From data compilation to model validation: A comprehensive analysis of a full deep-sea ecosystem model of the Chatham Rise

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The Chatham Rise is a highly productive deep-sea ecosystem that supports numerous substantial commercial fisheries, and is a likely candidate for an ecosystem based approach to fisheries management in New Zealand. We present the first end-to-end ecosystem model of the Chatham Rise, which is also the first end-to-end ecosystem model of any deep-sea ecosystem. We describe the process of data compilation through to model validation and analyse the importance of knowledge gaps with respect to model dynamics and results. The model produces very similar results to fisheries stock assessment models for key fisheries species, and the population dynamics and system interactions are realistic. Confidence intervals based on bootstrapping oceanographic variables are produced. The model components that have knowledge gaps and are most likely to influence model results were oceanographic variables, and the compilation species groups 'seabird' and 'cetacean other'. We recommend applications of the model include alternatives that vary these components.

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Abstract

The Chatham Rise is a highly productive deep-sea ecosystem that supports numerous substantial commercial fisheries, and is a likely candidate for an ecosystem based approach to fisheries management in New Zealand. We present the first end-to-end ecosystem model of the Chatham Rise, which is also the first end-to-end ecosystem model of any deep-sea ecosystem. We describe the process of data compilation through to model validation and analyse the importance of knowledge gaps with respect to model dynamics and results. The model produces very similar results to fisheries stock assessment models for key fisheries species, and the population dynamics and system interactions are realistic. Confidence intervals based on bootstrapping oceanographic variables are produced. The model components that have knowledge gaps and are most likely to influence model results were oceanographic variables, and the compilation species groups 'seabird' and 'cetacean other'. We recommend applications of the model include alternatives that vary these components.

Keywords: Chatham Rise; Atlantis; Ecosystem model; Deep sea; Fisheries; Validation; End-to-end

1 Introduction

The body responsible for fisheries management in New Zealand, Fisheries New Zealand, is seeking to move away from single species management towards a more ecosystem approach, both to fulfil Fisheries Act obligations and Marine Stewardship Council (MSC) expectations (Ministry for Primary Industries (2008), Marine Stewardship Council (2014)). The Chatham Rise is the location of several nationally important MSC certified fisheries (Deepwater Group, 2018), and a growing understanding of trophic interactions exists there (Stevens et al. (2011b), Dunn et al. (2009)).

Chatham Rise is a submarine ridge running eastwards for about 1000 km from the east coast of South Island, New Zealand, rising up from depths of about 3000 m, to about 50 m at the western end, and sea level around the Chatham Islands at the eastern end (Figure 1). The subtropical front (STF), a relatively broad permanent feature where warmer, more saline, and nutrient poor subtropical water from the north meets nutrient rich subantarctic water from the south, extends up the east coast of South Island, and then eastwards along Chatham Rise (Heath (1985), Uddstrom and Oien (1999)). The demersal fish assemblage on Chatham Rise has the highest fish species richness in New Zealand waters (Leathwick et al. 2006). The range of habitats and depths, and the influence of the STF, are expected to provide a wide variety of foraging opportunities for demersal and pelagic organisms.

The Chatham Rise is perhaps New Zealand's most productive fishing ground. It supports substantial commercial fisheries for finfish and invertebrates, with notable examples being: trawl fisheries for hoki (*Macruronus novaezelandiae*), orange roughy (*Hoplostethus atlanticus*),

hake (*Merluccius australis*), and black and smooth oreos (*Allocyttus niger*, *Pseudocyttus maculatus*); a longline fishery for ling (*Genypterus blacodes*); and a potting fishery for rock lobster (*Jasus edwardsii*) (Ministry for Primary Industries 2014).

Analyses of trawl survey series and commercial fishery catch rates have shown that marked variations over time have occurred in the relative abundance of some common species on Chatham Rise, e.g., hoki, hake, orange roughy, scampi (*Metanephrops challengeri*), and rock lobster (Maunder and Starr, 1995; Dunn et al., 2008; Stevens et al., 2017). Some factors driving these fluctuations have been identified (i.e., high exploitation levels, variation in recruitment), but there will certainly be other physical and biological factors that will influence animal behaviour and survivability, resulting in changes to the ecosystem. A knowledge of how particular biological and ecological changes could affect the abundance and distribution of species will usefully inform the management of those species.

In an ecosystem, nothing exists independently. When assessing biological risks, it is difficult to conceptualise risk to the whole system. A system-level model within which different scenarios can be explored is an extremely valuable tool for gaining conceptual understanding of economic and biological risks for a whole system, as well as for individual parts.

Atlantis is an ecosystem modelling approach that can be used to create an environment in which different scenarios can be played out to test for different results and learn how a system may be reacting to changes within it. Reviewed as one of the best modelling frameworks for exploring 'what-if' type questions (Plagányi, 2007), it includes the ability to compare social, conservation, and economic outcomes. With sufficient data, this modelling approach can be extremely useful for management strategy evaluation (Plagányi, 2007), and has been applied to multiple marine systems (from single bays to millions of square kilometres) in Australia, the United States, Europe, and South Africa (Savina et al. (2005), Fulton et al. (2007), Link et al. (2010), Ainsworth et al. (2015), Smith et al. (2015), Sturludottir et al. (2018), Ortega-Cisneros et al. (2017)).

In this paper, we describe the first end-to-end ecosystem model for the Chatham Rise, New Zealand (hereafter referred to as CRAM). We present analyses of the model, comparing its state and dynamics to current knowledge. We identify and assess the likely influence of current knowledge gaps and uncertainties.

In developing such models, knowledge gaps become evident, and we are provided with the opportunity to analyse the importance of these gaps, thus guiding direction of future research. The model was assessed for single species dynamics and inter-species connectivity. We conducted a skill assessment on species groups for which we have surveys capable of indexing abundance, and compared responses to historical fishing for species groups that have stock assessments or reliable catch per unit effort (CPUE) indices. We simulated changes in biomass for each species group and analysed responses throughout the system. This latter part formed the basis for analysing influence and importance of knowledge gaps, and where a species group performed poorly in the skill assessment it often highlighted a knowledge gap.
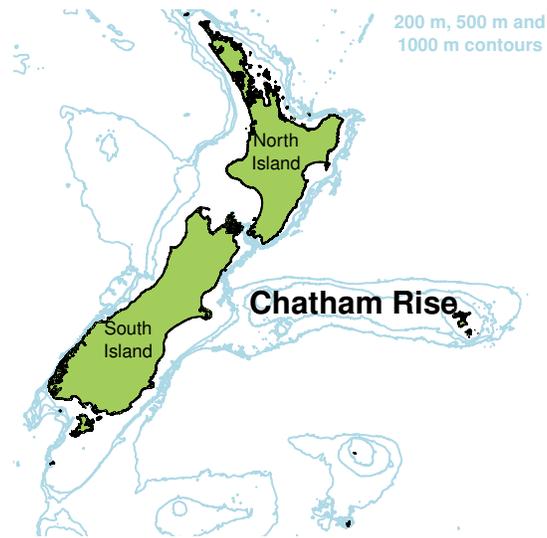
Figure 1: Map of New Zealand with Chatham Rise marked, including 200 m, 500 m, and 1000 m isobaths.

2 Model design

2.1 Model area

The Chatham Rise Atlantis model area comprises waters from the shore-line around Chatham Islands (but excluding estuaries on the islands) to depths of 1300 m along the Chatham Rise, New Zealand (Figure 2). The western boundary of the area is defined as the 400 m contour on the western edge of the Mernoo Gap, a trough that separates the Chatham Rise from the coastal shelf off the mid east coast of South Island.

An Atlantis model requires the modelled region to be split into polygons and depth layers. Each polygon/depth layer is referred to as a cell. The intention of the splits is to capture important aspects of the region but at a simplified level such that modelling the region over many years becomes possible. If we were modelling a smaller temporal scale, we may have considered a finer spatial scale. The polygons within the modelled area are referred to as dynamic polygons, and these are surrounded by non-dynamic polygons which act as a buffer between the modelled area and surrounding area.

Several investigations of fish communities or fish species richness indicated that the division of the Chatham Rise into polygons for Atlantis modelling should occur primarily based on depth categories, with the northern and southern slopes separated (owing to the different water

masses and fish communities to the north and south of the STF), and with some longitudinal differentiation as well. McClatchie et al. (1997) analysed species richness from depths of 80 to 898 m depth on the Chatham Rise and Campbell Plateau. They found species-richness hotspots to be concentrated on the Chatham Rise (particularly the north Rise) and reported that richness increased with depth to reach a maximum at 500 to 1000 m. Leathwick et al. (2006) investigated factors affecting fish species richness around New Zealand, and concluded that depth was the single most important environmental predictor, with highest richness occurring at depths of 900 to 1000 m, but with a broad plateau of moderately high richness between 400 and 1100 m. Richness was higher both in waters with high surface concentrations of chlorophyll a and in zones of mixing of water bodies of contrasting origins (e.g. the STF). Water temperature was also important, with lower richness occurring in waters that were cooler than expected given their depth. On Chatham Rise, richness was high relative to other areas of the New Zealand EEZ, particularly on the northern slope (Leathwick et al. 2006). Tuck et al. (2009) analysed data exclusively from a series of trawl surveys of depths 200–800 m on Chatham Rise (described by Livingston et al. (2002)). Species communities were found to group in adjacent depth-defined strata, but with differences between depths on the northern and southern Rise, as well as some longitudinal differentiation (Tuck et al., 2009). The STF on the Chatham Rise has been shown to serve as a discontinuity for about 70% of the small mesopelagic fish species (Robertson et al., 1978). In the study most pertinent to the Atlantis model, Bull et al. (2001) investigated depths from 200 to 800 m on Chatham Rise and concluded that mean species richness peaked at 550 to 800 m on the north Rise, and was lower on the south Rise, and in depths between 200 and 550 m. They concluded that there were marked changes in fish community composition at depths of about 350 and 550 m, and that depth, latitude, and to a lesser extent longitude explained most of the variation in abundance and composition of catches.

A large amount of data on the abundance and distribution of demersal fish and invertebrate species has been collected from the series of trawl surveys of depths 200–800 m on Chatham Rise in January annually from 1992 to 2014 (Livingston et al. 2002, Stevens et al. (2017)). Some of the more recent surveys in the series also included strata to depths of 1300 m (Stevens et al., 2017). The survey area was stratified by depth, latitude, and longitude. It was logical, therefore, to base the Atlantis model polygon boundaries on the trawl survey strata boundaries. Consequently, the model area was divided into 23 dynamic polygons based on bottom depth bins (< 200 m, 200–400 m, 400–600 m, 600–800 m, 800–1300 m), with bins deeper than 400 m separated into northern and southern Rise polygons, and with longitudinal separation (where trawl survey strata allowed) aimed at producing western, central, and eastern polygons. The dynamic polygon area is surrounded by 6 additional non-dynamic polygons which allows for the exchange of water, nutrients and biota into and out of the dynamic model domain. The final configuration of the dynamic and non-dynamic polygons is shown in Figure 2.

All model polygons are further divided into water column depth layers, ranging from one

164   layer in some near-shore polygons to five layers for the deepest polygons. Depth layers are also

165   defined in Figure 2. Each box also contains one epibenthic and one sediment layer.
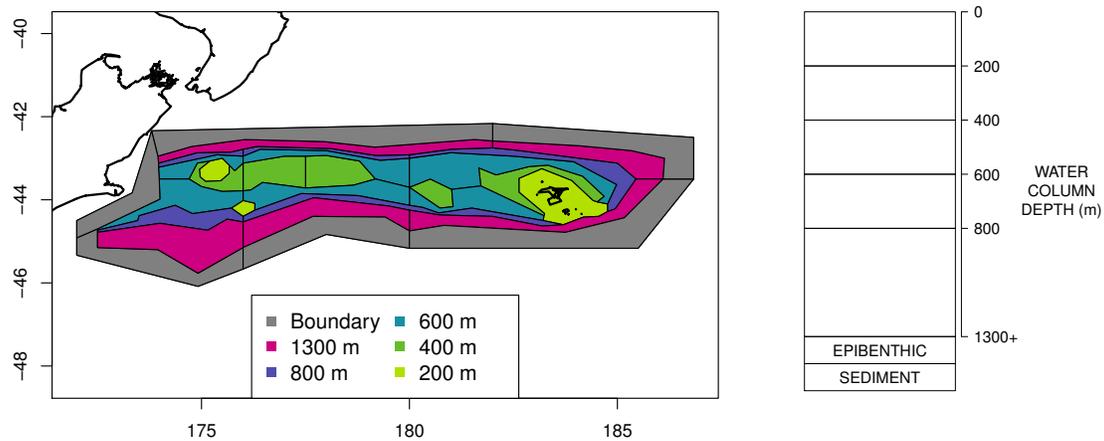
Figure 2: Polygons as defined for CRAM with maximum depths for each polygon shown by colour (left) and depth layer bins (right).

2.2   Time

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167   The model was run with a 35 year burn-in period (1865–1900) followed by a 115 year modelled

168   period (1900–2015). The burn-in period allows for the model to adjust from potentially unstable

169   initial conditions due to uncertainty of some of the parameters, to a state that is more stable.

170   A 35 year period was chosen as it covered initial fluctuations of most functional groups in the

171   model. All results presented here are from the modelled period 1900–2015. The model used 12

172   hour timesteps to allow for changes in temperature, light and feeding patterns between night

173   and day.

2.3   Oceanography

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175   Salinity, temperature and water exchange between cells were forced in the Atlantis model using

176   outputs from a ROMS (Regional Oceanographic Modelling System) model that covered years

177   1996–2004. Water currents across each box face cause the horizontal movement of nutrients

178   (such as ammonia and nitrate) available to primary producers. The speed and direction of

179   currents influence the spatial distribution of plankton groups. Water temperatures influence

180   biological process such as respiration Hoegh-Guldberg and Bruno (2010). Based on sea surface

181   temperatures (SST), the ROMS years (1996–2004) look to be fairly representative of those from

182   1961–2017 (Figure 3). The base model presented here repeated the available ROMS variables,

183   and we ran sensitivities varying the order of ROMS years or repeating one ROMS year.
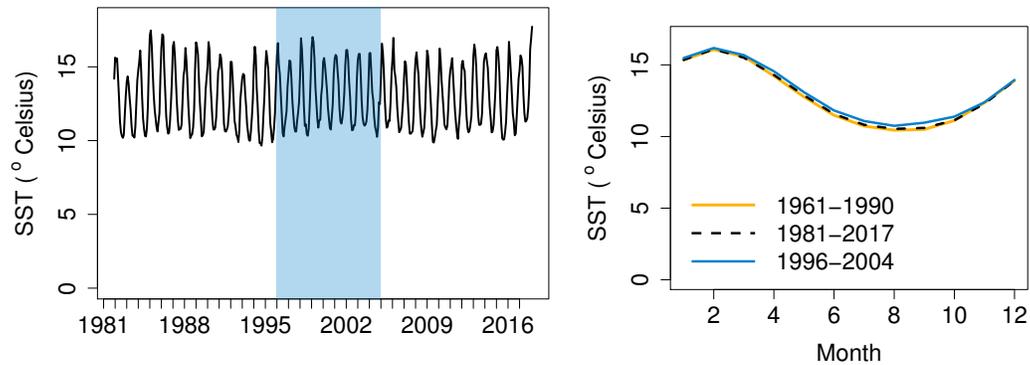
Figure 3: Sea surface temperature (SST) (^{o} Celsius) for 1981–2017 with ROMS years 1996–2004 shaded blue (left) and mean SST by month (right) from 1961–1990 (orange solid line), 1981–2017 (black dashed line), and 1996–2004 (blue solid line).

2.4   Nutrients

Atlantis models use nitrogen, an important and often limiting nutrient in marine systems Moore et al. (2013), to track the transfer of energy throughout the system. The nitrogen cycle can be seen in Figure 4. When biomass pools are tracked in the model, they are done so in mg N m^{-3}. When a fish (for example) eats another fish, it is nitrogen that is transferred up the food chain, with some nitrogen going to detritus and carrion, thus providing nitrogen to micro-organisms and filter feeders to fuel the cycle over again.
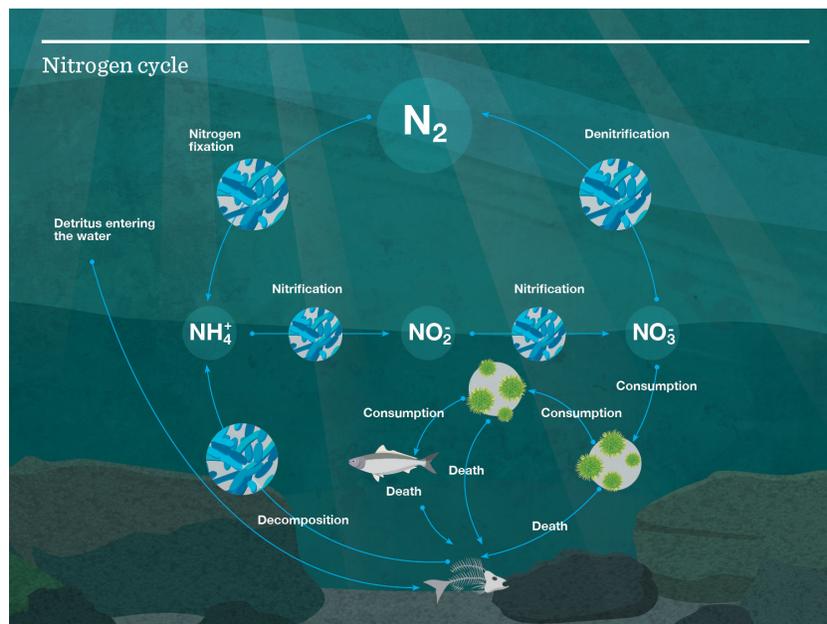
Figure 4: Nutrient cycle.

2.4.1 Nutrient data

Oxygen (O_2), nitrates (NO_3), ammonium (NH_4^+) and silica (SiO_2) were simulated in the model, and required spatially defined initial conditions (values for each cell in the model domain). Table 1 has a summary of the data sources for these nutrients. We used values from the World Ocean Atlas (WOA) for initial conditions for nitrate values down to 500 m, oxygen down to the full model depth of 1300 m, and silica down to 1300 m. The WOA contains objectively analysed climatological fields of *in situ* oxygen, temperature, salinity, and some nutrients (Locarnini et al., 2013; Zweng et al., 2013; Garcia et al., 2013a,b). NO_3 $\mu mol/m^3$ were converted to mg N/m^3 by multiplying by 14 as the molecular mass of nitrogen is 14 g/mol.

World Ocean Circulation Experiment (WOCE) (Deutsches Ozeanographisches Datenzentrum, 2006) data were used for nitrates at depths greater than 500 m, which were not covered by WOA. WOCE data were also used to compare values for oxygen, to inform initial conditions for silica, and to compare with salinity, temperature and chlorophyll *a*.

Ammonium values were available from NIWA oceanographic surveys, but only down to 50 m. This was not too concerning as ammonium is fairly small in terms of the nitrogen budget.

Table 1: Sources of data for Oxygen, Nitrates, Ammonium and Silica.

Variable	Source	Depth	Latitude	Longitude
Oxygen	WOA	1300 m	42–47 S	172 E –170 W
Oxygen	WOCE	1300 m	42.5 S	180 E
Nitrate	WOA	500 m	42–47 S	172 E –170 W
Nitrate	WOCE	1300 m	42.5 S	180 E
Silica	WOCE	1300 m	42.5 S	180 E
Ammonium	NIWA survey	0–50 m	43–46 S	172 E –180 E

2.5 Species groups

CRAM uses 53 functional groups to model the biological processes. Of these 53 groups, 15 vertebrates, and one invertebrate comprised single species; all other groups comprised two or more species. The main component species of the groups are shown in Tables 2 –5. All vertebrate groups and five invertebrate groups were modelled with age-structure using up to 10 age-classes and varying number of years per age-class, depending on the longevity of the primary species in the group. Within each age-class, the model simulated numbers of individuals and the average weight (mg N) of individuals within each age class. Weights were split into structural (S_N) and reserve (R_N) components following the definition in Broekhuizen et al. (1994) where reserve weight is the part that can be used during periods of starvation, which includes flesh, fat, reproductive components and other soft tissue. Primary producers and remaining invertebrate groups were modelled as biomass pools (mg N m^{-3}) with no age-structure.

Table 2: List of functional vertebrate groups for CRAM. Name is the species group name which is the same as the main speces name for single-species groups but without punctuation. Lifespan is the assumed maximum number of years an individual in that group may live. Ben, benthic; Dem, demersal; invert, invertivore; pisc, piscivore.

Name	Main species	Lifespan (years)
Baleen whales	Southern right whales (*Eubalaena australis*)	80
Basketwork eel	Basketwork eels (*Diastobranchus capensis*)	30
Baxters dogfish	Baxter's dogfish (*Etmopterus baxteri*)	50
Ben fish deep	Four-rayed rattail (*Coryphaenoides subserrulatus*)	20
Ben fish shal	Oblique banded rattail (*Coelorinchus aspercephalus*)	10
Black oreo	Black oreo (*Allocyttus niger*)	120
Bollons rattail	Bollons' rattail (*Caelorinchus bollonsi*)	20
Cetacean other	Primarily sperm & pilot whales & dolphins	30
Dem fish pisc	Giant stargazer (*Kathetostoma giganteum*)	20
Elasmobranch invert	Primarily skates & dogfish	20
Elasmobranch pisc	Primarily semi-pelagic sharks	50
Epiben fish deep	Spiky oreo (*Neocyttus rhomboidalis*)	100
Epiben fish shal	Common roughy (*Hoplostethus atlanticus*)	10
Ghost shark	Dark ghost shark (*Hydrolagus novaezealandiae*)	20
Hake	Hake (*Merlucciidae*)	30
Hoki	Hoki (*Macruronus novaezelandiae*	20
Javelinfish	Javelinfish (*Coelorinchus australis*)	10
Ling	Ling (*Molva molva*)	30
Lookdown dory	Lookdown dory (*Cyttus traversi*)	30
Mackerels	Slender jack mackerel (*Trachurus murphyi*)	30
Orange roughy	Orange roughy (*Hoplostethus atlanticus*)	120
Pelagic fish lge	Southern bluefin tuna (*Thunnus thynnus*)	20
Pelagic fish med	Barracouta (*Thyrsites atun*)	10
Pelagic fish sml	Myctophids (*Myctophidae*)	4
Pinniped	NZ fur seal (*Arctocephalus forsteri*)	20
Reef fish	Blue cod (*Parapercis colias*)	20
Seabird	Seabirds & shorebirds	20
Seaperch	Seaperch (*Helicolenus* spp.)	50
Shovelnosed dogfish	Shovelnosed dogfish (*Deania calcea*)	40
Smooth oreo	Smooth oreo (*Pseudocyttus maculatus*)	100
Spiny dogfish	Spiny dogfish (*Squalus acanthias*)	30
Warehou	Silver, white & blue warehou	20

Table 3: List of functional invertebrate groups for CRAM. Name is the species group name which is the same as the species name for single-species groups. Description includes main species. Lifespan is the maximum number of years an individual in that group may live. Those groups with no value for lifespan are modelled as biomass pools and hence do not have a lifespan defined as this is only relavent when modelling numbers. Zoo, zooplankton; Invert comm, commercial invertebrates; herb, herbivore; scav, scavenger.

Name	Description	Lifespan (years)
Arrow squid	Arrow squid	2
Benthic Carniv	Benthic carnivores	
Carniv Zoo	Planktonic animals (size 2–20 cm)	
Cephalopod other	Squid & octopus	2
Deposit Feeder	Detritivores and benthic grazers	
DinoFlag	Dinoflagellates	
Filter Other	Non-commercial benthic filter feeders	
Gelat Zoo	Salps, ctenophores, jellyfish	
Invert comm herb	Paua & kina	10
Invert comm scav	Primarily scampi & crabs	14
Meiobenth	Benthic organisms (size 0.1–1 mm)	
MesoZoo	Planktonic animals (size 0.2–20 mm)	
MicroZoo	Heterotrophic plankton (size 20–200 μm)	
Rock lobster	Rock lobster	12

Table 4: List of functional phytoplankton and algae groups for CRAM. Name is the species group name which is the same as the main speces name for single-species groups. Description includes main species.

Name	Description
Diatoms	Diatoms (large phytoplankton)
Macroalgae	Macroalgae
Microphytobenthos	Unicellular benthic algae
Pico-phytoplankton	Small phytoplankton

Table 5: List of functional bacteria and detritus groups for CRAM. Name is the species group name which is the same as the main speces name for single-species groups. Description includes main species.

Name	Description
Carrion	Dead and decaying flesh
Labile detritus	Organic matter that decomposes at a fast rate
Pelagic bacteria	Pelagic bacteria
Refractory detritus	Organic matter that decomposes at a slow rate
Sediment bacteria	Sediment bacteria

₂₁₉ **2.5.1 Initial conditions and biological parameters for species groups**

₂₂₀ Initial biomasses for each species group were estimated using a single species stochastic
₂₂₁ stock assessment model, CASAL (Bull et al., 2012). Biomass estimates were derived by
₂₂₂ using known biological parameters and a catch history to project back from an absolute
₂₂₃ abundance estimate in 2003. The values of absolute abundance for each group were
₂₂₄ obtained from a mean value of trawl survey relative abundance indices (from surveys
₂₂₅ conducted annually from 1992 to 2014 (see O'Driscoll et al. (2011)), and with a trawl
₂₂₆ catchability quotient derived by expert opinion applied to each mean. Where there
₂₂₇ was no available catch history (e.g. seabirds), or no useful estimates of relative abun-
₂₂₈ dance from the trawl surveys (e.g. rock lobster), initial biomasses were estimated using
₂₂₉ expert opinion. For age-structured groups, initial biomass estimates were assigned to
₂₃₀ age-classes using estimates of instantaneous natural mortality (M). Average weights
₂₃₁ at age were calculated using Von Bertalanffy growth and length-weight conversion pa-
₂₃₂ rameters. Values used for these parameters are in Table 6. Weights at age were split
₂₃₃ into reserve and structural components using ratio $R_N : S_N = 2.5 : 1$. This allows for
₂₃₄ an individual's body mass to decrease by approximately 70% before starving, which is
₂₃₅ within the 60–80% range suggested by Broekhuizen et al. (1994).

₂₃₆ All age-structured groups were modelled with Beverton-Holt recruitment, the steep-
₂₃₇ ness (h) values for which are in Table 6. These values are not ever well known, and
₂₃₈ scenarios explored using this model should consider sensitivities for these.

Table 6: Biological parameters assumed for age-structured species groups. VB, von Bertalanffy; M, instantaneous natural mortality rate; h, steepness value for the Beverton-Holt stock recruitment relationship. Length-weight parameters are: $W = aL^b$ (weight W in g, length L in cm). Where Reference is 'Trawl db' some data have been derived from the NIWA trawl survey database (see Mackay (2000)). Species group matches 'Name' in Tables 2 and 3 and are without punctuation.

Species group	VB Growth			Length-weight		M	h	Reference
	Linf (cm)	K	T_0	a	b			
Arrow squid	35	2.4	0	2.90E-02	3	4.6	0.8	Ministry for Primary Industries (2016)
Baleen whales						0.01	0.5	
Basketwork eel	47.3	0.283	-1.294	2.35E-03	3.25	0.19	0.8	Trawl db
Baxters dogfish	64.4	0.06	-2.97	5.95E-03	3.068	0.08	0.3	Irvine et al. (2006a)
Ben fish deep	36	0.3	-1.1	7.28E-03	2.632	0.2	0.8	Stevens et al. (2010), Trawl db
Ben fish shal	38	0.3	-1.1	2.35E-03	3.25	0.2	0.8	Stevens et al. (2010), Trawl db
Black oreo	37	0.1	-2	7.80E-03	3.27	0.044	0.75	Ministry for Primary Industries (2016)

Bollons rattail	47.3	0.283	-1.294	2.35E-03	3.25	0.19	0.8	Stevens et al. (2010)
Cephalopod other	45	2.4	0	2.90E-02	3	4.6	0.8	
Cetacean other						0.033	0.5	
Dem fish pisc	69.8	0.17	-0.53	1.50E-02	3.01	0.19	0.8	Sutton (1999), Ministry for Primary Industries (2016)
Elasmobranch invert	150.5	0.095	-1.06	2.68E-02	2.933	0.135	0.3	Ministry for Primary Industries (2016)
Elasmobranch pisc	84.7	0.1065	-4.56	1.50E-03	3.334	0.09	0.3	Irvine et al. (2006b)
Epiben fish deep	35.3	0.07	-0.5	2.83E-02	2.9322	0.05	0.75	Stewart and Smith (1994), Trawl db
Epiben fish shal	24	0.18	-0.3	2.65E-02	2.9126	0.2	0.8	Trawl db
Ghost shark	97	0.09	-1.17	2.02E-03	3.274	0.35	0.3	Ministry for Primary Industries (2016)
Hake	95.9	0.279	0.05	2.00E-03	3.288	0.19	0.8	Horn (2013)
Hoki	100.8	0.164	-2.16	4.79E-03	2.89	0.275	0.75	McKenzie (2016), Ministry for Primary Industries (2016)
Invert comm herb	155	0.15	0	3.00E-05	3.303	0.15	0.8	Breen et al. (2003)
Invert comm scav	50	0.25	0	3.73E-04	3.145	0.2	0.8	Tuck (2016)
Javelinfish	51.2	0.216	-1.618	1.38E-03	3.13	0.35	0.8	Stevens et al. (2010)
Ling	135.2	0.105	-0.72	1.07E-03	3.336	0.14	0.84	McGregor (2015)
Lookdown dory	50	0.075	-1	2.35E-02	2.97	0.15	0.8	Stewart and Smith (1994), Ministry for Primary Industries (2016)
Mackerels	74.25	0.111	-0.811	2.38E-02	2.7671	0.3	0.7	Cubillos et al. (1998), Kochkin (1994)
Orange roughy	37.2	0.065	-0.5	9.21E-02	2.71	0.045	0.75	Ministry for Primary Industries (2016)
Pelagic fish lge	182	0.205	0	1.88E-02	3.0078	0.2	0.8	Fournier et al. (1990), Ministry for Primary Industries (2016)
Pelagic fish med	85.2	0.298	-0.45	7.40E-03	2.94	0.3	0.7	Horn (2002), Ministry for Primary Industries (2016)
Pelagic fish sml	7	0.8	0	1.30E-02	2.81	1.58	0.7	Young et al. (1988), Trawl db
Pinniped						0.07	0.5	
Reef fish	51.7	0.087	-1.7	1.91E-02	2.9818	0.14	0.8	Ministry for Primary Industries (2016)
Rock lobster	85	0.15	0	4.16E-03	2.935	0.12	0.8	Ministry for Primary Industries (2017)
Seabird						0.11	0.5	
Seaperch	45.6	0.08	-0.8	7.77E-03	3.22	0.07	0.8	Paul and Horn (2009), Ministry for Primary Industries (2016)
Shovelnosed dogfish	106.4	0.106	-0.384	1.58E-03	3.192	0.13	0.3	Clarke et al. (2002), Trawl db
Smooth oreo	46	0.07	-1.5	3.05E-02	2.885	0.063	0.75	Ministry for Primary Industries (2016)

Spiny dogfish	104.8	0.093	-3.17	1.30E-03	3.2639	0.2	0.3	Hanchet (1986), Beentjes and Stevenson (2009)
Warehou	53.1	0.37	-0.88	8.28E-03	3.214	0.25	0.8	Horn and Sutton (1996), Ministry for Primary Industries (2016)

2.6 Predation

Simulated predation was a four step process that occurred within each cell and at each timestep. From the predator's perspective the steps modelled can be summarised as: 1.) Am I allowed to eat it? 2.) Is it in the same place at the same time as me? 3.) Does it fit in my mouth? 4.) How much can I eat? Further details are in the Atlantis User's Guide (Audzijonyte et al., 2017).

Diets of each species group were summarised in categories Algae, Bacteria, Bird, Cetacea, Coelenterate, Crustacean, Detritus, Echinoderm, Elasmobranch, Microzooplankton, Mollusc, Phytoplankton, Polychaete, Teleost, and Tunicate similar to that done in the diet study of Stevens et al. (2011a) (Figure 5). While this summary misses the temporal, spatial, age and size components of the predator-prey interactions, it is useful to check overall diets. For example, warehou and smooth oreos eat mostly salps (tunicates) as expected; Baxter's dogfish eat mostly fish, crustaceans, molluscs and tunicates as expected; and invertebrate herbivores (kina and paua) eat mostly algae, although they should also eat some phytoplankton, which they do but it is lost with the detail.
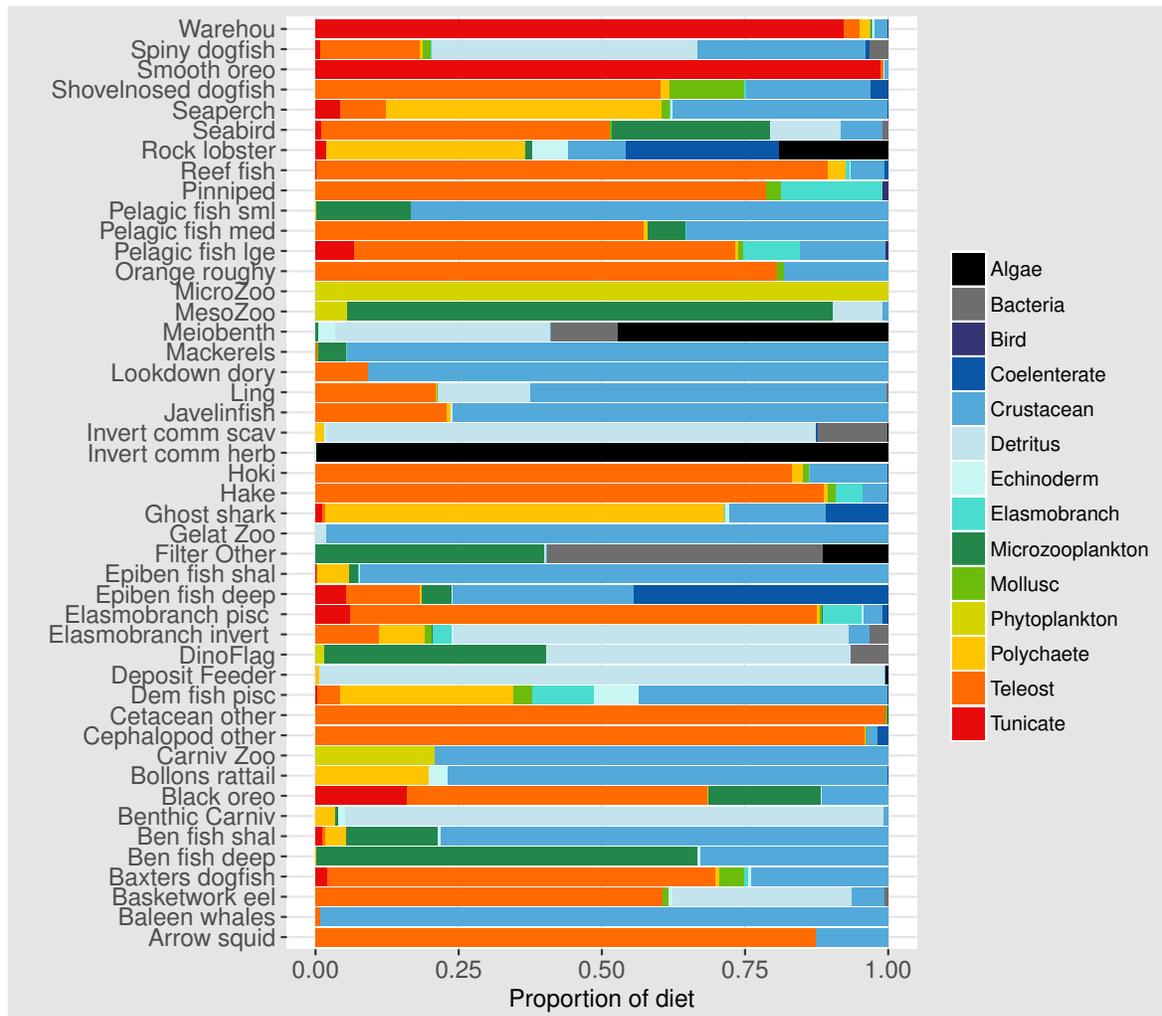
Figure 5: Summary of the proportion of prey groups in the diets of species functional groups (Tables 2 and 3) over model years 1900–2016 from the fished model where the proportion is by mg N consumed.

3 Calibration

Calibration of the model included ensuring stable biomass trajectories when applying no fishing; realistic realised diets; realistic growth and mortality (size-at-age and proportions-at-age); and biomass decreasing with increasing trophic level following the PREBAL (Link, 2010) guidelines.

Biomass trajectories should reach a quasi-equilibrium when modelled with constant oceanography and no fishing (Kaplan and Marshall, 2016). While oceanography is not constant in our non-fishing model as it changes by year (Section 2.3), most of the age-structured groups should still be fairly stable. This was generally the case; all biomass trajectories remained within CVs of 20% over the simulated 1900–2016 model period, except for invertebrate scavengers - commercial and seaperch. Invertebrate scavengers - commercial are primarily scampi, and they are likely responding to changes resulting from the oceanographic variables. Biomass trajectories for all age-structured groups from the un-fished model are in Appendix 10. Seaperch biomass was trending downward initially, but they seem to have reached an equilibrium by about 1950, with expected growth and mortality rates.

Simulated growth rates of age-structured species groups were assessed by comparing the simulated size-at-age with those expected based on growth curve estimates from the literature (Table 6). The overlaid simulated and 'observed' figures were generally very similar (Appendix 10. For each species group, we estimated CVs required to satisfy the hypothesis that the modelled size-at-age were not significantly different from the 'observed' with probability of 0.95. The required CVs were all less than 30% except for epibenthic fish (deep and shallow), invertebrate herbivore (commercial), invertebrate scavenger (commercial), ling, rock lobster and small pelagic fishes. For all these groups, the first age class, and sometimes the first few, were larger in size than expected. Deep epibenthic fish were larger than expected at all age classes, but for all other groups the characteristic of larger than expected size at age had been remedied by the time they were adults.

Natural mortality in the model consists of mortality intrinsic within the model from predation, starvation, and light, oxygen or nutrient deprivation, and additional forced mortality. The latter was applied for modelled species groups that would not otherwise suffer sufficient natural mortality within the model, such as those that have little known predation. Age-structured simulated natural mortality rates from the stable base model were compared to estimates of M from the literature where available (Table 6) by comparing the proportions-at-age. The overlaid simulated and 'observed' figures were generally very similar (Appendix 10, although rock lobster and invertebrate herbivore

commercial (primarily paua and kina) had slightly more mortality in the model, and demersal piscivores, epibenthic fish small, pelagic fish medium, and warehou had slightly less mortality.

We summarised biomass by trophic level for the base model as at 2016 on a log-scale, and biomass reduced with increasing trophic level with a fitted slope of -1.6 (Figure 6). This was close to the recommended range of PREBAL of (-1.5, -0.5). The biomass at trophic level 4 was slightly higher in this summary than in the model, as the summary was based on adult trophic level and many of the fish species are trophic level 4 as adults, but lower as juveniles. This resulted in the biomass of the juveniles for these fish adding to the level 4 biomass whereas in the model they were perhaps functioning as a level 3.
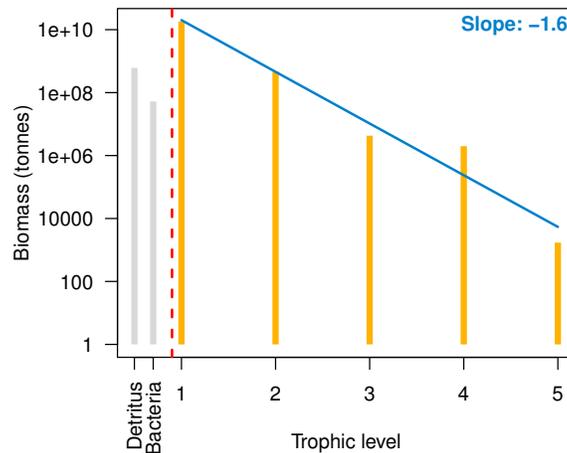
Figure 6: Biomass by trophic level as at 2016 in the Chatham Rise Atlantis model simulation.

4   Sensitivity analyses

4.1   Oceanography

Oceanographic variables from a ROMS (Regional Oceanographic Modelling System) model for years 1996–2004 were used to define temperature, salinity and flux (water exchange). As our model spanned more than these years, we needed to recycle the ROMS variables in some way. The purpose of this section has two parts: 1.) establishing confidence intervals for our model simulations with respect to oceanographic variability; 2.) assessing the effect of repeating oceanographic variables from any one year, and whether these take the model outside of the established confidence intervals.

To retain realistic within-year dynamics, the ROMS variables from each year were

kept together as a unit, and the years covered by the ROMS model were considered
the samples. We ran two sets of simulations: the first sampled ROMS years at random
with replacement for each model year simulated (bootstrapped the ROMS years) and
repeated this for 50 model runs; the second repeated one ROMS year for all model
years simulated and did a separate model run for each of the nine ROMS years. In both
cases, the 2003 ROMS was repeated for a 35-year burn-in period, followed by a 50 year
simulation. The 2003 ROMS was chosen for the burn-in period as this year had the
closest sea temperatures to the means from all ROMS years (Figure 7). Bootstrapping
the ROMS years was used to establish confidence intervals with respect to between-year
oceanographic variability. Repeating each ROMS year in turn was testing the effect of
multiple years being different to the other years in some consistent way, such as cooler
or warmer.

The established confidence intervals were fairly narrow for most species groups, with
CVs < 10%. Of the exceptions, diatoms had the highest CV of 79%, followed by carniv-
orous zooplankton (46%), labile detritus (23%), sediment bacteria (13%), invertebrate
scavengers (commercial) (12%), refractory detritus (12%), meso-zooplankton (11%) and
pelagic bacteria (11%).

The years with cooler sea temperatures (1996, 1997, and 2004) when repeated for
50 years produced the most species groups that went above the established confidence
intervals, with the on average warmer years (1999, 2000, and 2001) having the most
species groups that went below (Figure 8). Years 2003 and 1998 were closest to the
average sea temperatures and had the least number of species groups outside the boot-
strap confidence intervals. The Base Model that repeated the ROMS from all nine years
in order for the entire model simulation had roughly average numbers of species groups
that went above and below the bootstrap bounds, with 16 species groups exceeding the
bounds at some point and six species groups going below them (Figure 8).

4.2 Connectivity and influence

Understanding which species groups are most influential or responsive in the model is
another test for realistic dynamics, and may be useful to help understand results of
scenarios explored using this model in the future. To do this, we need to perturb each
species group in turn, then assess the responses of the other groups in the system. For
each age-structured species group, we ran two simulations, one with a small additional
mortality and one larger; M(per year) + (0.1, 0.005). We assessed responses of the
groups with respect to the Base Model at the completion of 50-year simulations. We
analysed the 'keystoneness' and responsiveness of the groups based on biomasses relative
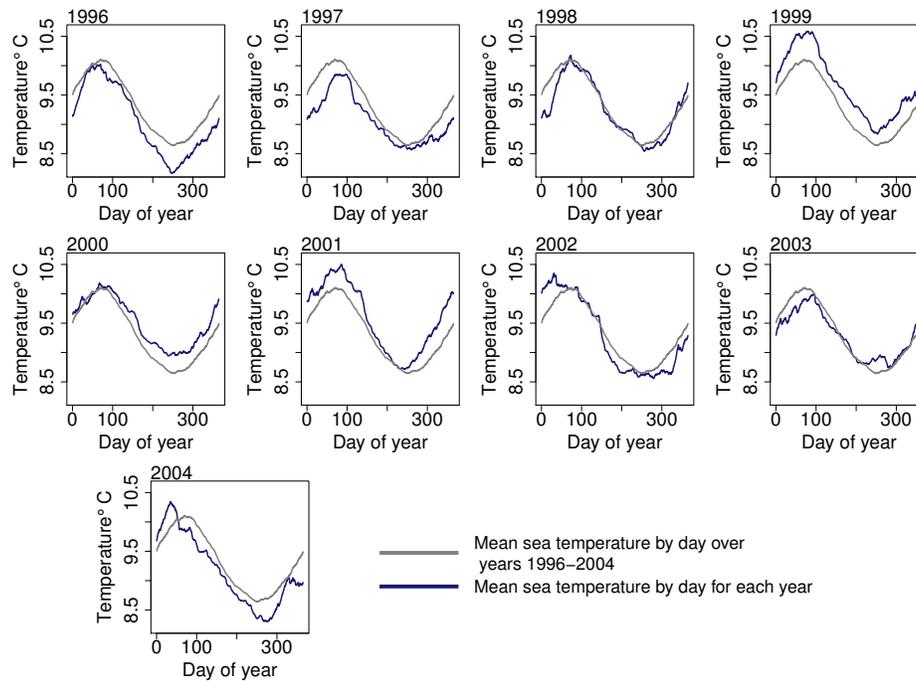
Figure 7: Sea temperature (^{o}C) from ROMS model outputs by day for each year 1996–2004 (dark blue line) and median sea temperature over all ROMS model years 1996–2004 (grey line).
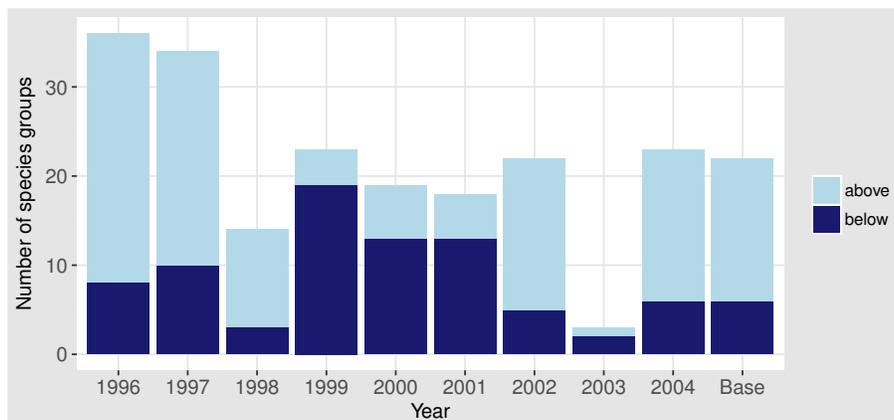
Figure 8: Number of species groups for each simulation with one ROMS year repeated that went above (light blue) or below (midnight blue) the limits of bootstrapped ROMS simulations and for the Base Model where the years were repeated in order for the entire model simulation.

347   to the Base Model.

348   We calculated keystoneness using an adaption of the method in Libralato et al.

349   (2006). It is a measure of the effect the group has on the rest of the system (change in

350   biomass of the other species groups), that takes into account its proportion of the total

351   biomass. For example, if two species groups have the same effect, but one has a large

biomass and one a small biomass, the smaller would have a larger keystoneness. We used simulation outputs to estimate the total effect (ϵ) of each species group (Equation 1) which used the change in biomass of each group relative to the Base Model (Equation 2). As the additional mortality caused larger and smaller changes to the focus groups, we scaled the focus groups' biomass proportions by their change in biomass (Equation 4). Hence, the resulting keystoneness allowed for the effect changing each group had on the other groups, the focus groups biomass as a proportion of the total, and the proportional change in biomass of the focus group relative to the base model.

$$\epsilon_f = \sqrt{\sum_{g \neq f}^{G} m_{f,g}^2} \tag{1}$$

$$m_{f,g} = \frac{B_{f,g} - B_{b,g}}{B_{b,g}} \tag{2}$$

$$\kappa_f = log(\epsilon_f(1 - p_f)) \tag{3}$$

$$p_f = \frac{B_{b,f}}{\sum_{g=1}^{G} B_{b,g}} \times |m_{f,f}| \tag{4}$$

ϵ_f, effect group f has on the other groups

$m_{f,g}$, proportional change in biomass of group g when group f was reduced, relative to the Base Model

B_{b_g}, B_{b_f}, biomass in base model of group g, f

B_{f_g}, biomass of group g in model with group f mortality increased

κ_f, keystoneness of group f

p_f, biomass proportion of group f

There were four species groups that stood out as having more effect than the other groups: orange roughy, hoki, pelagic fish small (primarily myctophids) and spiny dogfish. These remain the top four for keystoneness, but the order changes due to the proportional biomasses (Figure 9).

We calculated responsiveness in a similar way to keystoneness, but from the perspective of the response group (Equation 5).

$$R_g = \sqrt{\sum_{f \neq g}^{G} \left(m_{f,g}^2 \times p_f \right)} \tag{5}$$

1 Hoki
2 Orange roughy
3 Spiny dogfish
4 Pelagic fish sml
5 Ben fish shal
6 Seabird
7 Pelagic fish med
8 Epiben fish shal
9 Cetacean other
10 Hake
11 Ling
12 Shovelnosed dogfish
13 Warehou

14 Cephalopod other
15 Mackerels
16 Bollons rattail
17 Elasmobranch pisc
18 Basketwork eel
19 Arrow squid
20 Lookdown dory
21 Invert comm herb
22 Epiben fish deep
23 Smooth oreo
24 Reef fish
25 Baleen whales
26 Black oreo

27 Javelinfish
28 Baxters dogfish
29 Pelagic fish lge
30 Ghost shark
31 Dem fish pisc
32 Elasmobranch invert
33 Invert comm scav
34 Seaperch
35 Ben fish deep
36 Pinniped
37 Rock lobster

Figure 9: Keystoneness (y-axis) and relative overall effect (x-axis) for all age-structured species groups, with numbers giving keystoneness ranking (1 is the most influential using Equation 3). Colours indicate biomass proportion scaled by proportional change in biomass (Equation 4).

373   R_g responsiveness of group g to increased mortality in all other groups

374   The most responsive group was pelagic fish small (primarily myctophids), followed

375 by smooth oreo, invertebrate scavengers commercial (primary scampi), and pelagic fish

376 medium (primarily barracouta) (Figure 10). The pelagic fish small species group ranked

377 high for keystoneness and responsiveness, and so may be most important and influential

378 in scenarios explored with this model.

5   Fishing

380   Most of the fisheries on the Chatham Rise became established after the mid-1970's,

381 with the exception of the blue cod (*Parapercis colias*) (reef fish species group) fishery

382 which extends back to the early 1900's. Individual catch histories are in Appendix 10

383 and Figure 11 presents a summary of catches from the Chatham Rise with the top six

384 species by total catch shown in colour and the others combined into an 'other' category.
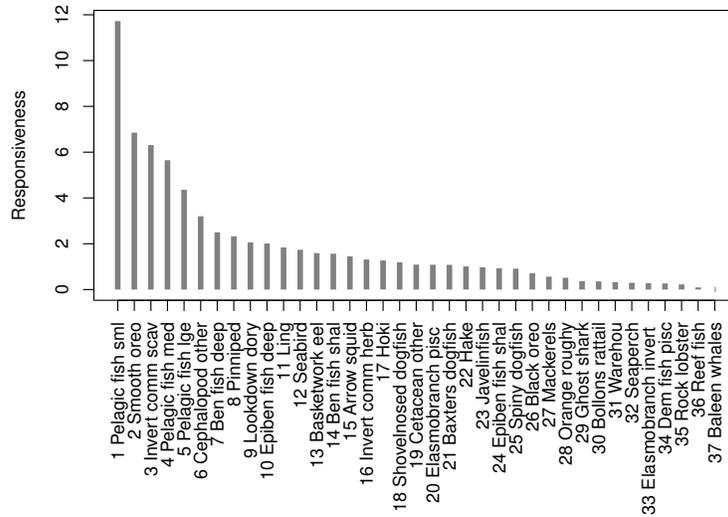
Figure 10: Responsiveness of age-structured species groups after 50 years of perturbation, as calculated in Equation 5.

385 Hoki had the largest total catch, followed by orange roughy, smooth oreo, ling, black
386 oreo, then barracouta. Orange roughy comprised the largest individual fishery in the
387 late-1970's–early-1990's after which it declined markedly; from the 1990's hoki was the
388 dominant fishery.

389 The fisheries were modelled with six fleets, defined in Table 7. The demersal line
390 fishery was dominant until mid–late 1960's when the demersal trawl fishery became
391 dominant, catching approximately 70 000 tonnes per year (Figure 12).
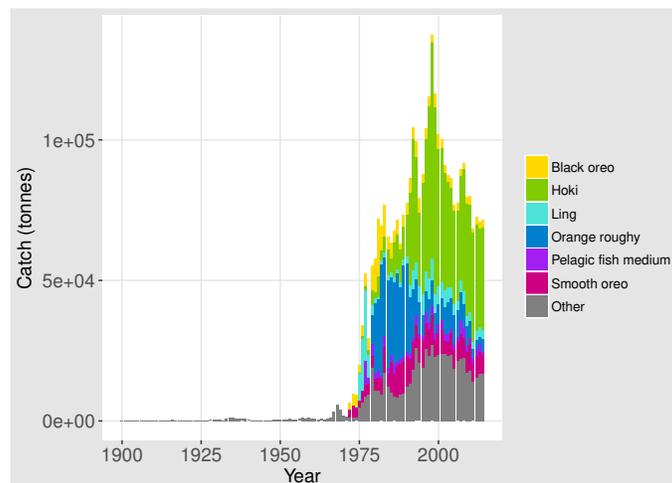
Figure 11: Tonnes caught from Chatham Rise 1900–2014 for all species with top six species groups by total catch coloured seperately.

Table 7: Fishing fleets defined for Chatham Rise Atlantis model. Number of species groups is the number of species groups that have been caught by each fishing fleet; total catch is the total tonnes caught by each fishing fleet from 1900–2014.

Code	Description	Number of species groups	Total catch (t)
trawlDEM	trawl on demersals and mesopelagics	33	2 850 000
lineDEM	line on demersals and mesopelagics	16	1 200 000
snetDEM	setnet on demersals and sharks	6	45 700
potIVS	potting on lobster and blue cod	4	241 000
jigCEP	jig on squid	1	1 700
diveIVH	diving on paua and kina	2	158 000
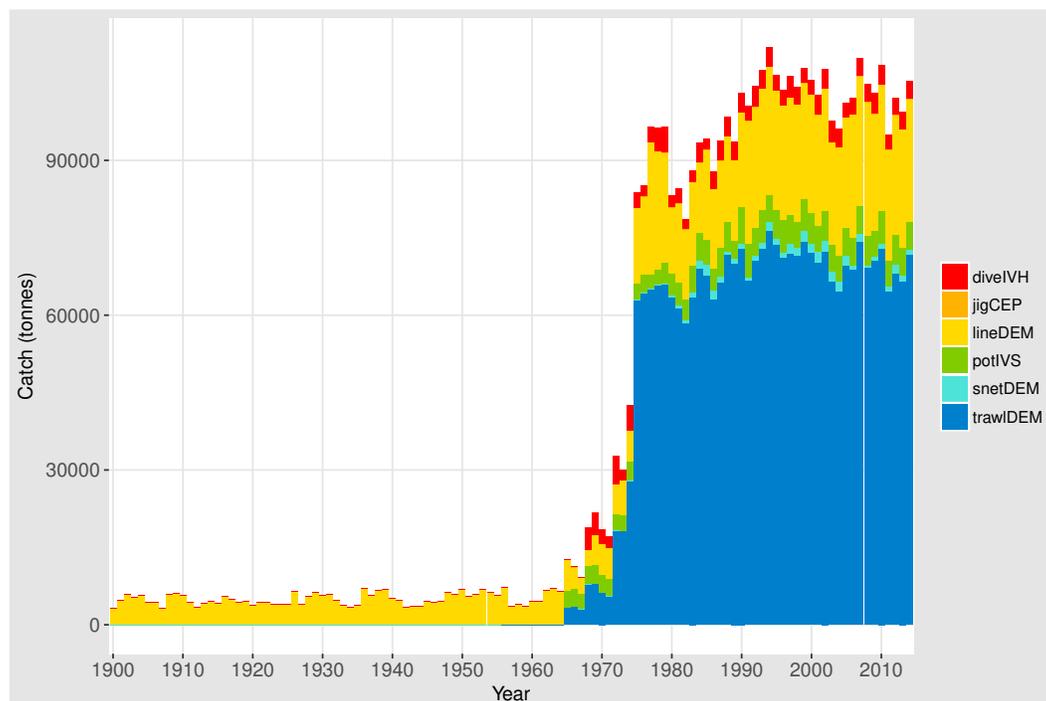
Figure 12: Total tonnes caught by fishing fleet from the Chatham Rise 1900–2014. Descriptions for the fleet codes are in Table 7.

5.1 Comparison with fisheries CPUE and Stock Assessment indices

CRAM model estimates of biomass trends for key fisheries species were compared to CPUE and/or stock assessment indices where these were available. The Atlantis model captures the main biomass trends of hoki in response to historical fishing (Figure 13). Hoki are the largest fishery on the Chatham Rise, and has one of the most complex stock assessment models in New Zealand, with multiple areas, intricately defined migration,

and annual recruitment deviates (McKenzie, 2016). The Atlantis model results are very similar to the stock assessment model results for hake and ling, and although the stock assessment models for these are not as complicated as hoki, they still have between-year recruitment deviates (Horn, 2013; McGregor, 2015) that are not present in the Atlantis model. The species group 'Invertebrate scavengers - commercial' is primarily scampi, and the matched increase in the late 1990s–early 2000s is particularly pleasing as catches were fairly constant over this time (Tuck, 2016), so the increase is coming from dynamics within the model. Orange roughy is a close match to the stock assessment, even though this stock assessment model also has between-year recruitment deviates (Dunn and Doonan, in press) that are not in the Atlantis model.

6   Skill assessment

Quantitative skill assessments have become popular as part of assessing the performance of Atlantis models (Sturludottir et al., 2018; Ortega-Cisneros et al., 2017; Olsen et al., 2016). A quantitative skill assessment was carried out, comparing model biomass estimates with those from trawl surveys where available (O'Driscoll et al., 2011; Stevens et al., 2017). The trawl surveys target hoki, hake and ling, and as such the biomass indices are most reliable for these three species. The metrics selected were three of those suggested in Olsen et al. (2016) and Stow et al. (2009): Modelling efficiency (MEF) used to asses model predictions relative to the mean of the observations (Equation 6); Reliability index (RI) gives the average factor the model predictions differ from observations (Equation 7); Pearson's correlation (r) assesses whether model predictions are correlated with observations (Equation 8). The full set of CRAM biomass trajectories with historic catches and trawl survey indices are in Appendix 10.

$$MEF = \frac{\sum_{i=1}^{n} \left(O_i - \bar{O}\right)^2 - \sum_{i=1}^{n} \left(O_i - P_i\right)^2}{\sum_{i=1}^{n} \left(O_i - \bar{O}\right)^2} \tag{6}$$

$$RI = \exp \sqrt{\frac{1}{n} \sum_{i=1}^{n} \left(\log \frac{O_i}{P_i}\right)^2} \tag{7}$$

$$r = \frac{\sum_{i=1}^{n} \left(O_i - \bar{O}\right)\left(P_i - \bar{P}\right)}{\sqrt{\sum_{i=1}^{n} \left(O_i - \bar{O}\right)^2 \sum_{i=1}^{n} \left(P_i - \bar{P}\right)^2}} \tag{8}$$

Each skill assessment metric was calculated using single point estimates from the trawl survey, and variants on RI and MEF were calculated allowing for the trawl survey
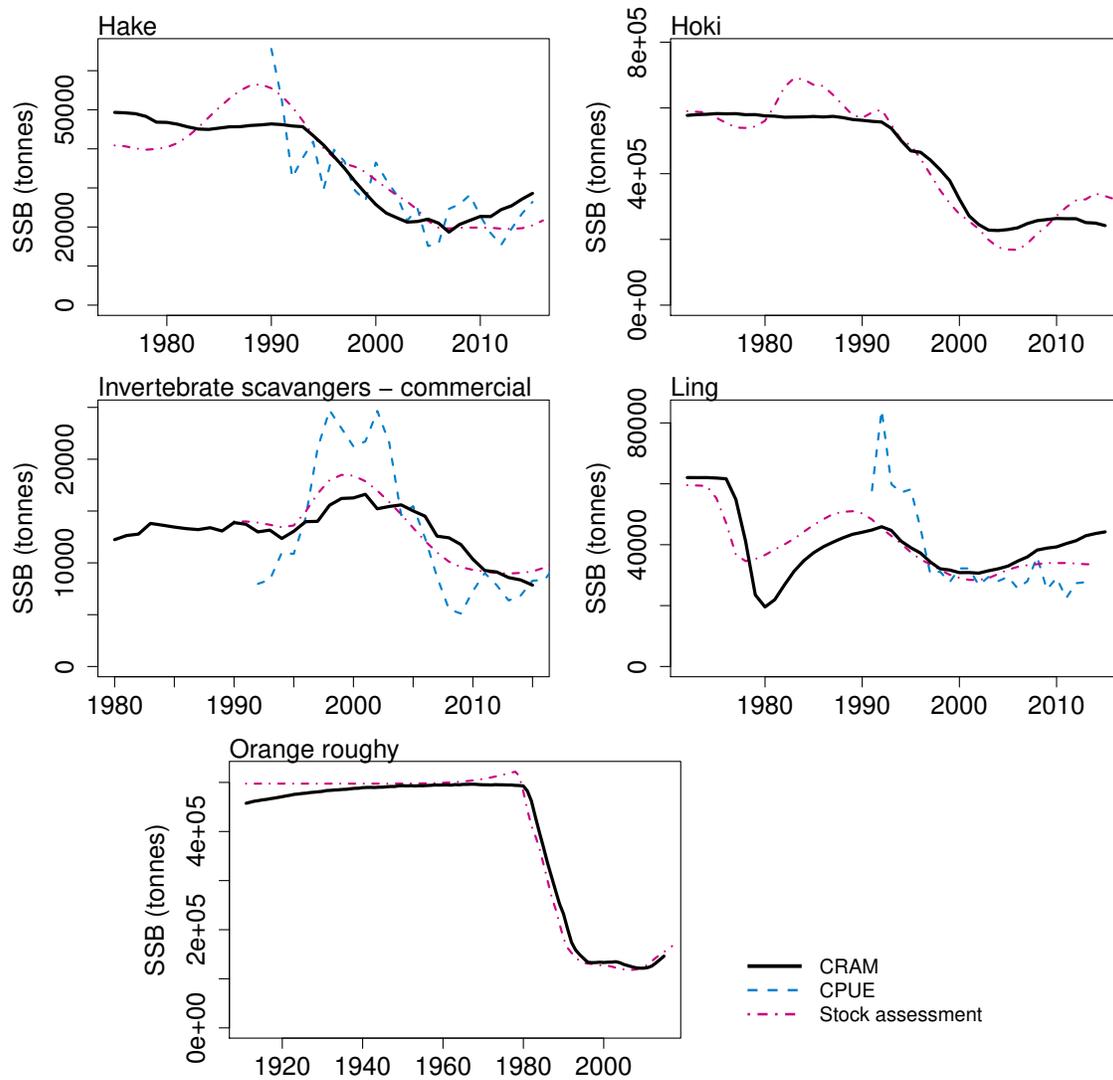
Figure 13: CRAM estimated spawning stock biomass (SSB) (black solid), stock assessment estimated SSB (red dot-dash), and CPUE (blue dash) where available for the hake (top left), hoki (top right), invertebrate scavengers - commercial (primarily scampi) (middle left), ling (middle right), and orange roughy (bottom) . CPUE and stock assessment SSB were rescaled to match the mean of the CRAM estimated SSB.

₄₂₄   estimated 95% confidence intervals. Both variants only penalised the skill metric for

₄₂₅   terms outside of the 95% confidence intervals of the trawl survey.

₄₂₆   An MEF close to one indicates a close match between model predictions and ob-

₄₂₇   servations, with zero indicating the mean of the observations is as close as the model

₄₂₈   predictions, and a negative value indicating the model predictions fit the observations

₄₂₉   worse than the mean of the observations. Ling stands out at approximately -2.5 when

₄₃₀   compared to the trawl survey point estimates, but as all the predicted points for ling sit

within the 95% confidence interval, it receives a score of one when taking the bounds into account (Figure 14). Benthic invertivores (shallow) and lookdown dory are slightly negative with respect to the trawl survey point estimates.

A reliability index (RI) of one indicates the model predictions are on average equal to the observations. All groups were between 1 and 1.5 (Figure 14).

A Pearson's correlation close to one indicates trends in the predictions vary with those in the observations, close to zero indicates there is little relationship between the trends, and negative indicates the predicted trends tend to be opposite from the observed trends. Hake and hoki had good correlation, close to 0.8. The other groups were either close to zero or negative (Figure 14). This is neither surprising nor concerning as the trawl survey estimates for these groups tend to have high variability and high CVs which are not taken into account here.
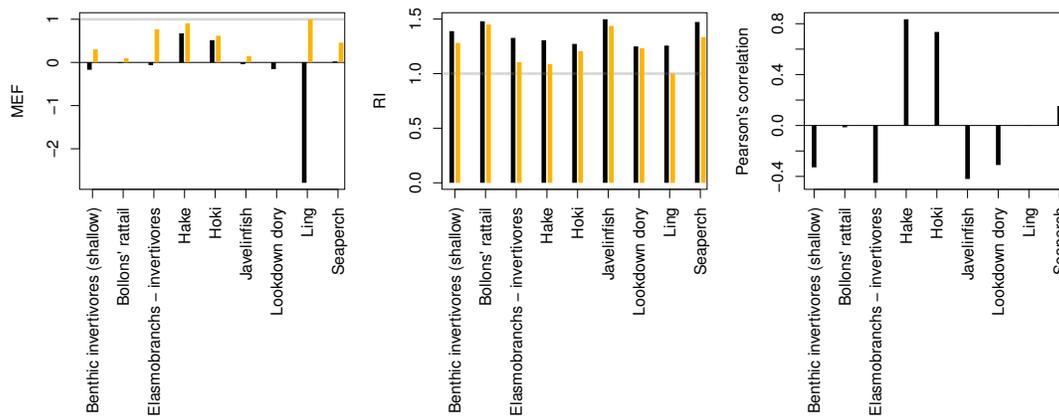
Figure 14: Skill assessment metrics MEF (left), RI (middle) and Pearson's correlation (right) for CRAM species groups that have trawl survey indices for abundance. Metric definitions in Equations 6–8. The black bars are the skill metrics with respect to single point estimates from the trawl survey. The orange bars are the skill metrics with respect to the trawl survey 95% confidence intervals. The grey horizontal lines in the MEF and RI figures mark the value for a perfect fit, which is 1 for both of these.

7   Bringing it together

We qualitatively graded the species groups by how well they performed in the model and how well informed they were by data, information and other research (referred to as 'informance'). We compared these gradings with the keystone and responsiveness from Section 4.2. Figure 15 gives a visual guide for how well the most influential or responsive

species groups did for informance and performance. While poor knowledge may not be concerning if paired with high responsiveness, the triple of highly responsive, a keystone species, and poorly defined may need consideration for future scenarios.

The groups that were highest for keystoneness and highest for informance and performance were hoki, orange roughy, benthic fish shallow (primarily oblique banded rattail), and hake. These all have abundance indices available, biological parameters, diet information, and all perform well with respect to these in the model. Hoki, orange roughy and hake (groups 1, 2, and 10 for keystoneness) have full stock assessments, which the model matches well. These are important groups for fisheries and will likely feature strongly in any fisheries scenarios explored with this model.

Species groups Pelagic fish small (primarily myctophids) and Pelagic fish medium (primarily barracouta) were both high with respect to keystoneness and responsiveness, and while both were fairly well defined, these had some areas of poor model performance and do not have abundance indices to compare. The estimated length at age 1 from CRAM for small pelagic fish is larger than expected, although values from age 2 onwards are acceptable (Appendix 10) so this is probably not influential on the model overall. Medium pelagics have slightly less natural mortality in the model than they should (Appendix 10), and may be less responsive to fishing mortality as a result. As they are 7th with respect to keystoneness and high for responsiveness, they could affect scenario outcomes and are worth considering when analysing results. They make up approximately 1% of the age-structured biomass.

Spiny dogfish were third for keystoneness, and low for responsiveness. They fit well to mortality and growth curves, but we do not have an index of abundance with which to compare the model simulated biomass in response to historical fishing. They make up approximately 5% of the age-structured biomass.

Epibenthic fish shallow (primarily common roughy) were 8th for keystoneness, but low for responsiveness. They compare reasonably well to the trawl survey abundance index, but have less natural mortality in the model than they should. They make up approximately 1% of the age-structured biomass.

Species groups 'Seabird' and 'Cetacean other' are both poorly defined and rank within the top 10 for keystoneness, although lower for responsiveness. They are both composite groups, with Seabird consisting of all sea and shore birds, and Cetacean other consisting primarily of sperm whales, pilot whales and dolphins (Table 2). Scenarios explored in the future may benefit from sensitivities with respect to these two groups to understand their effect on the outcomes, or perhaps some more work to better define them.
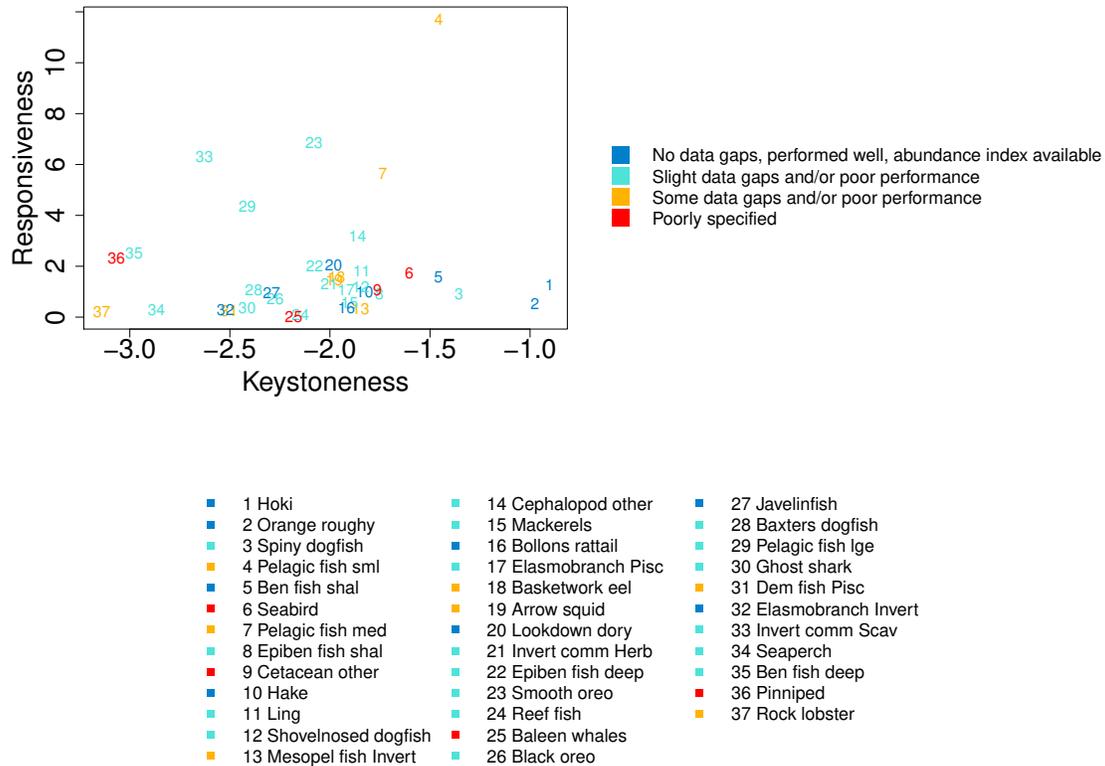
Figure 15: Keystoneness (x-axis) and responsiveness (y-axis) with numbers showing keystoneness ranking and colours how well each species group was informed and/or performed in the model (legend).

8   Discussion

Ecosystem-based fisheries management (EBFM) is most likely to be achievable with the best information and modelling available (Heymans et al., 2010). The Chatham Rise Atlantis model presented here uses the wealth of data and information available for the Chatham Rise and its fisheries, and one of the best ecosystem models for exploring 'what-if' type questions (Plagányi, 2007) and ecosystem-level management strategy evaluation (Fulton et al., 2014). This comprehensive ecosystem model with realistic population dynamics and flow-on effects has the potential to be a valuable tool for understanding potential system-wide responses to fisheries management strategies in one of New Zealand's largest fishing grounds.

Some key aspects of this model performed convincingly well, such as responses of key fisheries species under fishing, realised diets, and the keystone rankings. That the key fisheries species results were very similar to the corresponding stock assessment results

gives confidence that the model can respond to fishing in a way that is realistic, and that the ecosystem effects relative to these species are realistic. The stock assessment models fit data such as proportions at length and biomass indices with the help of between-year recruitment deviates, which are not present in the Chatham Rise Atlantis model. Conversely, the stock assessment models do not have time-varying natural mortality or growth rates, which are present in the Chatham Rise Atlantis model. As such, both modelling approaches achieve similar results but in very different ways. It is possible that the recruitment deviates in the stock assessments are proxy's for the other ecosystem dynamics that the Atlantis model is able to capture (or vice versa). However, the Atlantis model is too complex to fit to data. Hence, the Chatham Rise Atlantis model's ability to achieve the same results as the stock assessment models, that were fitted to data, is the best outcome.

Realistic diets and the influence of species groups on the rest of the ecosystem are key to the model's potential to explore and gain understanding of flow-on and cascading effects. It may be possible, for example, for a species to have realistic growth rates, but it is not very useful in an ecosystem modelling context if they do so by eating the wrong things. While they might respond realistically to direct pressure such as fishing, the flow-on effects would not likely reflect reality. Due to the complex nature of the Atlantis model, the summary of realised diets, together with analysing the keystoneness and responsiveness, are appropriate for determining whether species interactions are generally realistic, at a level of complexity that can be comprehensible. The Chatham Rise Atlantis model has realistic diet summaries for all species groups, and the top keystone species groups were all those we would expect to be most influential within this ecosystem.

While there are of course some knowledge gaps, for the current model we have identified those most likely to influence scenario outcomes through analysing how influential (keystoneness) and influenced (responsiveness) the species groups are on and to each other. The composite groups 'cetacean other' and 'seabirds' were highly influential while poorly specified. Two solutions would be to a.) split these groups into smaller groups that can be better specified; b.) run sensitivities with respect to these groups when exploring scenarios using this model.

The oceanographic variables that require repeating due to only covering years 1996–2004, were found to be influential on the simulated biomasses of the species groups, and the order they were repeated changed the results, with CVs of up to nearly 80%. This suggests scenarios carried out using this model need to consider oceanographic variability in simulated results, using multiple runs with different oceanographic years repeated or

changing the order. This may be true for many ecosystem models, but we are unaware of similar analyses completed elsewhere. Further work understanding which species groups and/or spatial areas of the model are most affected by oceanographic variability might be helpful in understanding potential impacts on scenario results.

While we have confidence in this model for exploring fisheries type scenarios in support of an ecosystem based approach to fisheries management, the model still stands to benefit from further exploration. Key to understanding the implications of any results from such a complex model is to first ask what in the model is producing the results, before asking what it tells us about the system. The analyses presented in this paper such as responsiveness and keystoneness, dynamics and diets, are intended to set the stage for an understanding of how the model is specified and how it behaves, but it is not exhaustive. Any future use of the model can be expected to add to our understanding of the model first, and then possibly our understanding of the ecosystem.

9   Conclusions

The model produces very similar results to fisheries stock assessment models for key fisheries species, and the population dynamics and system interactions are realistic. Confidence intervals based on bootstrapping oceanographic variables were fairly narrow for most species groups, with diatoms, carnivorous zooplankton and labile detritus having the largest CVs. The species groups with the highest keystoneness were orange roughy, hoki, pelagic fish small (primarily myctophids) and spiny dogfish. The model components that have knowledge gaps and are most likely to influence model results were oceanographic variables, and the compilation species groups 'seabird' and 'cetacean other'. We recommend applications of the model include alternatives that vary these components.

10   Acknowledgements

Mark Hadfield for development of the ROMS model for oceanographic variables. Bec Gorton (CSIRO) for converting the ROMS variables into Atlantis model inputs. Ian Tuck for providing a comprehensive internal review of the manuscript. Cliff Law and Graham Rickard (NIWA) for help with ocean physics data and conversions. Matt Pinkerton for trophic level results from stable isotope analyses and visible band radiation at sea surface data. James Bell, Victoria University supervisor.

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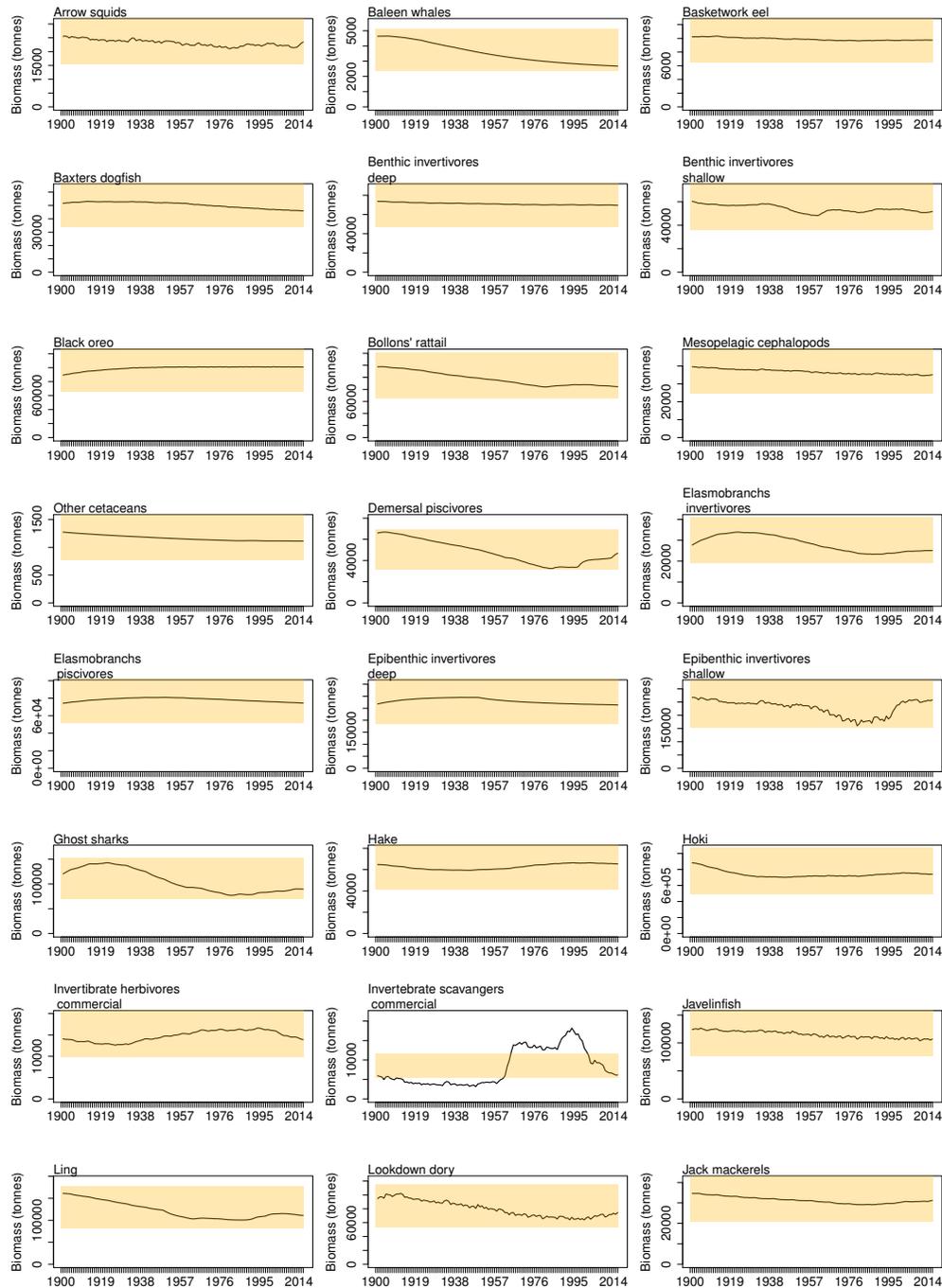
757 **Appendix A: Simulated biomass by species group from**

758 **no-fishing model**

759 Simulated biomass from the un-fished model (black line) with 95% confidence intervals

760 based on 20% CVs (Coefficient of Variation) shaded orange by species group.

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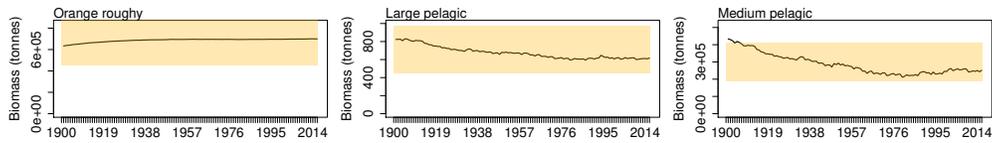
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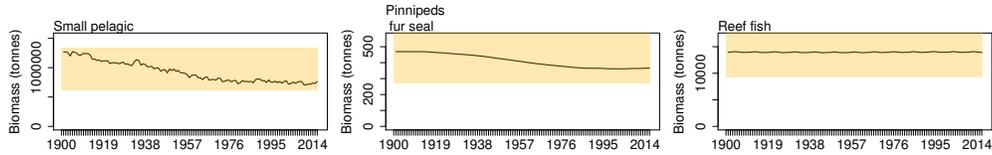
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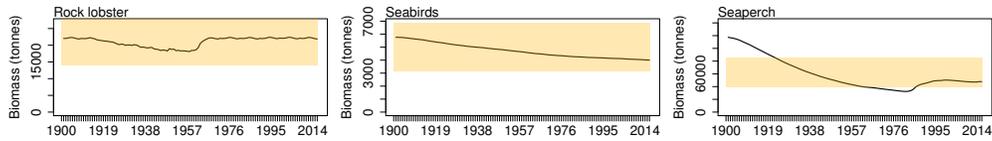
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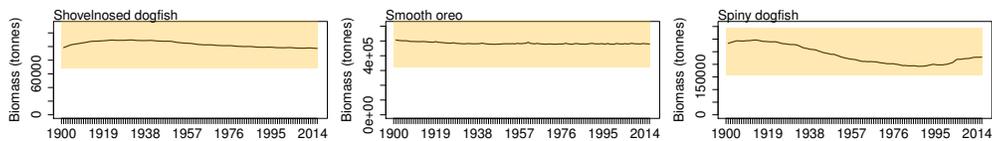
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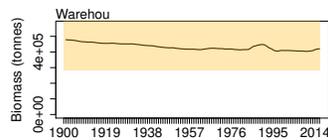
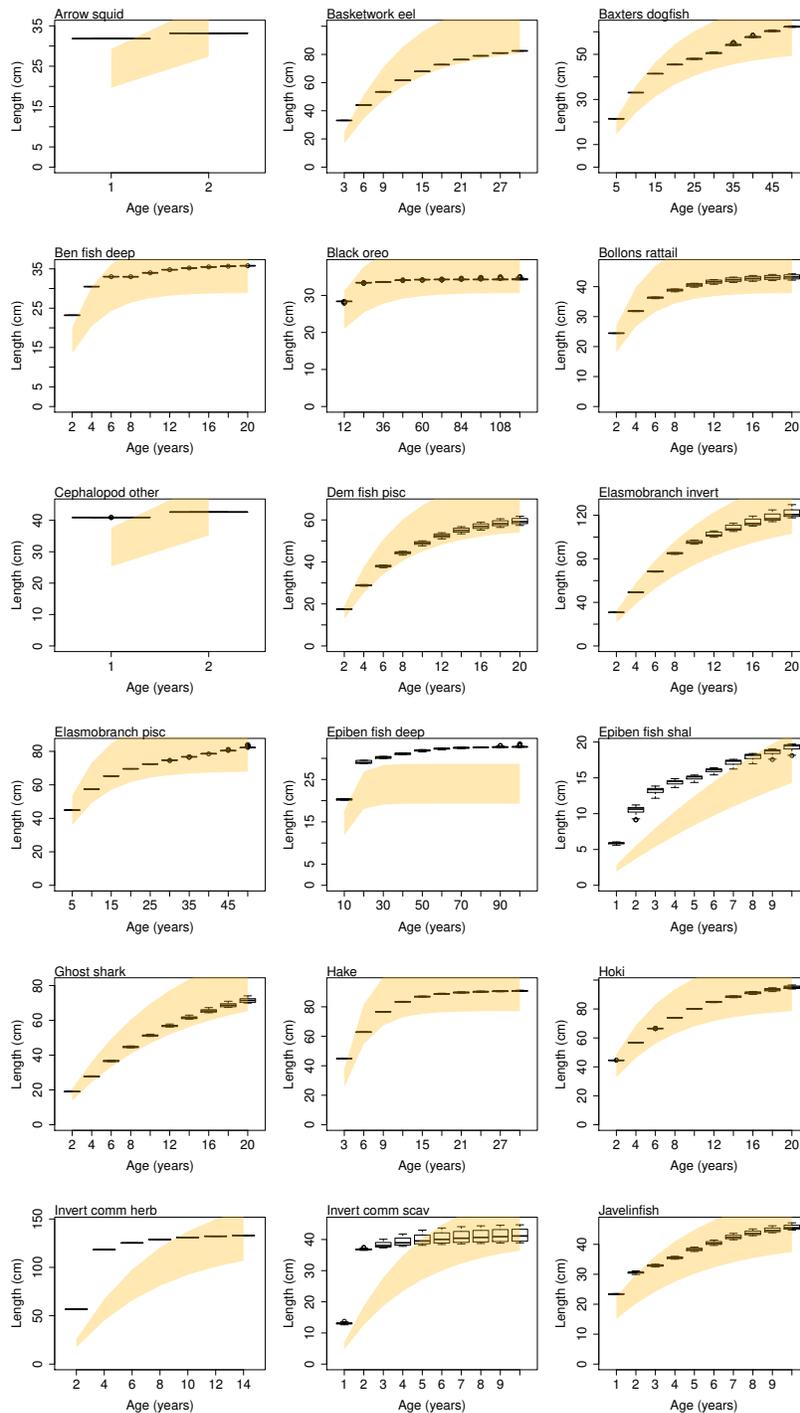

Appendix B: Size-at-age

Size-at-age using values based on literature (Table 6) where available (orange shaded shows 95% confidence intervals using CV 10%) and from CRAM simulated years 1900–2015 (boxplots).

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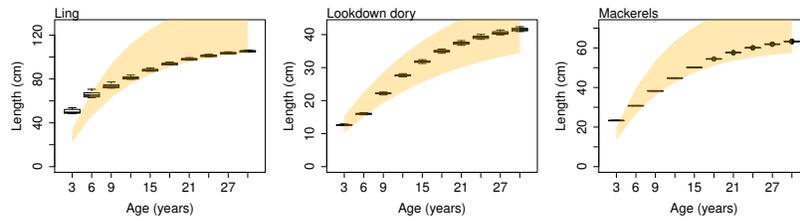
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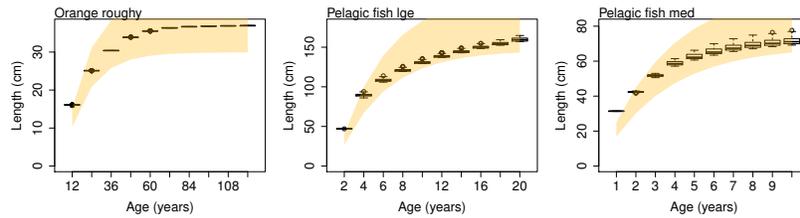
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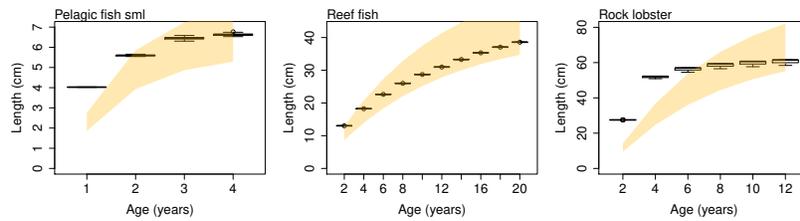
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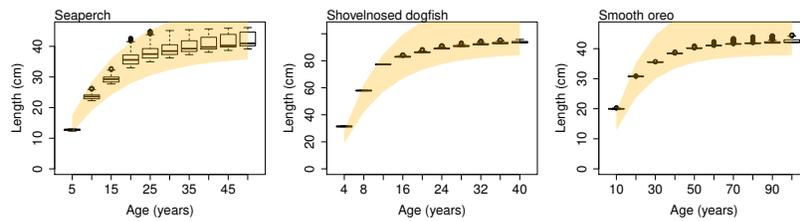
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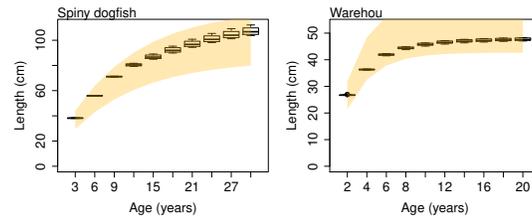
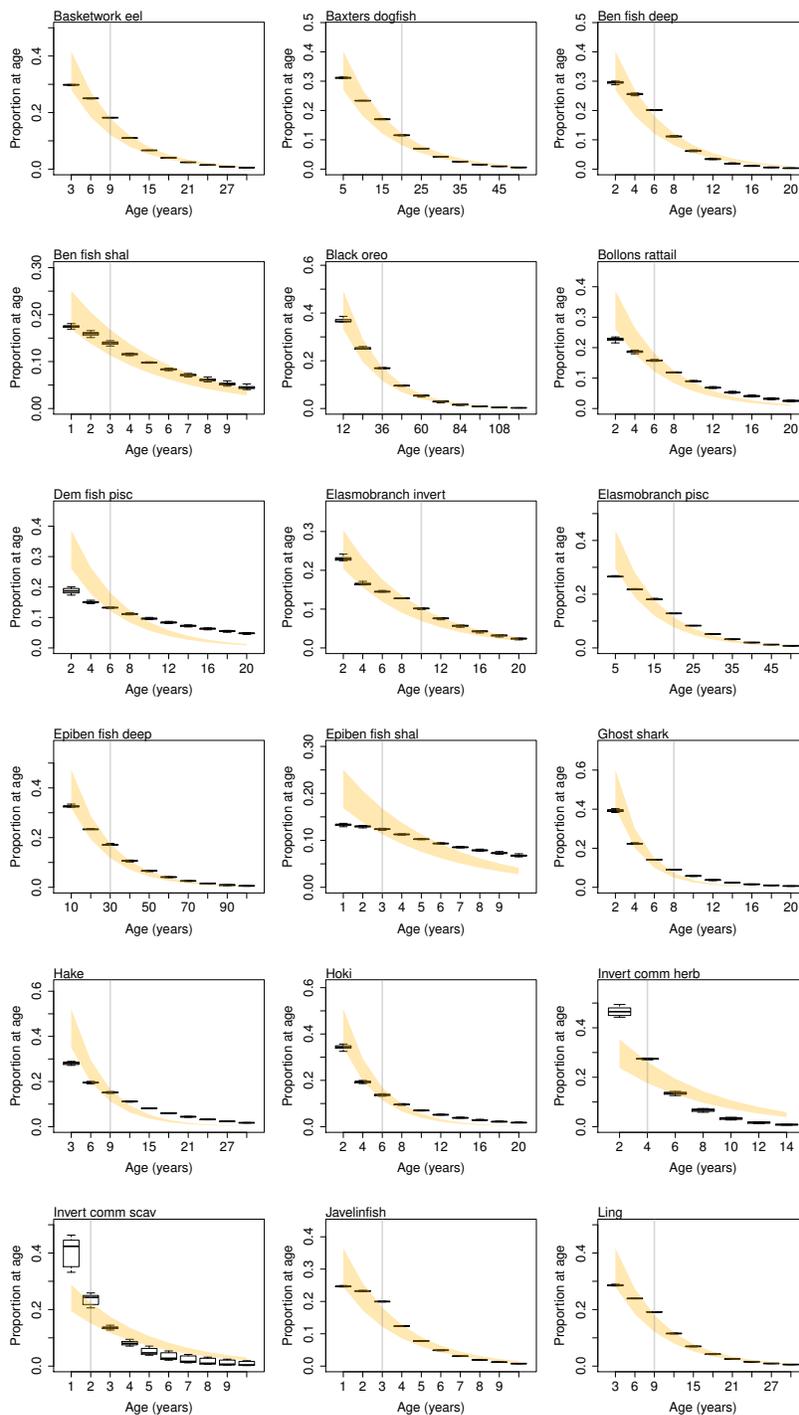

Appendix C: Proportion-at-age

Proportions at age using M based on literature (Table 6) where available (orange shaded shows 95% confidence intervals using CV 10%) and from CRAM simulated years 1900–2015 (boxplots).

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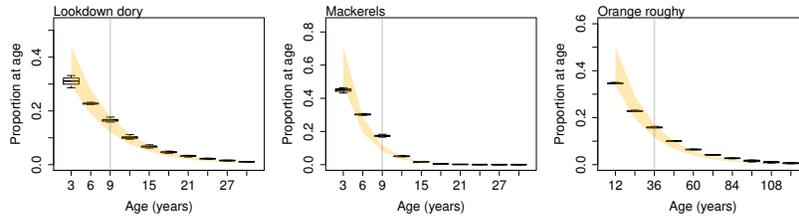
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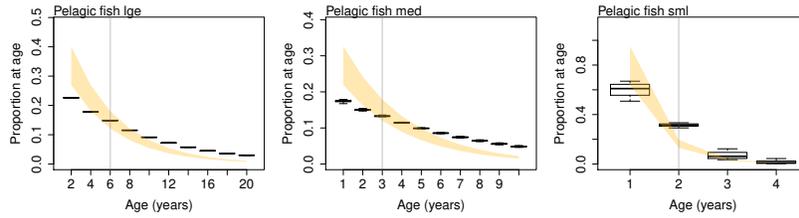
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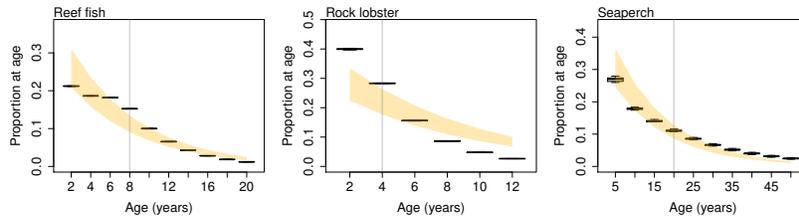
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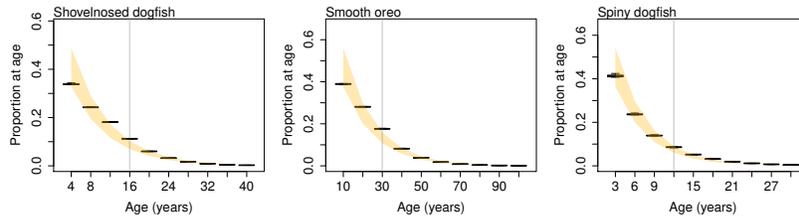
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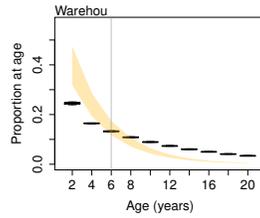
Appendix D: Observed vs estimated

Observed biomass estimated from trawl surveys (red), estimated biomass from CRAM (black) and forced catch history (grey) for all groups with trawl survey estimates.

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