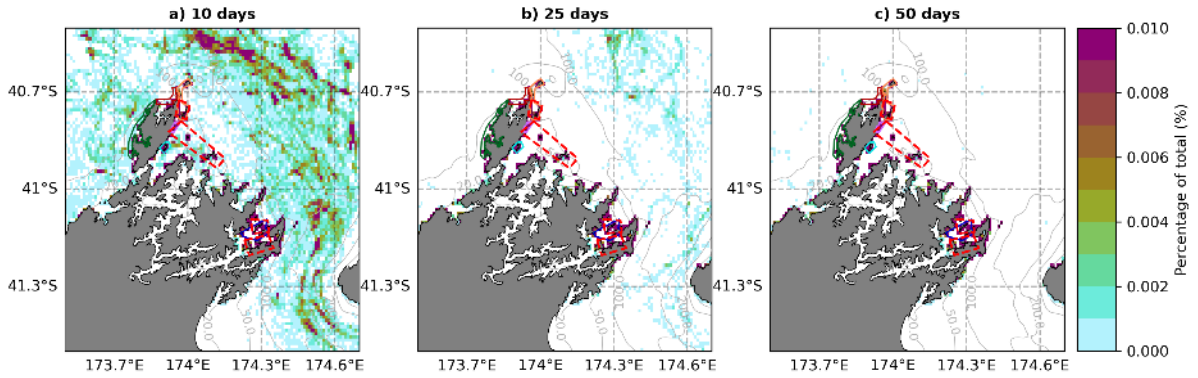

Figure 22: The same as Figure 21 but for particles released under the buoyancy-modified scenario. Red dashed polygons indicate the target polygons. The 100 m and 1000 m isobaths are shown in grey.

The two polygons along the west coast of D'Urville Island (RP1 and RP2, see Figure 14) exhibit low connectivity with all target polygons across all three time periods under both the passive and buoyancy-modified scenarios (Figure 23 and Figure 24). In contrast, RP3 shows high connectivity (>15%) with the two target polygons in Queen Charlotte Sound (TP3 and TP4), with slightly higher values under the buoyancy-modified scenario. In both scenarios, RP4 and RP5 exhibit high connectivity with the target polygon along the east coast of northern D'Urville Island (TP1), while RP6 demonstrates moderate connectivity with the same target polygon (Figure 23 and Figure 24). Additionally, RP4 and RP6 display moderate connectivity with the target polygon located outside of Pelorus Sound (TP2). The minimal variation in connectivity over time suggests that, in both scenarios, connectivity is primarily driven by particles stranding along the coastline.

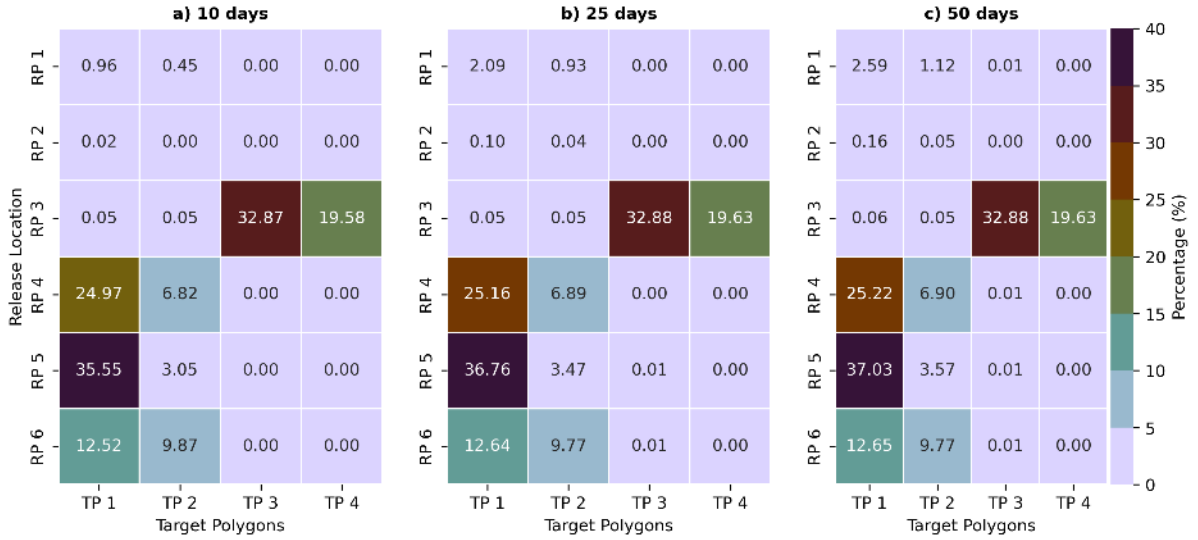

Figure 23: Connectivity between the six wider Marlborough sounds release polygons and the four target polygons (see Figure 14) under the passive scenario after a) 10 days, b) 25 days, and c) 50 days. Connectivity is calculated as the fraction of particles (expressed as percentage) released from a release polygon that resides inside a target polygon after a certain number of days.

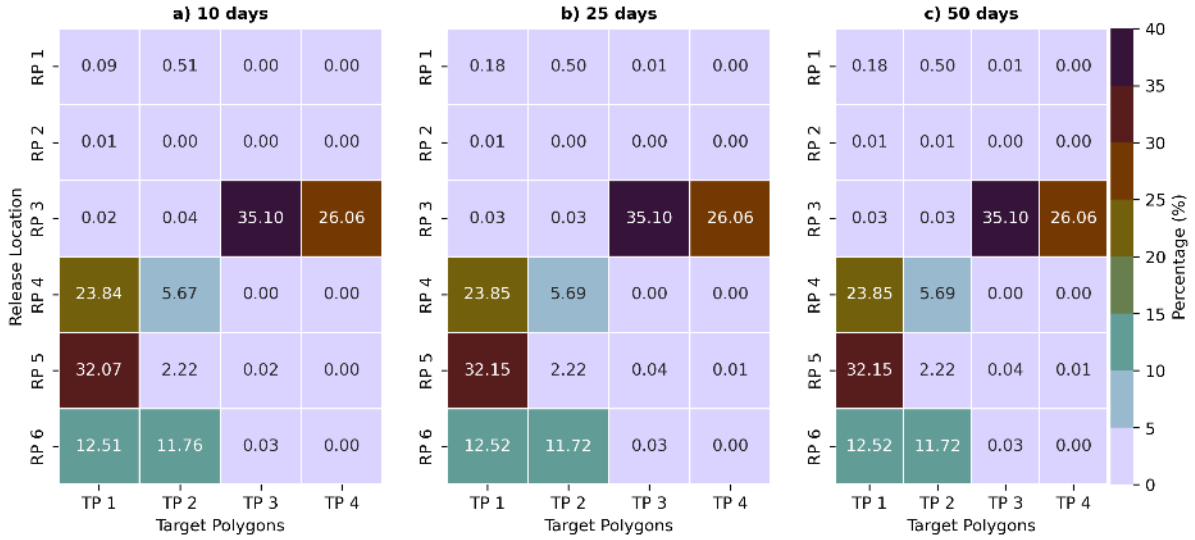

Figure 24: The same as Figure 23 but for particles released under the buoyancy-modified scenario.

Inner Marlborough sounds

A total of 861 000 simulated particles were released across the seven inner Marlborough Sounds polygons and tracked for one year under both particle tracking scenarios. The consistently low particle densities (<0.002%) observed outside of Marlborough Sounds in both scenarios (Figure 25 and Figure 26) suggest limited advection of particles from within the sounds into Cook Strait. Furthermore, the progressive decline in particle concentrations outside of Marlborough Sounds over time indicates rapid transport of particles out of Cook Strait. In both scenarios, high particle concentrations occur along the coast of Pelorus and Queen Charlotte Sound, with minimal temporal variation (Figure 25 and Figure 26), primarily due to coastal stranding.

Particle densities calculated separately for each release polygon reveal significant localised retention within both Pelorus and Queen Charlotte Sound. For example, particles released from the Double Cove polygon contribute notably to the high particle concentrations observed along the coastline between Onahau Bay and Blackwood/Tahuahua Bay. Similarly, particles released from the Maud Island polygon are a major source of the elevated concentrations along the coastlines of Waitata and Tawhitinui Reach.

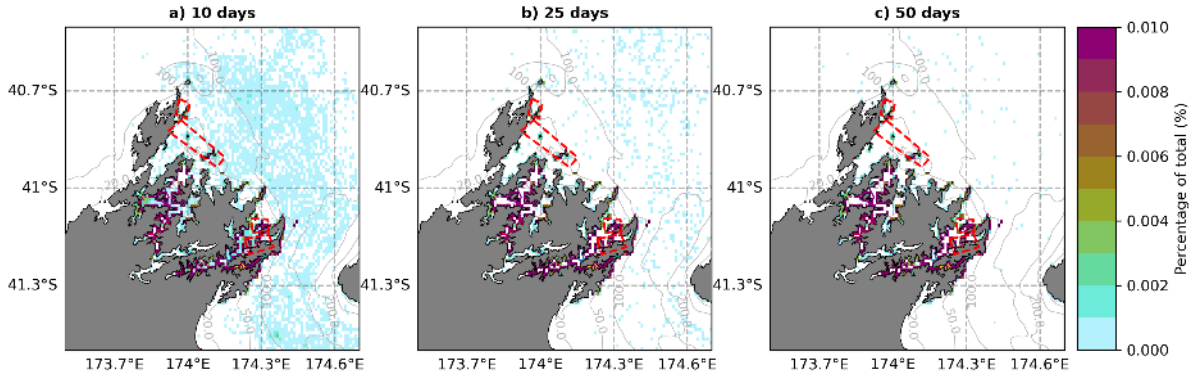

Figure 25: Particle densities of the seven inner Marlborough Sounds release polygons (shown in Figure 14) combined under the passive scenario. Particle densities were calculated on a 1 × 1 km grid and are based on the spatial distribution of particles after a) 10 days, b) 25 days, and c) 50 days. Warmer colours indicate a higher probability of a particle being located in a particular grid cell, whereas cooler colours signify lower probabilities. Red dashed polygons indicate the target polygons. The 100 m and 1000 m isobaths are shown in grey.

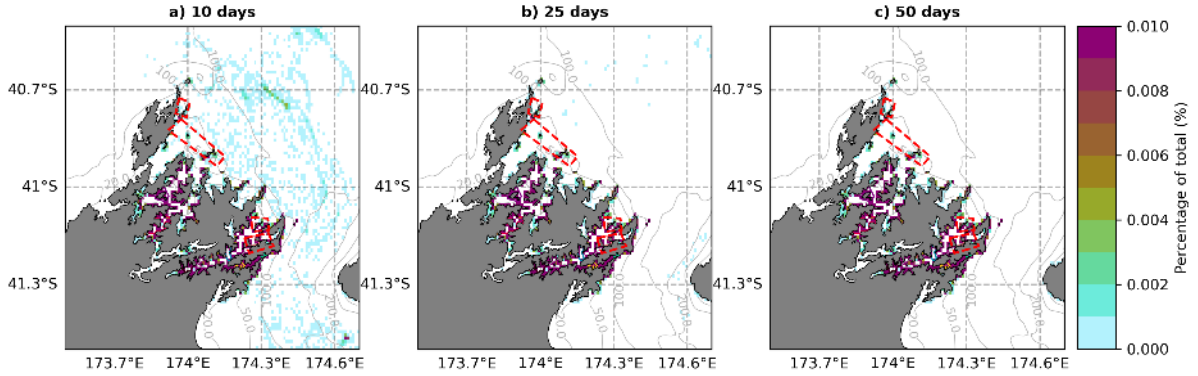

Figure 26: The same as Figure 25 but for particles released under the buoyancy-modified scenario. Red dashed polygons indicate the target polygons. The 100 m and 1000 m isobaths are shown in grey.

The connectivity calculated between the inner Marlborough Sounds polygons, and the target polygons, indicates limited exchange between the inner sounds and areas outside of the Sounds under both the passive and buoyancy-modified scenarios (Figure 27 and Figure 28). In both scenarios, particles released from the Double Cove, Erie Bay and Inner Pelorus polygons exhibit little to no connectivity with any of the target polygons. The Bay of Many Coves polygon shows some connectivity (<1%) with the more southern target polygon in Queen Charlotte Sound (TP4) but none with the other target polygons. In contrast, the Whekenui Bay polygon contributes particles to the two polygons outside of Pelorus Sound (TP1 and TP2) as well as with the more northern polygon in Queen Charlotte Sound (TP3) but exhibits limited connectivity with the other target polygon in Queen Charlotte Sound (TP4). Particles from the Whekenui Bay polygon are advected into the Cook Strait Narrows, from where strong tidal currents transport them back toward the outer Marlborough Sounds. The Maud Island polygon demonstrates some connectivity with the target polygon outside Pelorus Sound (TP2) under both particle tracking scenarios (Figure 27 and Figure 28), suggesting that a small proportion of particles released there are transported out of the sounds. Notably, Blumine Island is the only inner sounds polygon that exhibits some connectivity with all four target polygons, with the strongest link to TP4 (>80%). The limited connectivity between inner Marlborough Sounds polygons and the outer Marlborough Sounds region under the passive and buoyancy-modified scenarios, along with the elevated connectivity between release polygons and nearby target polygons reinforce the premise of localised retention.

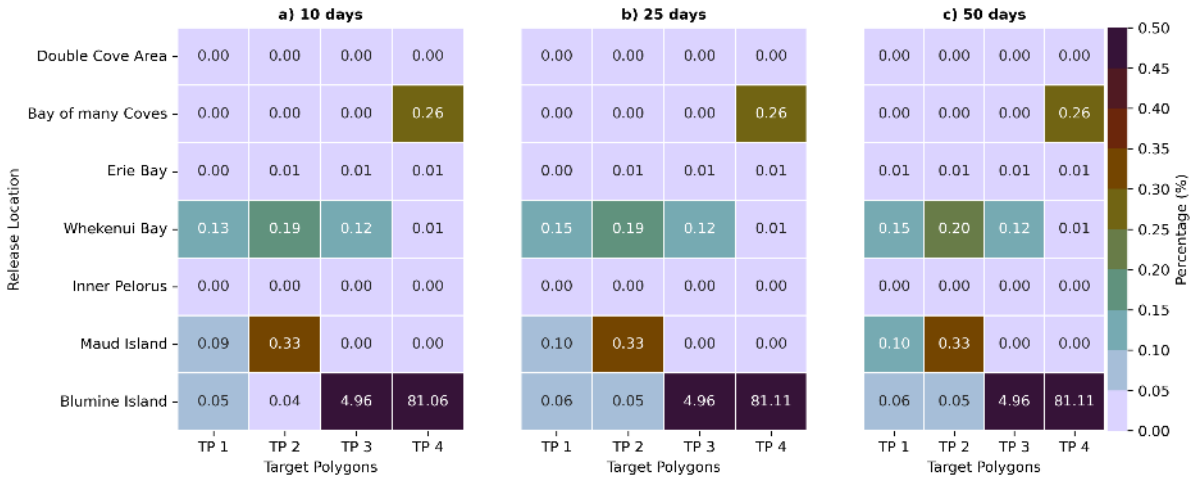

Figure 27: Connectivity between the seven inner Marlborough sounds release polygons and the four target polygons (see Figure 14) under the passive scenario after a) 10 days, b) 25 days, and c) 50 days. Connectivity is calculated as the fraction of particles (expressed as percentage) released from a release polygon that resides inside a target polygon after a certain number of days.

Figure 28: The same as Figure 27 but for particles released under the buoyancy-modified scenario.

3.3 Spatial scenarios

A total of ten spatial management scenarios were configured by the research team, and were identified largely based on the highest predicted female biomass (given the area's habitat characteristics) for a given region within the sound (i.e., inner, outer, Tory Channel) and where predicted spawning habitat had the largest continuous extent. The overlay of occurrence data on biogenic habitat forming taxa was also considered and contributed to the selection of most scenarios (Figure ***7***).

Six areas were configured for Queen Charlotte Sound (including Tory Channel), which were distributed throughout the Queen Charlotte Sound complex and included an area in the inner sound (Double Cove), mid sound (Bay of Many Coves, Tory Junction), outer sound (Blumine Island) and in Tory Channel (Erie Bay, Whekenui Bay) (Figure ***29***). Four areas were configured for Pelorus Sound including areas in the inner sound (inner Pelorus, Tennyson Inlet), mid sound (around Maud Island), and outer sound (Port Ligar) (Figure ***30***). Generally, the scenarios were slight modifications of areas used as release locations for the particle tracking analysis (see Section 2.4), with some changes to their shape and size to better encapsulate known spawning or biogenic habitat.

There was significant variability among the 10 scenarios with respect to their shape, size, the proportion of spawning habitat covered within each area, overlap with biogenic habitat forming taxa and connectivity (Table ***6***). This variability was expected given a request to have representative scenarios throughout the inner, middle reaches, and outer areas of Queen Charlotte and Pelorus sounds to inform management discussions (Section 2.5) (i.e., if the task were to identify areas with high predicted biomass, we would likely have selected more areas in outer Queen Charlotte Sound). However, to assist Fisheries New Zealand, we have provided rankings of each scenario according to the aforementioned factors, with the percentage of spawning habitat included within a scenario being the key metric (but see Section 4.4 on the subjectivity involved in this ranking). In particular, less weight was given to overlap with biogenic habitat forming taxa and connectivity with juvenile habitats, as the full extent of both habitat types are unknown and thus low overlap (or connectivity) is based on our current, incomplete understanding of these areas. Blumine Island was the highest ranked of the ten scenarios, as it contains the greatest percentage of predicted female spawning biomass (5.6% of total inner sounds female biomass), overlapped with several biogenic habitat forming taxa, and had high connectivity with known juvenile habitats and larval retention within the inner sounds. The second ranked scenario was Erie Bay, which contained 2.7% of female biomass, high overlap with biogenic taxa and moderate larval retention. Inner Pelorus (3rd ranked) contained a comparatively high percentage of spawning habitat, however this is due to the large size of the area (20.23 km^2), and a high area to boundary ratio which

would limit edge effects of fishing. Double Cove was the fourth ranked scenario, for similar reasons, but also contains an area of existing protection that likely enhances the success of spawning recovery. Maud Island (5th ranked) is the largest scenario (31.11 km^2), yet the area has only moderate spawning potential (2.2%). However, Maud Island does overlap with existing protection, has high larval retention and overlap with several biogenic taxa. Tennyson Inlet, Bay of Many Coves, and Port Ligar were the 6th, 7th, and 8th ranked scenarios respectively. Tory Junction (9th ranked) contained a low percentage of inner sounds spawning potential (0.4%) and has only moderate larval retention despite overlapping with several biogenic habitat forming taxa. The lowest ranked scenario was Whekenui Bay which also had low spawning potential (0.7%), only moderate larval retention, and limited overlap with biogenic habitat forming taxa distribution.

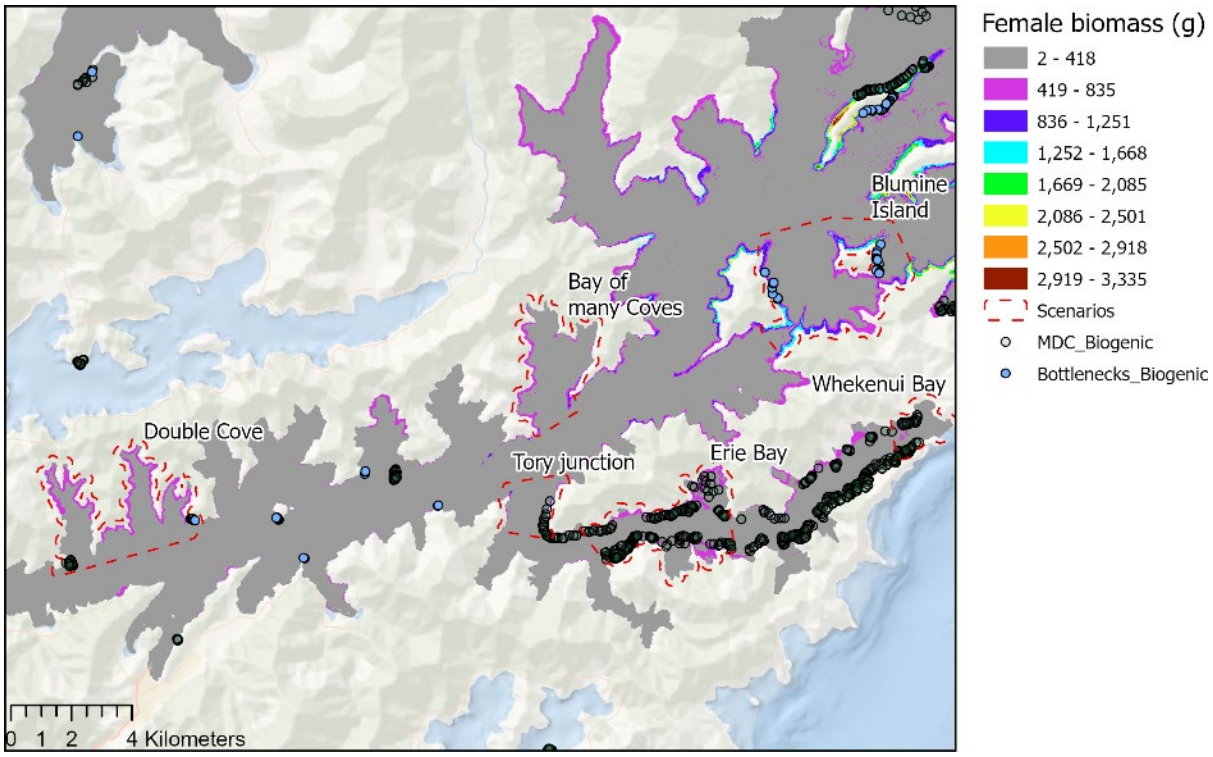

Figure 29: Potential management scenarios for Queen Charlotte Sound. The circles represent sites where occurrence of biogenic habitats has been noted from Marlborough District Council's (MDC) Significant Ecological Areas programme and NIWA's Juvenile bottlenecks programme. The coloured background indicates female biomass as predicted by the hurdle model for the inner sounds.

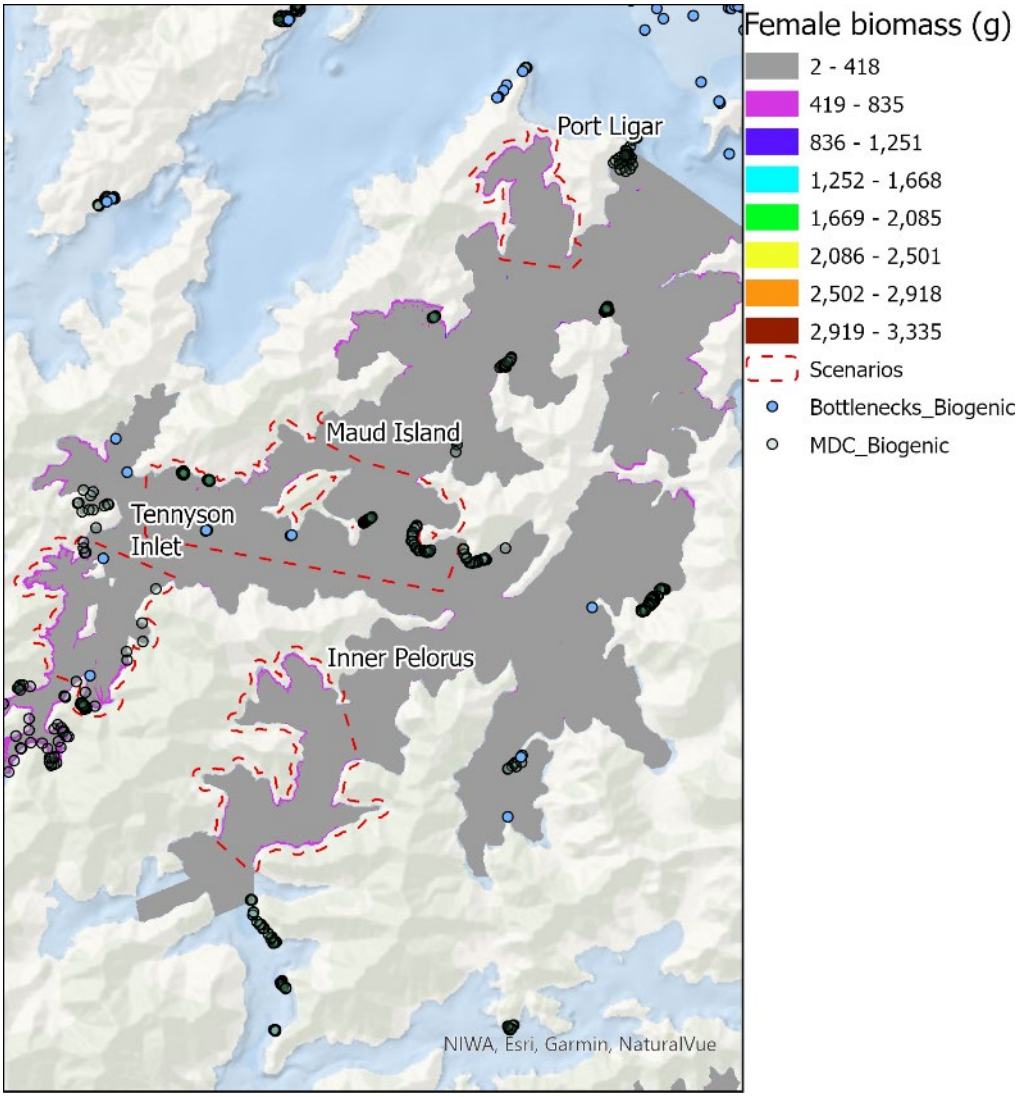

Figure 30: Potential management scenarios for Pelorus Sound. The circles represent sites where occurrence of biogenic habitats has been noted from Marlborough District Council's (MDC) Significant Ecological Areas programme and NIWA's Juvenile bottlenecks programme. The coloured background indicates female biomass as predicted by the hurdle model for the inner sounds.

Table 6: Attributes of area closure management scenarios expressed as size (km2), shape (area to seaward boundary ratio), % spawning (percent female biomass of the total within the inner sounds domain – excluding Long Island MR (as it is already protected). Biogenic habitat forming taxa is shown as presence of occurrence data. PLS: Pelorus Sound, QCS: Queen Charlotte Sound.

	Size (km^2)	Shape	% Spawning habitat	Biogenic occurrence	Known habitats	Connectivity – juv. habitat	Connectivity – larval retention	Rank	% of inner sounds domain
Pelorus									
Inner Pelorus	20.23	5.3	3.2		None	Low	High	3	3.5
Tennyson Inlet+	15.22	3.3	2.3	✓	Horse mussels in past	Low	High	6	2.6
Maud Island*	31.11	2.1	2.2	✓	Reef edges on headlands	Low-Moderate	High	5	5.4
Port Ligar	9.10	2.8	1.4		None	Moderate	High	8	1.6
% PLS									13.1
Queen Charlotte									
Double Cove*	8.51	1.6	2.3	✓	None	Low	High	4	1.5
Bay of Many Coves	6.49	3.4	1.6		Reef edges (?)	Low-Moderate	High	7	1.1
Tory Junction	2.37	0.6	0.4	✓	Biogenic clumps reef edges	Low-Moderate	Moderate	9	0.4
Erie Bay	7.85	3.0	2.7	✓	Biogenic clumps reef edges	Low	Moderate	2	1.4
Whekenui Bay	1.92	1.1	0.7	✓	Biogenic clumps reef edges (likely)	Low-Moderate	Moderate	10	0.3
Blumine Island	13.12	1.8	5.6	✓	Dog cockles (Patten and Pickersgill channels), emergent tubeworm patches (reef)	High	High	1	2.3
% QCS									7.0
% Total inner sounds									20.1

*Maud Island and Double Cove areas have existing fisheries restrictions, and Tennyson Inlet(+) is designated a 'significant ecological area' by Marlborough District Council.

4. DISCUSSION

This study provided insights into the distribution and restoration potential of spawning habitat for blue cod in the Marlborough Sounds and on the connectivity among key spawning locations and with juvenile habitat. Based on this information, we have configured ten potential 'example' spatial scenarios that provide generalisable insights that could inform discussions on spatial management of blue cod spawning stock through fishing controls. Due to a desire to enhance spawning capacity and the fishery within the inner sounds where it is most depleted, and a lack of connection between the inner sounds and coastal areas (Section 3.2), the ten candidate scenarios are restricted to and distributed throughout Pelorus and Queen Charlotte Sounds. These scenarios provide a solid starting point for Fisheries New Zealand to begin stakeholder engagement to develop areas for management in the Marlborough Sounds. Key considerations and broader outcomes of this study are discussed below.

4.1 Environmental drivers of spawning distribution

A broad range of environmental and habitat characteristics contributed to models used to predict the distribution of spawning potential, including variables that relate to physical seafloor characteristics, water quality and oceanographic conditions, and various combinations of these features. The environmental signature for 'good-quality' spawning habitat consisted of areas with low turbidity (both in terms of particulate material, e.g., suspended solids, and detritus), relatively shallow and reef associated habitat with high sand content and slope, high wave disturbance at the seafloor, low productivity and high tidal current. This combination of environmental conditions was similar between the inner and wider sounds domain – suggesting that the models captured a consistent characterisation of good quality spawning habitat. It is likely that the key drivers of distribution combine in different ways to result in high quality habitat, and such combinations will involve proxy relationships (where a variable is a proxy for another, unmeasured characteristic) and interactive relationships that are not easily discernible. However, by examining predicted spawning biomass, the univariate relationships exemplified by the partial dependence plots (e.g., Figure 18), and mapped values of the predictor variables (Figure 31), it is possible to determine how each variable contributes to identification of the key areas for spawning biomass in the inner sounds.

There were some generic relationships that acted equally on the predicted extent and value of biomass across all areas, with the most significant of these being the relationship between depth, slope and habitat suitability within the presence-absence component of the hurdle model (Figure 18). Together, these variables described over 75% of the variation in habitat suitability index. While the univariate relationships are not particularly strong (apart from bathymetry) (Figure 18), these variables are likely to have multivariate effects that combine to represent the extent of reef and reef-adjacent habitat. The effect of this combination is the narrow ribbon of predicted biomass, between 100 and 400 m, out from the coastline and islands of the inner sounds, with the extent becoming wider or narrower depending on the extent of reef/coastal slope habitat (
Figure A - *1*). Within this coastal fringe, while biomass will vary somewhat according to 'optimum' values of bathymetry, slope and reef complexity (proxied by bathymetric position), the key differences are attributable to variation in the drivers of the biomass component of the hurdle model, which differ among the 10 key areas. In general, areas with higher predicted biomass have a greater number of characteristics that are correlated with high biomass, as well as having values within the optimum range of each characteristic. The environmental variables that were key drivers of the biomass component of the hurdle model are mapped in Figure 31.

For each of the Pelorus Sound scenarios, the key drivers of higher predicted biomass are:

Tennyson Inlet

- Low turbidity according to variables that describe water quality based on total suspended particulate material (BBP), and those that are related to concentration of detrital material

(ADET) that often include signatures from riverine inputs (Álvarez-Romero et al. 2013, Ortiz-Rosa et al. 2020).

- Moderate to high wave action on the seafloor (BedDist), which relates to both wind and swell driven waves but also incorporates variability associated with depth (i.e., shallower seafloor is more impacted by waves). Thus, in the case of Tennyson Inlet it is likely that BedDist is acting as a proxy for bathymetry and shows the contribution of shallow habitat for blue cod spawning in the inner sounds.
- Warmer water temperatures than expected at the seafloor (TempRes), given the area's depth (i.e., > 3 °Cwarmer than average) and warmer surface waters (> 14 °C, SST). Blue cod generally show sensitivity and negative relationships with warmer than average conditions (Brough et al. 2023) and thus it is likely that the temperature signature is a proxy for shallow reef habitat.

Inner Pelorus

- Moderate to high tidal current velocity compared to other inner sound locations, and areas where high velocity coincides with the reef-edge fringe.
- Warmer water temperatures than expected at the seafloor (TempRes), given the area's depth (i.e., warmer than average) and warmer surface waters (SST). Blue cod generally show sensitivity and negative relationships with warmer than average conditions (Brough et al. 2023) and thus it is likely that the temperature signature is a proxy for shallow reef habitat.
- Several areas of high reef complexity indicated by high bathymetric position index (BPI) values.

Note – the high turbidity values (BBP/ADET) are likely to describe why this area has slightly reduced spawning habitat compared to other key areas.

Maud Island

- Low turbidity according to variables that describe water quality based on total suspended particulate material (BBP), and those that are related to concentration of detrital material (ADET), particularly on the western side of Maud Island.
- Moderate tidal current velocity on the eastern side of the area (Tapapa Point), and areas where high velocity coincides with the reef-edge fringe.
- Areas of high reef complexity indicated by high bathymetric position index (BPI) values, particular around and west of Maud Island itself.
- High slope values in the east of the area around Tapapa Point

Note – Maud Island had lower predicted biomass but was retained as a key area due to existing protection and occurrence of biogenic habitats.

Port Ligar

- Low turbidity according to variables that describe water quality based on total suspended particulate material (BBP), and those that are related to concentration of detrital material (ADET).
- Areas of high reef complexity indicated by high bathymetric position index (BPI) values, particularly around both headlands.
- Steep slopes in some areas around the coastal reef fringe, particularly adjacent to points within the bay.

For each of the Queen Charlotte Sound areas, the key drivers of higher predicted biomass are:

Double cove

- High to moderate sand concentration in seafloor sediments, which indicates a lack of mud content (i.e., sedimentation).
- Moderate wave action on the seafloor (BedDist), which relates to both wind and swell driven waves but also incorporates variability associated with depth (i.e., shallower seafloor is more impacted by waves). Thus, in the case of Double Cove it is likely that BedDist is acting as a

proxy for bathymetry and shows the contribution of shallow habitat for blue cod spawning in the inner sounds.
- Warmer water temperatures for the inner bays. Blue cod generally show sensitivity and negative relationships with warmer than average conditions (Brough et al. 2023) and thus it is likely that the temperature signature is a proxy for shallow reef habitat.
- Broader and shallower reef margin according to multibeam bathymetry, and bathymetric position index.

Bay of Many Coves

- Low turbidity according to variables related to concentration of detrital material (ADET).
- Low primary productivity derived from phytoplankton growth (VGPM), particularly within the bay. While a preference for low productivity might be counter intuitive, VGPM can also be a proxy for water quality, where high values may be related to high nutrients and land-based runoff.
- High reef complexity (BPI), particularly around the headlands.
- Moderate tidal current velocity around the headlands.

Blumine Island

- Low turbidity according to variables that describe water quality based on total suspended particulate material (BBP), and those that are related to concentration of detrital material (ADET).
- Low primary productivity derived from phytoplankton growth (VGPM), particularly within the Bay. While a preference for low productivity might be counter intuitive, VGPM can also be a proxy for water quality, where high values may be related to high nutrients and land-based runoff.
- High wave action on the seafloor (BedDist), particularly around East Bay. BedDist relates to both wind and swell driven waves but also incorporates variability associated with depth (i.e., shallower seafloor is more impacted by waves). Thus, in the case of Blumine Island it is likely that BedDist is acting as a proxy for bathymetry and shows the contribution of shallow habitat for blue cod spawning in the inner sounds.
- High reef complexity (BPI), particularly around the channels and headlands of both islands.
- Moderate tidal current velocity, particularly in the channels between the islands and the mainland.
- Warmer water temperatures than expected at the seafloor (TempRes), given the area's depth (i.e., warmer than average). Blue cod generally show sensitivity and negative relationships with warmer than average conditions (Brough et al. 2023) and thus it is likely that the temperature signature is a proxy for shallow reef habitat
- Broad reef margin with steep slopes in places – particularly around the channels between the islands and the mainland.

Tory junction

- High tidal current velocity intersecting with coastal reef fringe.
- Highly complex reef structure (BPI) on both sides of the channel, with steep slopes in places.
- High sand content in sediments adjacent to reef fringe, which also equates to low mud content (i.e., sedimentation).
- Moderate turbidity related to total suspended particulates (BBP) and detrital material (ADET).

Erie Bay

- High tidal current velocity intersecting with coastal reef.
- Highly complex reef structure (BPI) on both sides of the channel, with steep slopes in places.
- High sand content, particularly at the western end of Tory Channel.

- Low primary productivity derived from phytoplankton growth (VGPM). While a preference for low productivity might be counter intuitive, VGPM can also be a proxy for water quality, where low values may be related to low nutrients and land-based runoff.
- High diversity in physical seafloor characteristics (depth, slope, complexity), including broad, steeply sloping and complex reef habitat and shallow shelves. Together, these contribute to a wide extent of blue cod spawning habitat. Very shallow (<3m) habitat in some bays shows decline in spawning potential as expected.

Note – while sea surface temperatures were positively associated with spawning biomass, the considerably lower average temperatures in Tory Channel (Figure 31) should be kept in mind given potential impacts of climate change on blue cod, which may be particularly extreme in the Marlborough Sounds (see Brough et al. 2025).

Whekenui Bay

- Low primary productivity derived from phytoplankton growth (VGPM). While a preference for low productivity might be counter intuitive, VGPM can also be a proxy for water quality, where low values may be related to low nutrients and land-based runoff.
- Low turbidity according to variables related to concentration of detrital material (ADET). However, note that turbidity according to suspended particulates (BBP) is high – potentially due to tidal current or wave resuspension.
- High wave action on the seafloor (BedDist). BedDist relates to both wind and swell driven waves but also incorporates variability associated with depth (i.e., shallower seafloor is more impacted by waves). In the case of Whekenui Bay, the importance of BedDist may be related to both swell exposure, and the shallowness of the habitat.
- High sand content in sediments adjacent to reef fringe, which also equates to low mud content (i.e., sedimentation).
- High tidal current velocity intersecting with coastal reef.

The relationships between environmental/habitat variables and spawning biomass are highly consistent with other studies on blue cod habitat selection. For example, Brough et al. (2023) found the key drivers of blue cod distribution in Canterbury were related to reef edge habitat, turbidity, temperature, and substrate characteristic (particularly sand and gravel). These characteristics of blue cod habitat selection have also been reported elsewhere within the species range and are thus likely to be a consistent component of blue cod habitat. While it is highly likely these physical characteristics of blue cod habitat are important, the species also has known associations with biogenic habitats formed by oysters (Carbines et al. 2004), bryozoans (Carbines 2004), tubeworms (Morrison et al. 2014), sponges, ascidians, and macroalgae (Carbines 2004; Carbines et al. 2004). We were unable to directly include information on biogenic habitats in the models used to predict spawning distribution due to a lack of data on biogenic occurrence that matched the scale of data on blue cod from the potting surveys. However, for the inner sounds domain it is likely that the use of high resolution multibeam data on physical characteristics provides an appropriate proxy for some biogenic habitat forming taxa. That the available data on the occurrence of (some) biogenic taxa regularly coincides with areas of importance for spawning, substantiates this claim (Figure *7*). However, we cannot rule out that including detailed data on the distribution of biogenic habitats of importance for blue cod (i.e., extension of layers similar to Ribó et al. 2021), would not change the predicted distribution of spawning potential.

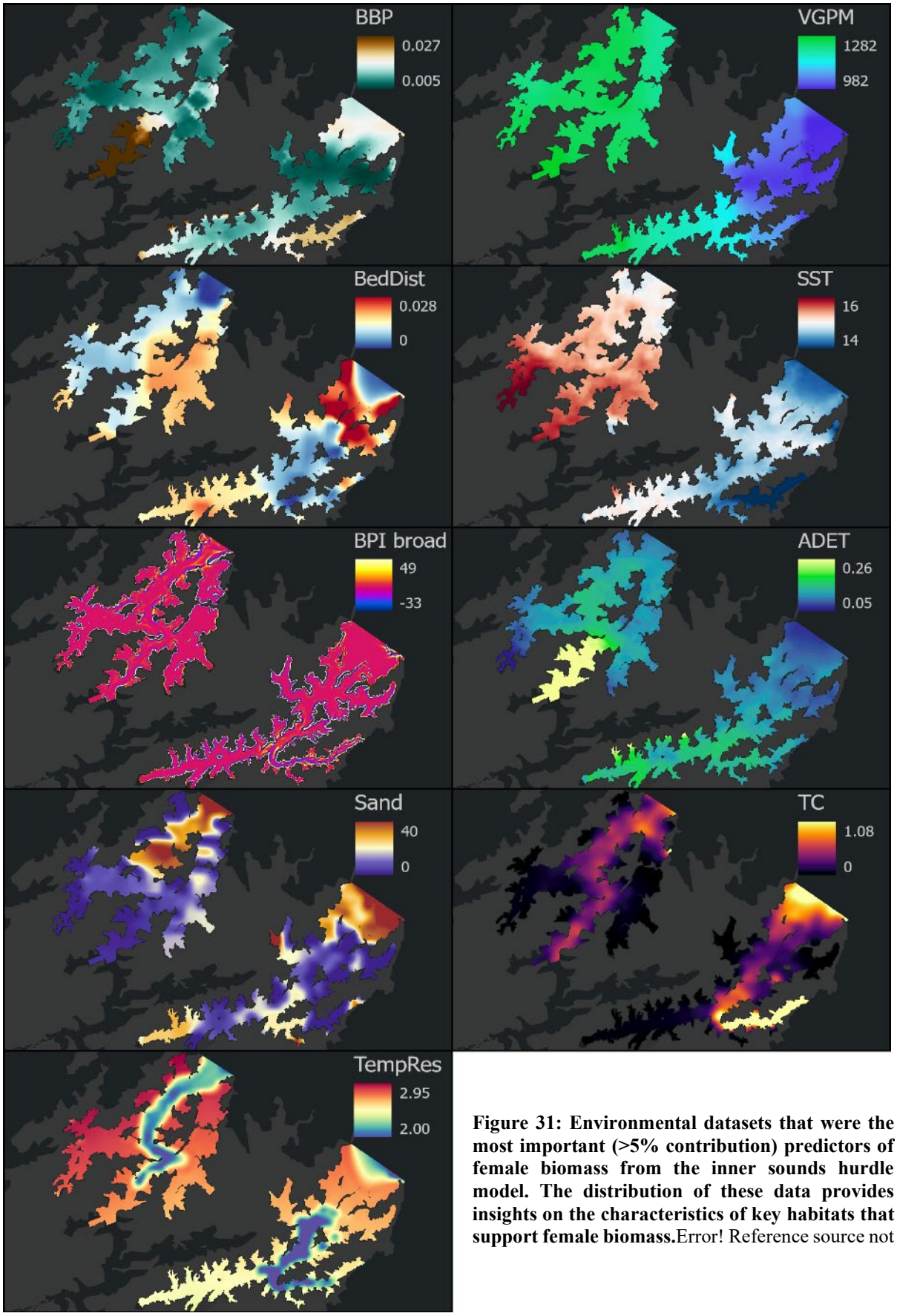

Figure 31: Environmental datasets that were the most important (>5% contribution) predictors of female biomass from the inner sounds hurdle model. The distribution of these data provides insights on the characteristics of key habitats that support female biomass. Error! Reference source not

4.2 Connectivity

The dispersal modelling indicates rapid advection of particles out of the wider Marlborough Sounds region, suggesting that spawning locations outside of the sounds are unlikely to contribute significantly to the rebuilding of spawning stocks in the inner sounds, at least via passive settlement of larvae (i.e., active movement of juvenile/adult fish may still be possible). Connectivity between Pelorus Sound and Queen Charlotte Sound is limited, but both regions exhibit high localized retention. Similarly, Atalah et al. (2022), using dispersal modelling to identify potential source areas of green-lipped mussel spat in the Marlborough Sounds, also found high retention in Queen Charlotte Sound as well as in the mid and inner Pelorus Sound.

The circulation in Pelorus Sound is characterised by strong tidal flows along the central channel, which break down into eddy fields within the surrounding embayments (Stevens et al. 2019). While the tidal flow along the central channel facilitates particle transport throughout the sound, the eddies formed in the embayments enhance particle retention.

Queen Charlotte Sound is characterized by well-defined estuarine circulation, whereas Tory Channel is dominated by strong tidal flows (Hadfield et al. 2014). The estuarine circulation in Queen Charlotte Sound promotes the advection of particles along the main channel while also limiting the export into Cook Strait. In contrast, the strong tidal currents in Tory Channel facilitate bi-directional exchange between Queen Charlotte Sound and Cook Strait.

4.3 Caveats

The SDMs developed in this study had good performance for predicting the distribution of present-day female blue cod biomass given the environmental and habitat characteristics of the Marlborough Sounds. There are, however, a range of factors that were unable to be included in the models that are likely to be the core drivers of where large, female fish are currently found – foremost among these is rates of historical fishing extraction (Bowden et al. 2021, Brough et al. 2023). Locations where female blue cod biomass is currently high, are likely those areas that have faced less commercial and recreational fishing pressure historically. The models use the unique environmental signature of these areas (e.g., coastal waters) to generate a proxy for this missing effect. However, not being able to include the direct influence of historical fishing pressure means that we cannot forecast likely changes in biomass for depleted areas (e.g., the inner sounds), and we therefore assume that the spawning stock will recover if the characteristics of the habitat are appropriate and exploitation is halted. This is a common assumption in the restoration of marine habitats and species due to the oftentimes unavailability of data on stressors at appropriate spatiotemporal scales (Tulloch et al. 2015, Zellmer et al. 2019, Lester et al. 2020). Improvements to the SDM approach used in this study could also determine exploring scale and resolution-dependent effects of the various spatiotemporal environmental/habitat variables used in the modelling (Mannocci et al. 2017, Porskamp et al. 2022). Such explorations were deemed out of scope for this study, however we note that Brough et al. (2023), found that environmental data extracted based on a pot's location, and for the month of the survey were the best predictors of blue cod abundance elsewhere in the South Island – which aligned with the approach taken here.

While the sample coverage used to develop the SDMs is high, there are some spatial gaps in the potting data which may mean that the characteristics of some areas and the female biomass they support may not be well represented. If some areas within the sounds have unique habitat characteristics or unexpectedly high/low female biomass (given their characteristics), this may exert bias on the model predictions. For example, there has been limited sampling in existing management areas other than the Long Bay Marine Reserve (e.g., Maud Island, Double Cove). If female biomass has recovered in these inner-sounds areas, the SDMs developed here would be greatly improved by data from these areas. Both Maud Island and Double Cove were included within scenarios for broader protection in this study based, in part, due to the possibility that there is unmeasured, existing recovery of female biomass in these areas.

In this study, we used a hurdle model approach largely to constrain the prediction of female blue cod biomass to an appropriate environmental envelope (i.e., coastal, nearshore habitat) using the PA component, and to allow biomass to vary within this envelope using the biomass component of the hurdle model (Pirathiban et al. 2015). Hurdle models are typically undertaken using true absences (Maunder & Punt 2004, Stephenson et al. 2021a, Bennion et al. 2024b), which were not available through the full Marlborough Sounds area due to potting surveys targeting places where blue cod are most well-known to occur. The use of randomly generated pseudo-absences (i.e., background data) in the hurdle model can skew the proportion of sites occupied which is an important component for the estimation of probability of occurrence (i.e., habitat suitability index) (Maunder & Punt 2004). However, simulation studies have found that this is a problem only when it is likely that many presences are found within the background dataset, and that the use of gradient boosting methods (i.e., BRTs/RFs) over multiple model runs with randomly selected background data can alleviate such issues (Maunder & Punt 2004, Ward et al. 2009, Di Lorenzo et al. 2011). We generated randomly selected background data with the same spatial structure as female blue cod presence, but that was structured according to data on commercial and recreational fishing effort to represent areas that are highly likely to be true absences. This approach is recommended for the use of background data in hurdle-type models, and allows the methods to realise the benefits of presence-only data (Di Lorenzo et al. 2011, Pirathiban et al. 2015, Charsley et al. 2025). Further work could undertake simulation experiments to characterise the uncertainty associated with including background data that may contain the environmental signature of presences (as per Charsley et al. 2025). However, the PA component of the hurdle model had very high predictive performance and the predictions align well with general knowledge on the habitats in which blue cod occur in this area.

In addition to caveats associated with the spatial modelling of female biomass, the following considerations apply to the results of the particle tracking analysis.

- Some physical processes that influence larval transport in nearshore environments - such as surface gravity waves (e.g. Stokes drift) and riverine-induced buoyancy currents – are either excluded or poorly resolved in the current hydrodynamic models. Uncertainties in larval transport arising from these limitations could be reduced through the development of a single, purpose-built, high-resolution hydrodynamic model.
- Similarly, the use of a merged velocity field derived from three different hydrodynamic models for the particle tracking can introduce inconsistencies in the particle trajectories, particularly at the boundaries between the model domains. These inconsistencies could be eliminated by implementing a single high-resolution hydrodynamic model that covers the entire Marlborough Sounds region.
- The constant release of 1000 eggs per day is not representative of the true spawning potential of blue cod and does not consider increased spawning at particular times of the spawning season.
- Many aspects of blue cod larval dispersal and settlement are simplified or neglected in the particle tracking models (e.g., chemical and environmental cues, predation), either due to limited biological knowledge or because further development of the particle tracking models is needed to incorporate these processes.
- The biological parameters (vertical velocity and density) prescribed to particles under the buoyancy-modified scenario are based on Northeast Arctic cod characteristics (Sundby 1983) due to limited information for New Zealand blue cod. Few marine fish have had the buoyancy characteristics of eggs investigated, with most other species being pelagic fish (that are likely less relevant for blue cod) or other gadids (that have similar characteristics to NEA cod) Sundby & Kristiansen, 2015. The buoyancy-modified scenario can be improved through the incorporation of species-specific biological characteristics, that can be determined via tank experiments to measure specific gravity using a vertical density gradient, or via in-situ field observations of the vertical distribution of eggs matched with vertical profiles of seawater density (Sundby & Kristiansen, 2015).

- The particle tracking was conducted over a single representative year; therefore, interannual variability and climate-driven influences (e.g., ENSO) on spawning potential, larval transport and recruitment were not accounted for.

4.4 Candidate scenarios

As stated in the methods, the ten scenarios that were used and ranked as examples for analysis are based on a suite of factors that included: (1) the predicted distribution of female biomass; (2) the distribution of other important habitats that may be important for blue cod including the occurrence of biogenic habitats (both from benthic invertebrates and kelp) or significant reef-edge habitat; (3) the results of the particle tracking analysis that indicate the connectivity of several broadly distributed 'candidate' areas; (4) the constraint that scenarios were to be widely distributed throughout the Queen Charlotte and Pelorus Sounds areas. The ten areas identified in Section 3.4, are likely to be the best scenarios to meet these criteria, based the outputs of this research alone. However, it should be noted that there is inherent subjectivity to the decision on where to delineate these scenarios. For example, while a scenario's approximate position is data driven, the shape and size of the scenarios relates directly to the percentage of spawning area protected (Figure ***29***, Figure ***30***, Table 6), and thus slight adjustments may result in reasonable variability in this key metric, which would in turn affect the ranking of the scenarios (Table ***6***). Additionally, the overlay with known biogenic habitat forming taxa should not be considered exhaustive as not all areas have been sampled for these habitats. Further, there are a range of information sources not considered, including local ecological knowledge, mātauranga Māori, social and economic values or considerations, and historical accounts of blue cod abundance beyond the potting survey time series that should be included in the wider spatial planning process. Thus, we reemphasise that these scenarios should be considered a starting point that provide a basis for future stakeholder engagement on spatial management approaches for increased spawning capacity. Further refinement should, however, include considering the same principles for successful spatial management used in this scenario approach, particularly:

- Ensuring that scenarios are the correct shape, size and level of protection to ensure viability and adequacy (i.e., considering home range size, spillover, likely response to management).
- Ensure scenarios are representative of areas within which restoration of spawning is the objective (i.e., considering sites throughout the inner sounds).
- Replication – utilising multiple scenarios to maximise the chances of recovery.
- Including areas of importance – ensuring scenarios cover a high proportion of key spawning habitat and other habitats that may be important (e.g., biogenic habitat).
- Connectivity – among scenarios and with juvenile habitats.
- Integration with other spatial management – both existing marine (e.g., MPA, MDC marine sites of ecological significance) and terrestrial management.

See Brough et al. (2021) for a full review of the application of these principles for the design of spatial management approaches.

The overall goal of these ten geographically widespread closure scenarios would be to increase blue cod abundance and size of both sexes, increase egg production, and restore the sex ratio balance. The particle tracking analyses indicated that there was almost no connectivity between Pelorus and Queen Charlotte Sound (see Section 3.2) and hence any spillover of eggs and larvae will benefit the neighbouring areas only within each of the sounds, with some loss of eggs and larvae to the wider prevailing currents that move eastward. The restricted movement and strong site fidelity of blue cod also (see Introduction section) indicates that it would be unlikely for there to be any significant movement of adults or juveniles between Pelorus and Queen Charlotte Sounds, and any benefits accruing from these protected areas would manifest independently. Thus, recovery of local populations within the inner sounds will require representative areas in each of the sounds. However, it is also vital to recognise the importance of the few remaining areas where blue cod spawning biomass is likely to

be present at significant levels (Gaines et al. 2010, Tong et al. 2021), and thus it also advisable for Fisheries New Zealand to consider management settings for areas within the wider sounds domain. While the particle tracking suggests that there is limited connectivity between the sites of highest spawning potential around D'Urville Island and the inner sounds, there is some connectivity with juvenile and coastal habitats in the outer sounds (Figure 23). Thus, the protection of these areas may contribute to the recovery of blue cod abundance in a step-wise manner that may ultimately lead to local enhancement in the inner sounds (Gaines et al. 2010, Le Port et al. 2017, Tong et al. 2021).

5. POTENTIAL RESEARCH

There are clear opportunities to build upon the spatial modelling undertaken in this study to generate layers of information that may be important for the management of blue cod and other fisheries in the Marlborough Sounds. Foremost among these are the use of existing occurrence and abundance data on biogenic habitat forming taxa to generate SDMs for these key habitats (e.g., Bennion et al. 2024a, Charsley et al. 2025, Brough et al. 2023). With this information, it may be possible to directly link fish abundance, density, and importance for particular life history processes (spawning) to the habitats that sustain these functions, thus providing significant advances for the mapping and protection of habitats of significance for fisheries. Additionally, further work could use decision-support tools to develop spatial scenarios for the protection of spawning and other biodiversity features using quantitative spatial prioritisations that could include trade-offs with human-use elements (i.e., fishing) (Lundquist et al. 2020a).

If area closures to enhance spawning capacity were to be implemented within the next few years, this provides an opportunity to sample the blue cod population in these areas before closure, and then periodically after closure to test the hypothesis that the closure to fishing has had an impact on blue cod abundance, size, sex ratio. These variables are all directly related to egg production. There is currently no acceptable method to sex blue cod non-lethally so any sampling of sex would need to sacrifice a number of blue cod during a survey. The next Fisheries New Zealand Marlborough Sounds potting survey is scheduled for October 2025, and this could be used to survey some of the candidate areas. It is likely that some of these areas have had pots set within their planned boundaries on previous surveys and these data could be easily collated. Ideally, it would be best to survey all planned protected areas before and after closure but, given the finite resources allocated to carry out a potting survey and lack of developed proposals on specific sites, high priority areas from this research would be: 1) Blumine Island in Queen Charlotte Sound; 2) Maud Island in Pelorus; and 3) Port Ligar in Pelorus Sound. Along with Long Island Marine Reserve, this would then provide survey coverage in the four highest ranked scenarios (two in each sound) that could be regularly monitored on potting surveys, or by other means, if closed to inform how effective these areas are at achieving the stated goals. Regardless, it is anticipated that collectively these areas will contribute to the overall health of the blue cod population within the inner sounds which should be tracked on routine potting surveys every four years. These areas could also be used to monitor the effects of fishing on the aquatic environment, using video or diver surveys of fish and benthic biodiversity in paired inner and outer locations.

6. FULFILMENT OF BROADER OUTCOMES

The broader outcomes of this project include provision of useful results that can be used to guide the Marlborough Sounds Blue Cod Advisory Group and Fisheries New Zealand to inform the development of new and novel fisheries management measures, including potential 'spawning recovery areas' as identified by the working group. Improved management and recovery of blue cod stocks will benefit a wide range of stakeholders such as iwi, recreational fishers, commercial fishers, environmental groups, and the wider public. The value of this taonga to stakeholders in Marlborough Sounds cannot be understated, and any success or learnings that stem from this research can theoretically be applied to other areas where blue cod are also in poor health.

In addition, this project has contributed towards capacity building within Earth Sciences NZ by involving five key staff (Mike Beentjes, Tom Brough, Eva Leunissen, Mark Morrison, and Charine Collins) most of whom have contributed in a meaningful way to research around the processes that contribute to understanding stressors on blue cod habitat, and ultimately to recovery of blue cod stocks. Two members are also female, contributing to gender diversity in science.

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APPENDIX 1: Additional model outputs

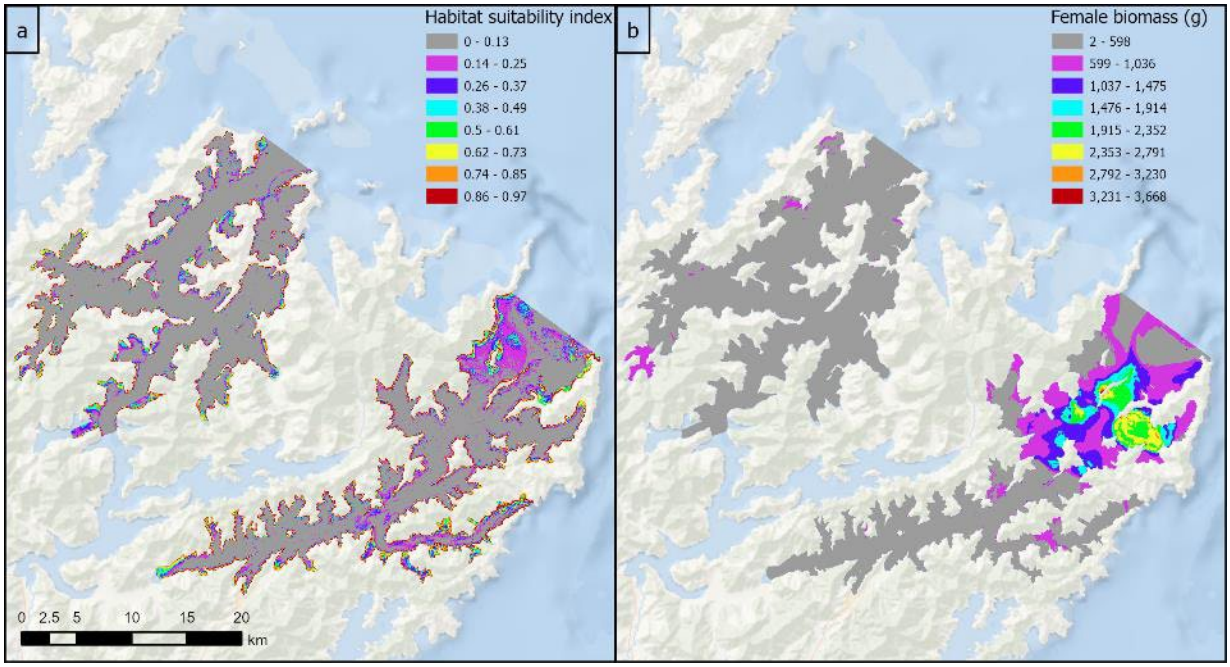

Figure A - 1: a) Presence-absence model output as habitat suitability index (HSI), b) abundance model output as female blue cod biomass (in grams).