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

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Abstract

17   The Chatham Rise is a highly productive deep-sea ecosystem that supports numerous sub-

18 stantial commercial fisheries, and is a likely candidate for an ecosystem based approach to

19 fisheries management in New Zealand. We present the first end-to-end ecosystem model of the

20 Chatham Rise, which is also to be best of our knowledge, the first end-to-end ecosystem model

21 of any deep-sea ecosystem. We describe the process of data compilation through to model

22 validation and analyse the importance of knowledge gaps with respect to model dynamics and

23 results. The model produces very similar results to fisheries stock assessment models for key

24 fisheries species, and the population dynamics and system interactions are realistic. Confidence

25 intervals based on bootstrapping oceanographic variables are produced. The model components

26 that have knowledge gaps and are most likely to influence model results were oceanographic

27 variables, and the aggregate species groups 'seabird' and 'cetacean other'. We recommend

28 applications of the model, such as forecasting biomasses under various fishing regimes, include

29 alternatives that vary these components.

1   Introduction

33 The goal of incorporating a holistic approach to understanding the system-wide repercussions

34 of how we manage our marine resources is admirable and ambitious (Long et al. (2015), Link

35 and Browman (2017)). Ecosystem Based Management (EBM) requires a range of tools, often

36 including ecosystem models (Smith et al. (2017), Stecken and Failler (2016)). Within ecosys-

37 tems there are many processes at play, and the models developed to support EBM vary in scope

38 and complexity (Plagányi (2007), Fulton (2010), Collie et al. (2016)). End-to-end ecosystem

39 models that can deal with bottom-up and top-down system controls have become popular

40 for exploring scenarios involving human induced impacts including fishing and climate change

41 (Rose, 2012).

43   The body responsible for fisheries management in New Zealand, Fisheries New Zealand, is

44 seeking to move away from single species management towards a more ecosystem approach,

45 both to fulfil Fisheries Act obligations and Marine Stewardship Council (MSC) expectations

46 (Ministry for Primary Industries (2008), Marine Stewardship Council (2014)). The Chatham

47 Rise is the location of several nationally important MSC certified fisheries (Deepwater Group,

48 2018), and a growing understanding of trophic interactions exists there (Stevens et al. (2011b),

49 Dunn et al. (2009)).

51   Chatham Rise is a submarine ridge running eastwards for about 1000 km from the east

52 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 end-to-end 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)). Atlantis is a deterministic simulation model such that for a given parameter set and model specification, the model outputs are identical. Atlantis models are too complex to statistically fit to observations, although subsets of key parameters can be estimated using statistical methods outside of the model. Analysing and understanding the model dynamics and potential weaknesses is essential before the model can be used to learn about the system.

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 biomass trends as the model responded 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.

2 Methodological Approach

The process of developing this model was not linear, but rather iterative and incremental. There were five main stages to the development, each of which was re-visited until we were satisfied with the performance of the model and our understanding of its dynamics. The main stages can be summarised as:

1.) Data and model inputs were collated and defined.

2.) The base historical model was calibrated without fishing such that this model had stable biomass trajectories over the 1900–2016 model period, realistic diets, growth rates, natural mortalities.

3.) Sensitivity analyses were carried out with respect to oceanographic variables and simulations aimed at understanding connectivity and influence between the species functional groups.

4.) Fishing was included in the model using forced catch removals.

5.) Skill assessment and comparisons to abundance indices and biomass estimates were carried out.
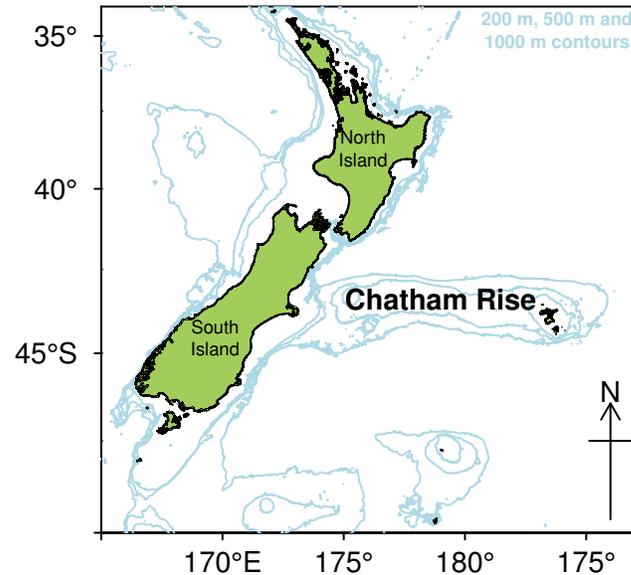
Figure 1: Map of New Zealand with Chatham Rise marked, including 200 m, 500 m, and 1000 m isobaths.

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131   Sections 3–7 cover each of these five main stages, followed by Section 8: Bringing it together,

132   which discusses some of the implications of the models' performance, dynamics and data gaps.

133

3   Model design

135   An Atlantis model simulates the ecosystem through time, calculating each new state based on

136   the previous state and the events of the current timestep. This section describes the physical,

137   biological, ecological, and fishing components of the Chatham Rise Atlantis Model. Further

138   details on Atlantis can be found in the Atlantis user manual (Audzijonyte et al., 2017).

139

3.1   Model area

141   The Chatham Rise Atlantis model area comprises waters from the shore-line around Chatham

142   Islands (but excluding estuaries on the islands) to depths of 1300 m along the Chatham Rise,

143   New Zealand (Figure 2). The western boundary of the area is defined as the 400 m contour

144   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 define the boundary conditions for the modelled domain.

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. 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).

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. This is also helpful for informing the model spatially based on trawl surveys. 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 layer in some near-shore polygons to five layers for the deepest polygons. Depth layers are also defined in Figure 2. Each box also contains one epibenthic and one sediment layer.
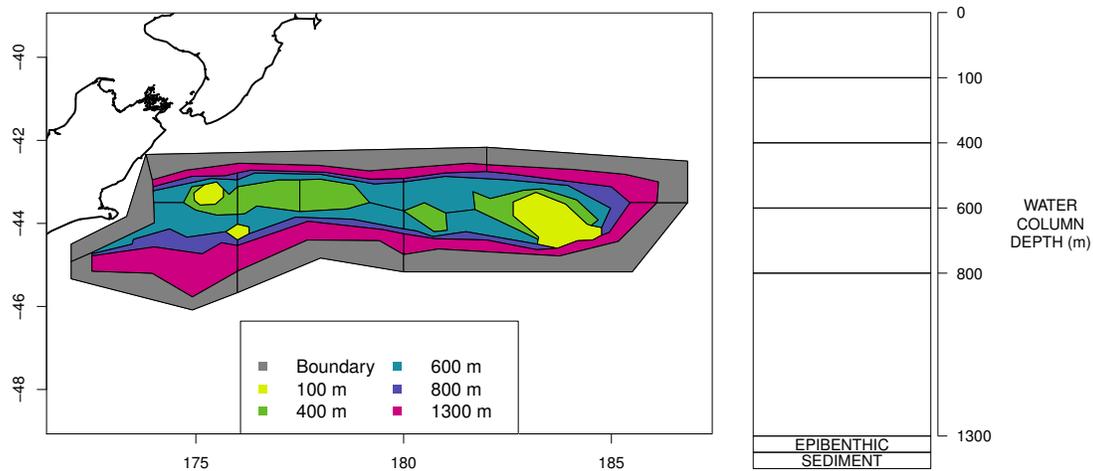
Figure 2: Polygons as defined for CRAM with maximum depths for each polygon shown by colour (left) and depth layer bins (right).

3.2   Time

The model was run with a 35 year burn-in period (1865–1900) followed by a 115 year modelled period (1900–2015). The burn-in period allows for the model to adjust from potentially unstable initial conditions due to uncertainty of some of the parameters and age distributions for the age resolved groups, to a state that is more stable. A 35 year period was chosen as it covered initial fluctuations of most functional groups in the model. All results presented here are from the modelled period 1900–2015. The model used 12 hour timesteps to allow for changes in temperature, light and feeding patterns between night and day.

3.3   Oceanography

Salinity, temperature and water exchange between cells were forced in the Atlantis model using outputs from a ROMS (Regional Oceanographic Modelling System) model (Hadfield et al., 2007) that covered years 1996–2004. Water currents across each box face cause the horizontal movement of nutrients (such as ammonia and nitrate) available to primary producers. The speed and direction of currents influence the spatial distribution of plankton groups. Water temperatures influence biological processes such as respiration (Hoegh-Guldberg and Bruno, 2010). Based on sea surface temperatures (SST), the ROMS years (1996–2004) look to be fairly representative of those properties from 1961–2017 (Figure 3). The base model presented here repeated the available ROMS variables as a nine-year cycle. Averaging the ROMS variables was not sensible due to the water exchange between cells, as these change every 12-hour timestep in strength and direction, and averaging them could easily result in implausible physical dynamics. We ran sensitivities varying the order of ROMS years or repeating one ROMS year to

202   help understand the effects of inter-annual oceanographic variability on this model.

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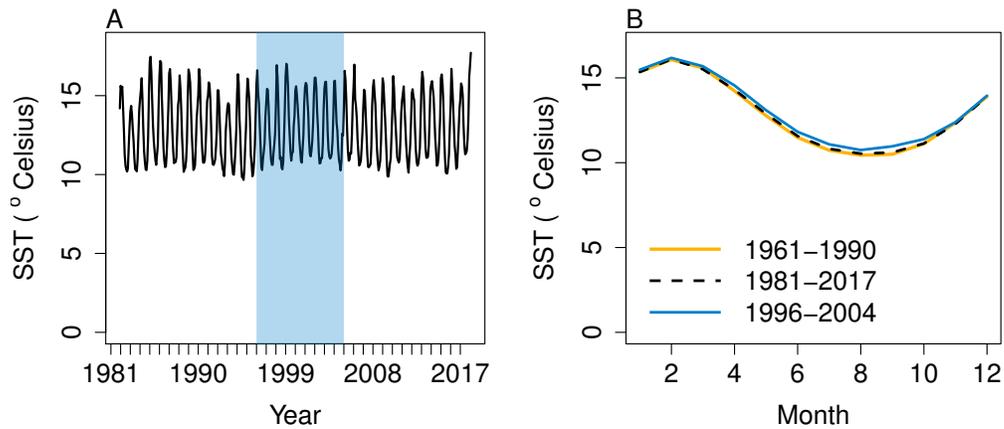
Figure 3: Sea surface temperature (SST) (^{o} Celsius) weekly averages for 1981–2017 with ROMS years 1996–2004 shaded blue (left) and mean SST by month (right) from the same data for 1981–2017 (black dashed line), with the subset from 1996–2004 (blue solid line), and additional historical SST data from 1961–1990, which were only available as monthly averages (orange solid line).

3.4   Nutrients

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

3.4.1   Nutrient data

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

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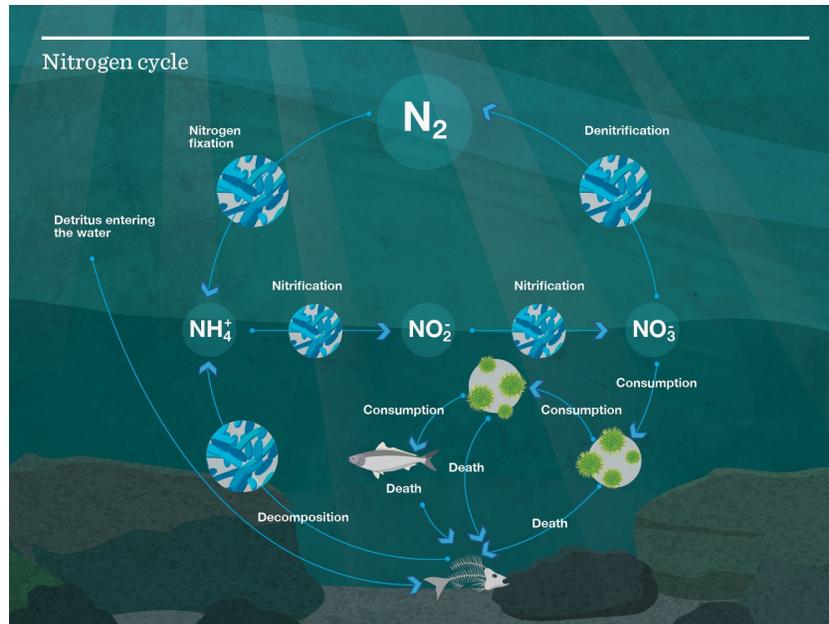
Figure 4: Nutrient cycle as modelled in Atlantis.

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 (National Institute of Water and Atmospheric Research) oceanographic surveys, but only down to 50 m. This was not too concerning as ammonium is a small component of the nitrogen budget.

Table 1: Sources of data for Oxygen, Nitrates, Ammonium and Silica. WOA, World Ocean Atlas; WOCE, World Ocean Circulation Experiment; NIWA, National Institute of Water and Atmospheric Research.

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

3.5 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

Table 2: List of functional vertebrate groups for CRAM. Name is the species group name which is the same as the main species 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 relevant 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 species 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 species 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

3.5.1 Initial conditions and biological parameters for species groups

Initial biomasses for each species group were estimated using a single species stochastic stock assessment model, CASAL (Bull et al., 2012). Biomass estimates for the entire Chatham Rise were derived by using known biological parameters and a catch history to project back from an absolute abundance estimate in 2003. Values of relative abundance were available for most species groups from trawl surveys conducted annually from 1992 to 2014 (see O'Driscoll et al. (2011)). For each survey, these abundance estimates were converted to absolute values using trawl catchability quotients (specific to each group) derived by our expert opinion, as fisheries scientists with experience dating back more than 30 years. Estimated absolute abundance for each group in 2003 (the midpoint of the survey series) was taken as the mean from all the survey estimates. For each species group, the initial biomass estimate was distributed across polygons in proportion to the survey series estimates (i.e., the mean proportion of total biomass by polygon over the survey series). The distribution of biomass by depth layer in each polygon was derived using our expert opinion. Where there was no available catch history (e.g. seabirds), or no useful estimates of relative abundance from the trawl surveys (e.g. rock lobster), initial biomasses (and their distribution by model polygon) were estimated using our expert opinion. For age-structured groups, initial biomass estimates were assigned to age-classes using estimates of instantaneous natural mortality (M). Initial average weights at age were calculated using Von Bertalanffy growth and length-weight conversion parameters. Values used for these parameters are in Table 6. Weights at age were split into reserve and structural components using ratio $R_N : S_N = 2.5 : 1$. This allows for an individual's body mass to decrease by approximately 70% before starving, which is within the 60–80% range suggested by Broekhuizen et al. (1994).

All age-structured groups were modelled with Beverton-Holt recruitment, the steepness (h) values for which are in Table 6. These values are not ever well known, and 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)

3.6 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? Full details are in the Atlantis User's Guide (Audzijonyte et al., 2017). Step 4 uses a feeding functional response, of which there are 12 options currently available in Atlantis. We have applied the Holling Type II functional response to all age-structured species groups in this model, thus influencing the amount of prey consumed by prey abundance, and the predators search rate and handling time.

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 in the detail.
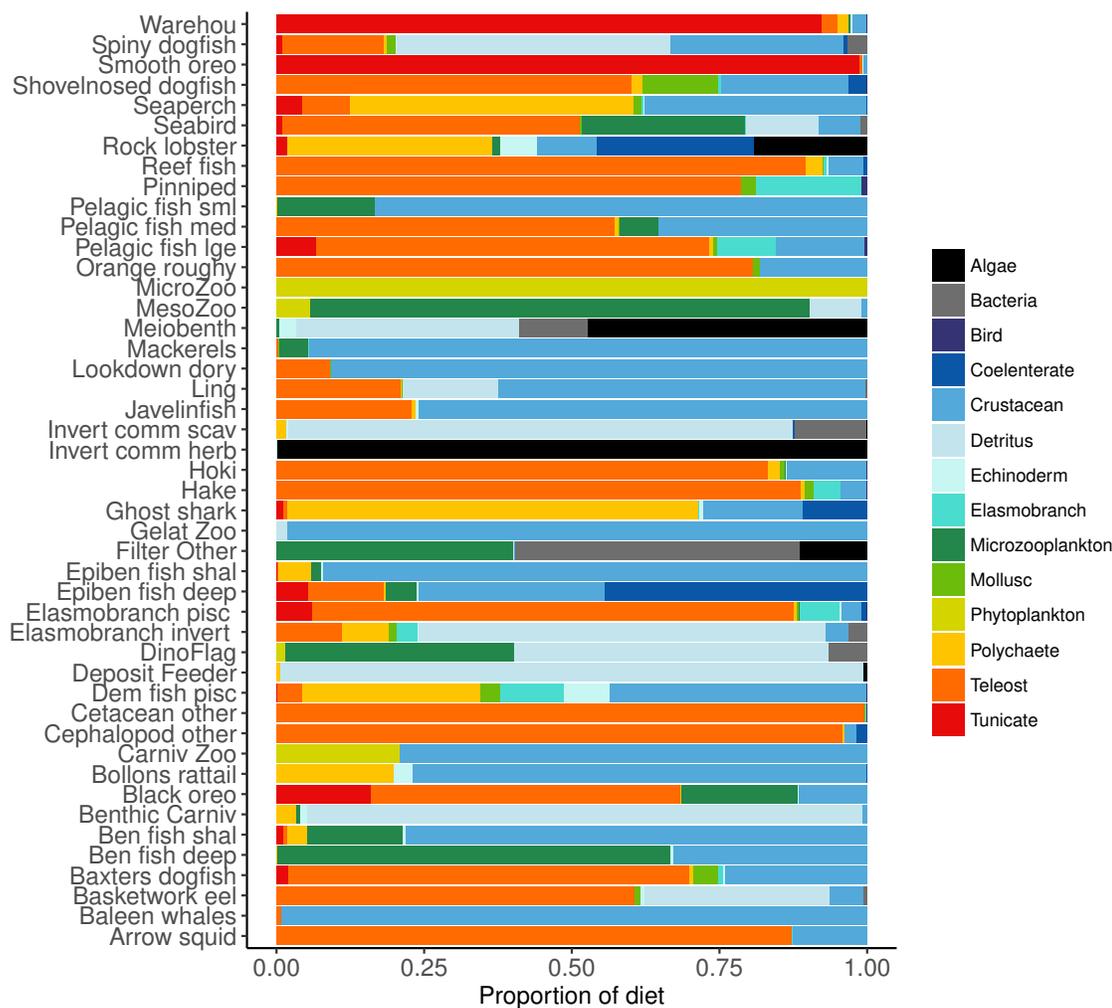
Figure 5: Summary of the proportion of prey groups in the diets of species functional groups (Tables 2 and 3) over model years 1900–2016 from the fished model where the proportion is by mg N consumed.

4   Calibration

Calibration of the model included ensuring stable biomass trajectories when apply-
ing 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 3.3), 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 A. Seaperch biomass was trending downward
initially, but they seem to have reached an equilibrium by about 1950, with expected
growth and mortality rates.

Atlantis simulates growth rates of age-structured groups as a function of consump-
tion. If growth is too slow, there may be insufficient food available, the feeding search
rate could be too low or handling time too high, and the reverse of these when growth
is too fast. Simulated growth rates of age-structured species groups were assessed by
comparing the simulated size-at-age with those expected based on growth curve esti-
mates from the literature (Table 6). The overlaid simulated and 'observed' figures were
generally very similar (Appendix B). 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), in-
vertebrate 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

331   mortality. The latter was applied for modelled species groups that would not other-

332   wise suffer sufficient natural mortality within the model, such as those that have little

333   known predation. Age-structured simulated natural mortality rates from the stable base

334   model were compared to estimates of M from the literature where available (Table 6) by

335   comparing the proportions-at-age. The overlaid simulated and 'observed' figures were

336   generally very similar (Appendix C), although rock lobster and invertebrate herbivore

337   commercial (primarily paua and kina) had slightly more mortality in the model, and

338   demersal piscivores, epibenthic fish small, pelagic fish medium, and warehou had slightly

339   less mortality.

340

341   We summarised biomass by trophic level for the base model as at 2016 on a log-scale,

342   and biomass reduced with increasing trophic level with a fitted slope of -1.6 (Figure 6).

343   This was close to the recommended range of PREBAL of (-1.5, -0.5). The biomass at

344   trophic level 4 was slightly higher in this summary than in the model, as the summary

345   was based on adult trophic level and many of the fish species are trophic level 4 as

346   adults, but lower as juveniles. This resulted in the biomass of the juveniles for these

347   fish adding to the level 4 biomass whereas in the model they were perhaps functioning

348   as a level 3.
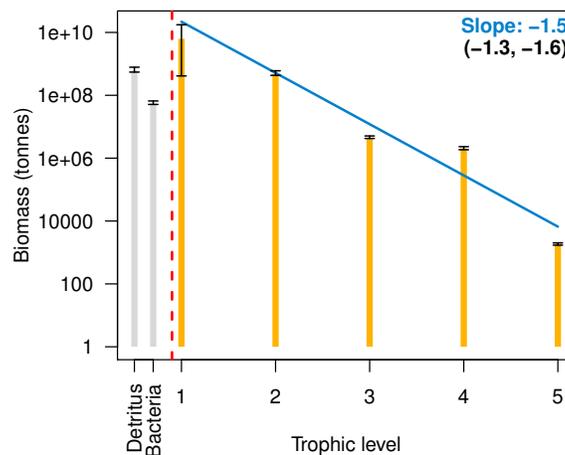
Figure 6: Biomass by trophic level with 95% confidence intervals from the 1900–2016 Chatham Rise Atlantis model simulation. The blue line is the fitted linear model to the median biomasses by trophic level, the slope which is in blue. The slopes of the linear models to fitted to the upper and lower 95% confidence interval limits are given in brackets.

349

5 Sensitivity analyses

5.1 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 biomass confidence intervals were fairly narrow for most species groups, with CVs < 10%. Of the exceptions, diatoms had the highest CV of 79%, followed by carnivorous zooplankton (46%), labile detritus (23%), sediment bacteria (13%), invertebrate scavengers (commercial) (12%), refractory detritus (12%), mesozooplankton (11%) and pelagic bacteria (11%). That these groups were found to be most sensitive to oceanographic variability in the model is a plausible and sensible result.

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 biomass confidence intervals, with the on average warmer years (1999, 2000, and 2001) having the most species groups that went below (Figure 8). These species groups affected by

385 warmer or cooler years had quite a bit of overlap, with meso-zooplankton, meiobenthos,
386 and black oreo most often affected. All of the species groups that went lower in warm
387 years also went higher in cool years. The reverse was not true; three species groups
388 (arrow squid, labile detritus, and ghost shark) went higher in the cool years, but not
389 lower in the warm years.

390 Years 2003 and 1998 were closest to the average sea temperatures and had the least
391 number of species groups outside the bootstrap confidence intervals. The Base Model
392 that repeated the ROMS from all nine years in order for the entire model simulation had
393 16 species groups that exceeded the bounds at some point (less than the warm years)
394 and six species groups that went below the bounds at some point (less than the cool
395 years) (Figure 8).

396
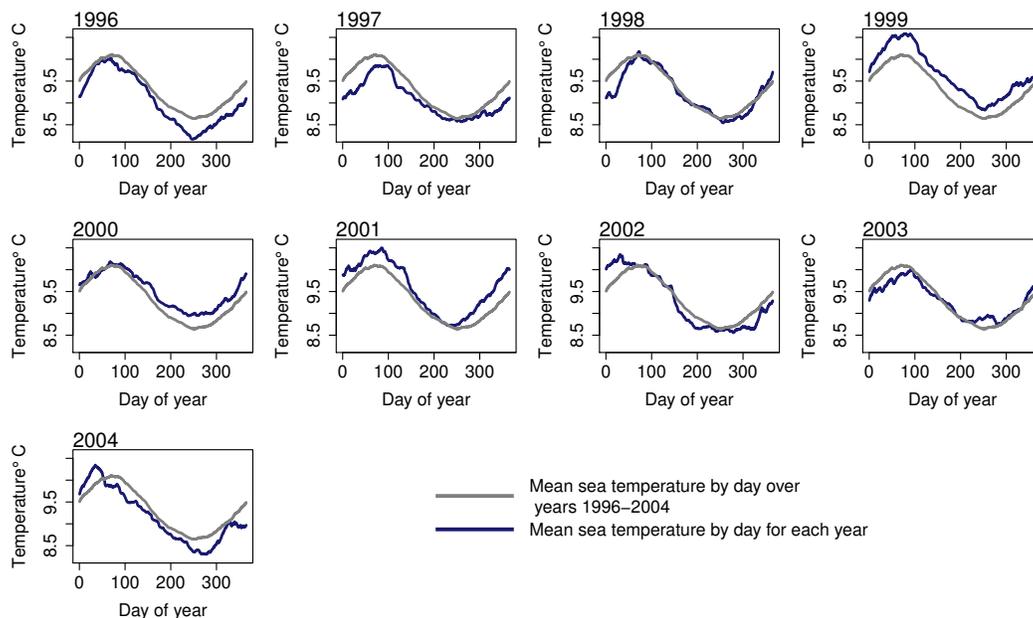
Figure 7: Sea temperature (^{o}C) from ROMS model outputs by day for each year 1996–2004 (dark blue line) and median sea temperature over all ROMS model years 1996–2004 (grey line).

5.2 Connectivity and influence

398 Understanding which species groups are most influential or responsive in the model is
399 another test for realistic dynamics, and may be useful to help understand results of
400 scenarios explored using this model in the future. To do this, we need to perturb each
401 species group in turn, then assess the responses of the other groups in the system. For
402 each age-structured species group, we ran two simulations, one with a small additional
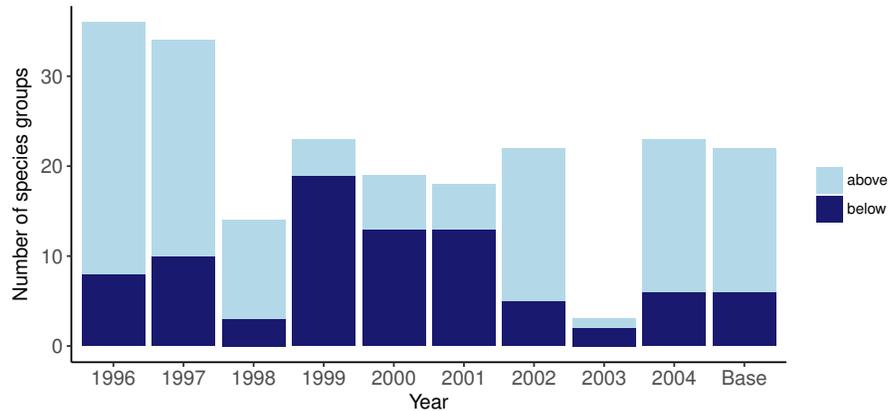
Figure 8: Number of species groups for each simulation with one ROMS year repeated that went above (light blue) or below (midnight blue) the limits of bootstrapped ROMS simulations and for the Base Model where the years were repeated in order for the entire model simulation.

403   mortality and one larger; M(per year) + (0.1, 0.005). We assessed responses of the

404   groups with respect to the Base Model at the completion of 50-year simulations. We

405   analysed the 'keystoneness' and responsiveness of the groups based on biomasses relative

406   to the Base Model.

407

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

409   (2006). It is a measure of the effect the group has on the rest of the system (change in

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

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

412   biomass and one a small biomass, the smaller would have a larger keystoneness. We

413   used simulation outputs to estimate the total effect (ϵ) of each species group (Equation

414   1) which used the change in biomass of each group relative to the Base Model (Equation

415   2). The simulated change in biomasses ($S_{f,g}$) were used in place of the mixed trophic

416   impact values calculated from mass balanced models and used by Libralato et al. (2006).

417   As the additional mortality applied in our simulations caused larger and smaller changes

418   to the focus groups, we scaled the focus groups' biomass proportions by their change in

419   biomass ($S_{f,f}$ in Equation 4). Hence, the resulting keystoneness allowed for the effect

420   changing each group had on the other groups, the focus groups biomass as a proportion

421   of the total, and the proportional change in biomass of the focus group relative to the

422   base model.

423

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

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

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

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

ϵ_f, effect group f has on the other groups

$S_{f,g}$, 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).

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

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

The most responsive group was pelagic fish small (primarily myctophids), followed by smooth oreo, invertebrate scavengers commercial (primary scampi), and pelagic fish medium (primarily barracouta) (Figure 10). The pelagic fish small species group ranked high for keystoneness and responsiveness, and so may be most important and influential in scenarios explored with this model.

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).

6   Fishing

Most of the fisheries on the Chatham Rise became established after the mid-1970's, with the exception of the blue cod (*Parapercis colias*) (reef fish species group) fishery which extends back to the early 1900's. Individual catch histories are in Appendix D and Figure 11 presents a summary of catches from the Chatham Rise with the top six species by total catch shown in colour and the others combined into an 'other' category. Hoki had the largest total catch, followed by orange roughy, smooth oreo, ling, black oreo, then barracouta. Orange roughy comprised the largest individual fishery in the late-1970's–early-1990's after which it declined markedly; from the 1990's hoki was the
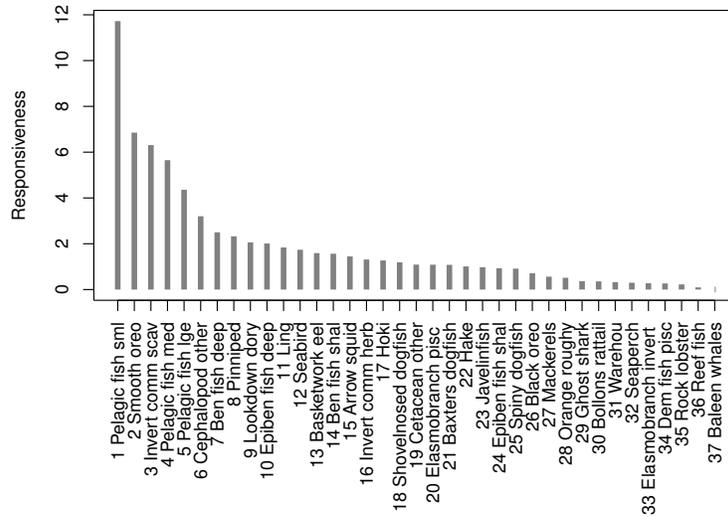
Figure 10: Responsiveness of age-structured species groups after 50 years of perturbation, as calculated in Equation 5.

456   dominant fishery.

457

458   The fisheries were modelled with six fleets, defined in Table 7. The demersal line

459   fishery was dominant until mid–late 1960's when the demersal trawl fishery became

460   dominant, catching approximately 70 000 tonnes per year (Figure 12). The historical

461   catches from these fleets were forced in the model using spatially and temporally resolved

462   inputs.
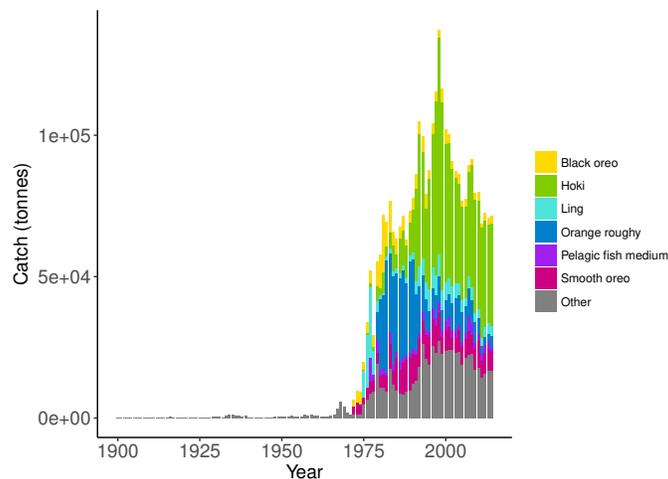
Figure 11: Tonnes caught from Chatham Rise 1900–2014 for all species with top six species groups by total catch coloured separately.

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
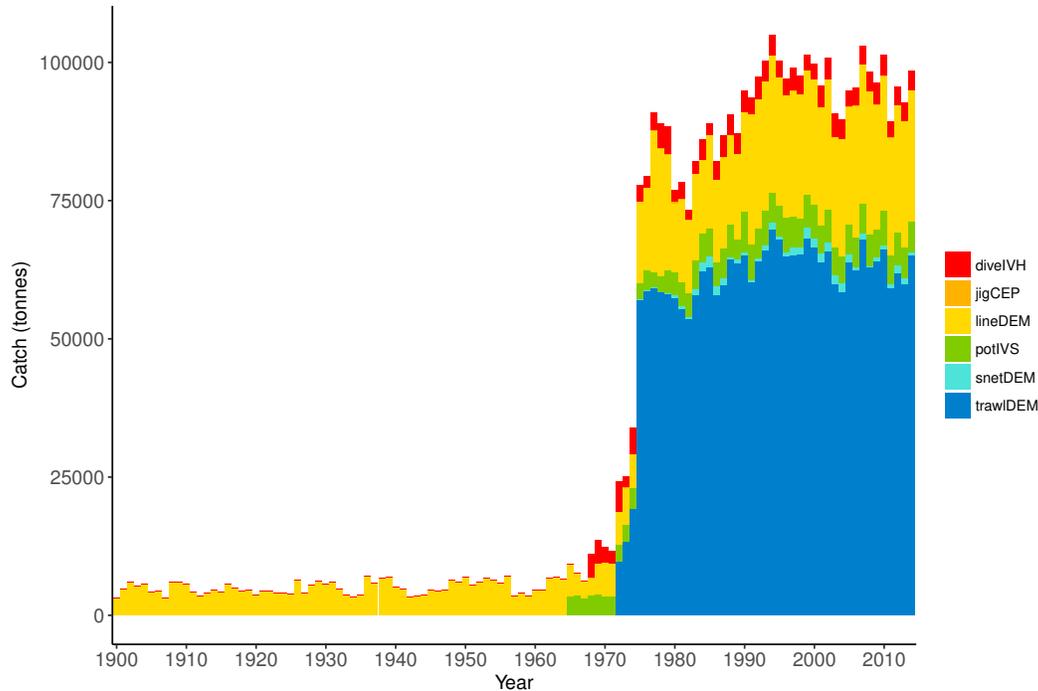
Figure 12: Total tonnes caught by fishing fleet from the Chatham Rise 1900–2014. Descriptions for the fleet codes are in Table 7.

6.1 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. The magnitude of the stock assessment biomasses (unscaled) are compared to the CRAM biomasses in the inset boxplots in Figure 13. Hoki, hake, and invertebrate scavengers (commercial) were all close to one, indicating matched magnitudes between the stock assessment and CRAM biomasses. Ling were generally less than one, indicating the CRAM biomasses were larger than the stock assessment biomasses. Orange roughy were greater than one, indicating CRAM biomasses were smaller than the stock assessment biomasses.

7 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 D.

$$MEF = \frac{\sum_{y=1}^{Y} \left(O_y - \bar{O}\right)^2 - \sum_{y=1}^{Y} \left(O_y - P_y\right)^2}{\sum_{y=1}^{Y} \left(O_y - \bar{O}\right)^2} \tag{6}$$

$$RI = \exp \sqrt{\frac{1}{Y} \sum_{y=1}^{Y} \left(\log \frac{O_y}{P_y}\right)^2} \tag{7}$$

$$r = \frac{\sum_{y=1}^{Y} \left(O_y - \bar{O}\right)\left(P_y - \bar{P}\right)}{\sqrt{\sum_{y=1}^{Y} \left(O_y - \bar{O}\right)^2 \sum_{y=1}^{Y} \left(P_y - \bar{P}\right)^2}} \tag{8}$$

where

Y is the number of years for which there are observations,

O_y is the observed biomass in year y,
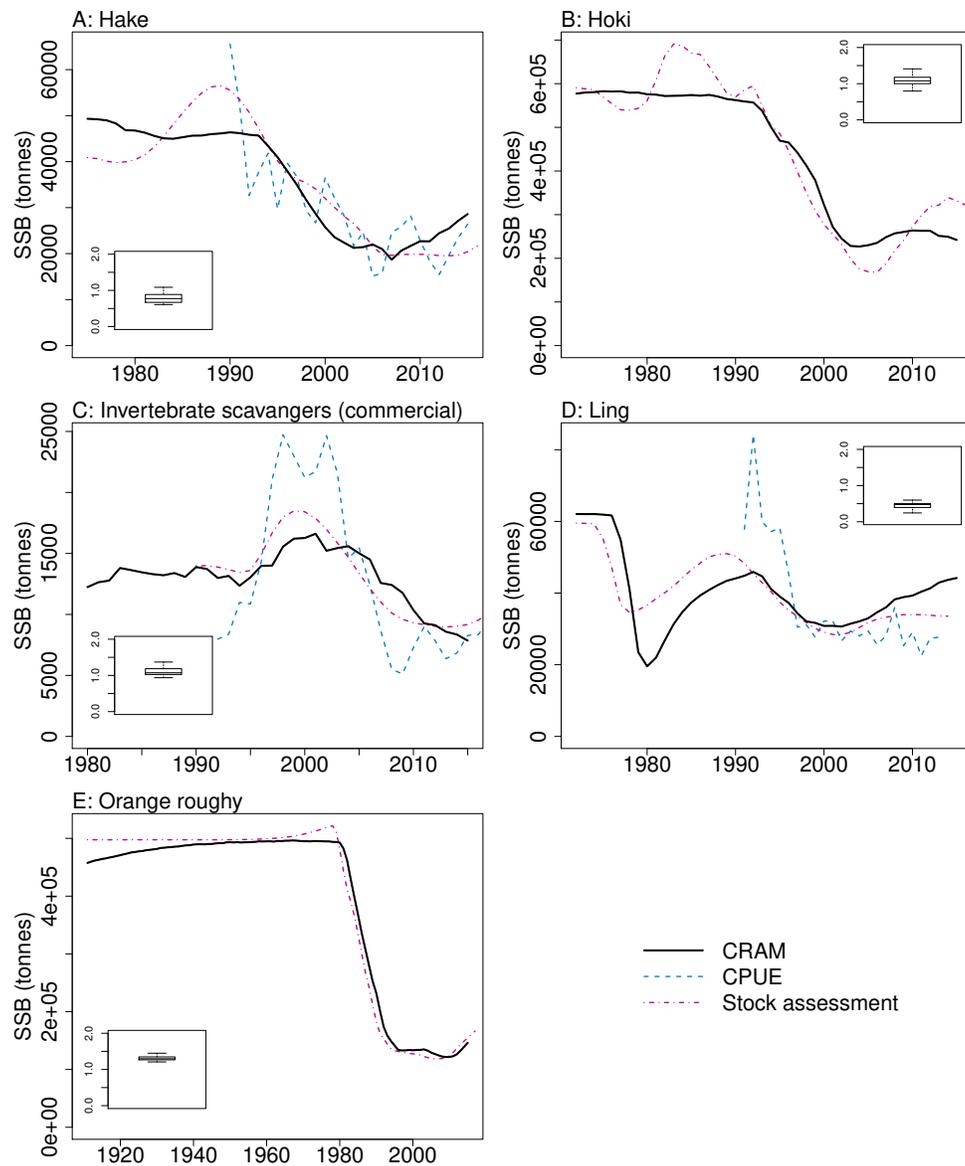
Figure 13: CRAM estimated spawning stock biomass (SSB) (black solid), stock assessment esti-
mated SSB (red dot-dash), and CPUE (blue dash) where available for the hake (A), hoki (B),
invertebrate scavengers (commercial) (primarily scampi) (C), ling (D), and orange roughy (E) .
CPUE and stock assessment SSB were rescaled to match the mean of the CRAM estimated SSB.
Inset boxplots show the range of values for the corresponding unscaled stock assessment SSB divided
by the CRAM estimated SSB.

504 P_y is the model biomass in year y

505

506 Each skill assessment metric was calculated using single point estimates from the

507 trawl survey, and variants on RI and MEF were calculated allowing for the trawl survey

estimated 95% confidence intervals. Both variants only penalised the skill metric for terms outside of the 95% confidence intervals of the trawl survey.

An MEF close to one indicates a close match between model predictions and observations, with zero indicating the mean of the observations is as close as the model predictions, and a negative value indicating the model predictions fit the observations worse than the mean of the observations. When the observed values are roughly stationary about the mean, as was the case for Ling, it is difficult for the predictions to improve on the mean of the observations. Ling stands out at approximately -2.5 when 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 exactly equal to the observations. RI greater than one (it cannot be less than one) indicates the factor by which observations are on average different to predictions. Since $log(O/P)$ is equal to $-log(P/O)$ and the RI squares these terms, an observation that is, for example, half the prediction will contribute exactly the same to this index as an observation that is twice a prediction. Hence, a RI of 2 indicates the observations differ from the predictions on average by 2, but these could be generally twice as big or half as big, or both. All groups had RIs between 1 and 1.5 (Figure 14), indicating the observations are at worse on average $1.5\times$ the predictions or $(2/3)\times$ the predictions.

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.
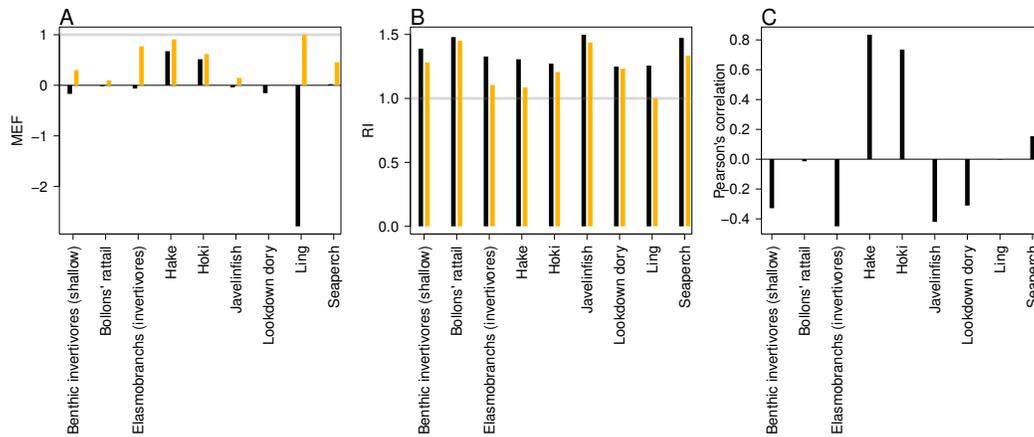
Figure 14: Skill assessment metrics MEF (A), RI (B) and Pearson's correlation (C) for CRAM species groups that have trawl survey indices for abundance. Metric definitions in Equations 6–8. The black bars are the skill metrics with respect to single point estimates from the trawl survey. The orange bars 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.

8   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 5.2. 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 providing keystoneness is low (since the effects may be more limited to this single species group), 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. This may be due to the size of recruits being larger than they should be, or the fish eating (and hence growing) more than they should in this first year. They are not so big that the effect transfers to the age-2's, as the age-2's are the correct size (Appendix B), so this is probably not influential on the model overall. Medium pelagics have slightly less natural mortality in the model than they should (Appendix C), 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 sensitivity analysis with respect to these two groups to understand their effect on the outcomes, or perhaps some more work to better define them.
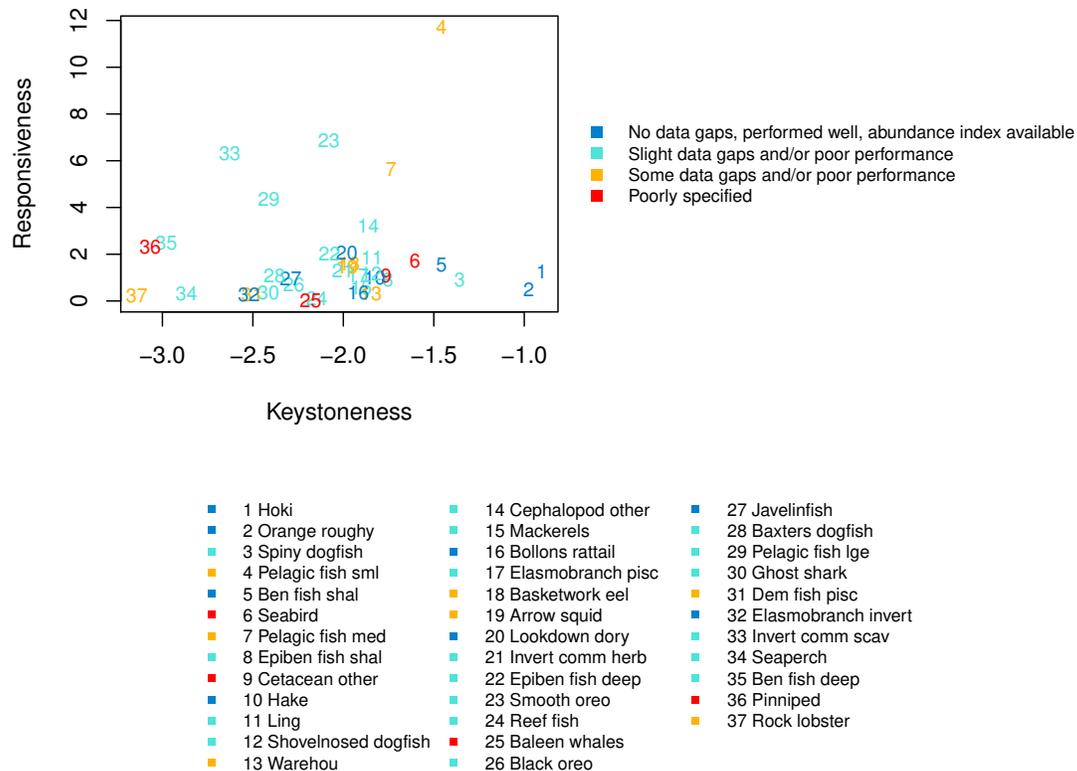
Figure 15: Keystoneness (x-axis) and responsiveness (y-axis) with numbers showing keystoneness ranking and colours how well each species group was informed and/or performed in the model (legend).

9   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 comprehensively to data and is entirely deterministic. 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. This is not to say the model could not benefit from further future work examining the realised diets at a finer scale - spatially, temporally, and by age-class.

Exploring the models sensitivity to initial conditions, while not an insignificant amount of work, may be worth doing at some stage in the future to add to our understanding of the models stability and persistence of dynamics. This has not, to the best of our knowledge, been done for Atlantis or OSMOSE models, likely due to the enormous complexity and computing resources required for the task. Sensitivities to initial conditions have been explored using Ecopath (Essington, 2007) and Ecopath with Ecosim (EwE) (Steenbeek et al., 2018). We are in the early stages of developing an EwE verison of CRAM, and it may be more feasible to explore ranges of initial conditions

within the EwE framework, with the possibility of then adapting the analyses to the Atlantis model. Sensitivities of high-ranking keystone species, such as spiny dogfish, would be simpler to implement and may produce greater understanding of the model.

While there are some knowledge gaps, 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. As option a.) would require more data than we currently have available, option b.) is the only currently viable option.

The oceanographic variables based on 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.

As Atlantis is spatially resolved, there is scope for a greater emphasis on the effects of features such as habitats, depth, and oceanographic features on responses to fisheries management scenarios. Kaplan et al. (2012) explored spatially resolved fisheries management scenarios using an Atlantis model of the California Current, including areas closed to bottom-contact fishing gear, and varying spatial management specification relating to Marine Protected Areas (MPAs). In the Chatham Rise ecosystem, it may be that repeating cooler or warmer years such as carried out in this study could influence the spatial distribution of some species. This could in turn influence the range of plausible responses to fisheries management scenarios that have a spatial aspect, such as MPAs, the effects of different fishing gear, serial depletion of fishing grounds, and potential effects on by-catch species that may overlap spatially with species that are targeted by fisheries.

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.

10   Conclusions

The analyses presented in this paper are intended to set the stage for an understanding of how the model is specified and how it behaves, but it is not exhaustive. The model produces 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 aggregate species groups 'seabird' and 'cetacean other'. We recommend applications of the model include alternatives that vary these components. It is expected that any future use of the model will add first to our understanding of the model, and then possibly to our understanding of the ecosystem.

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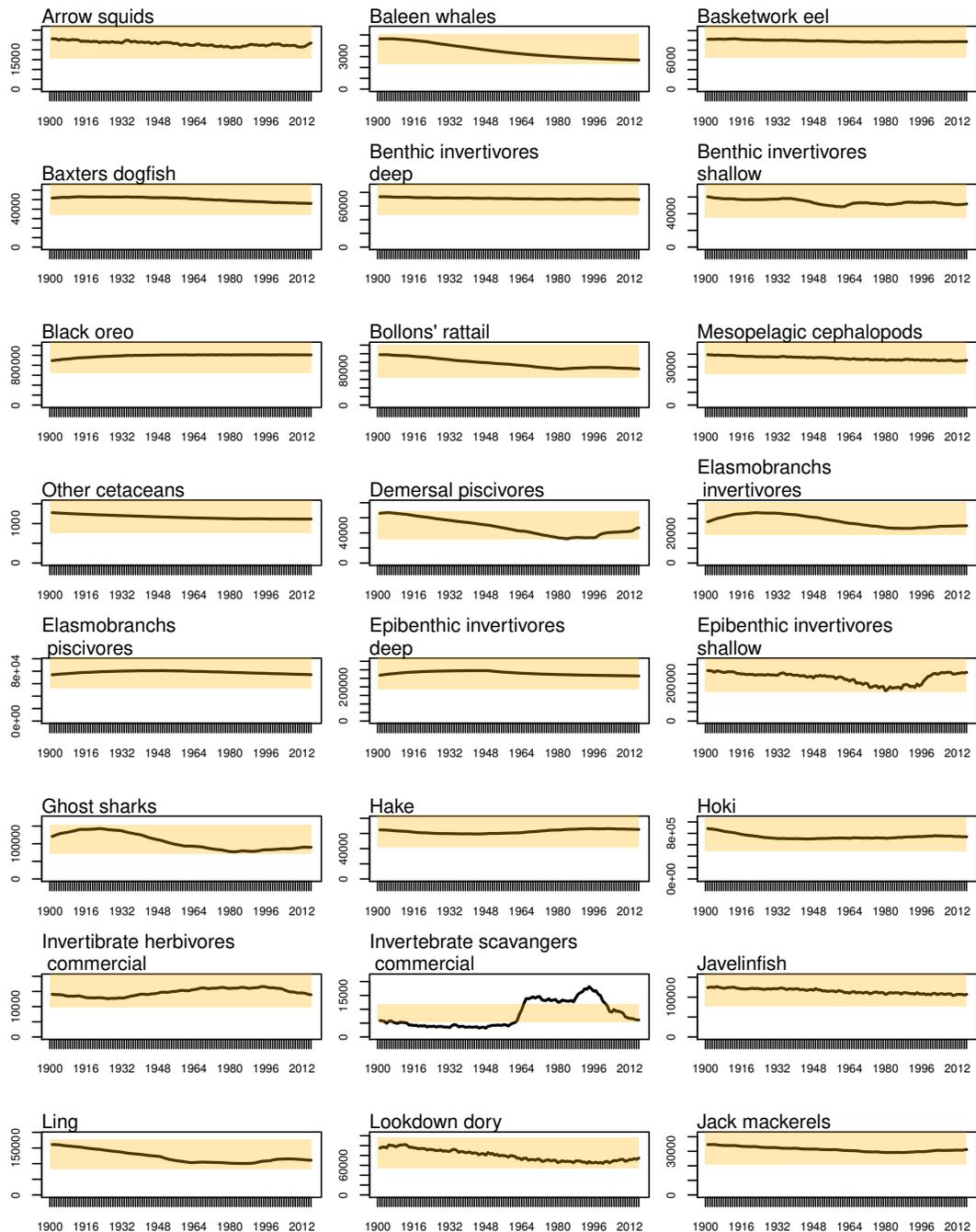
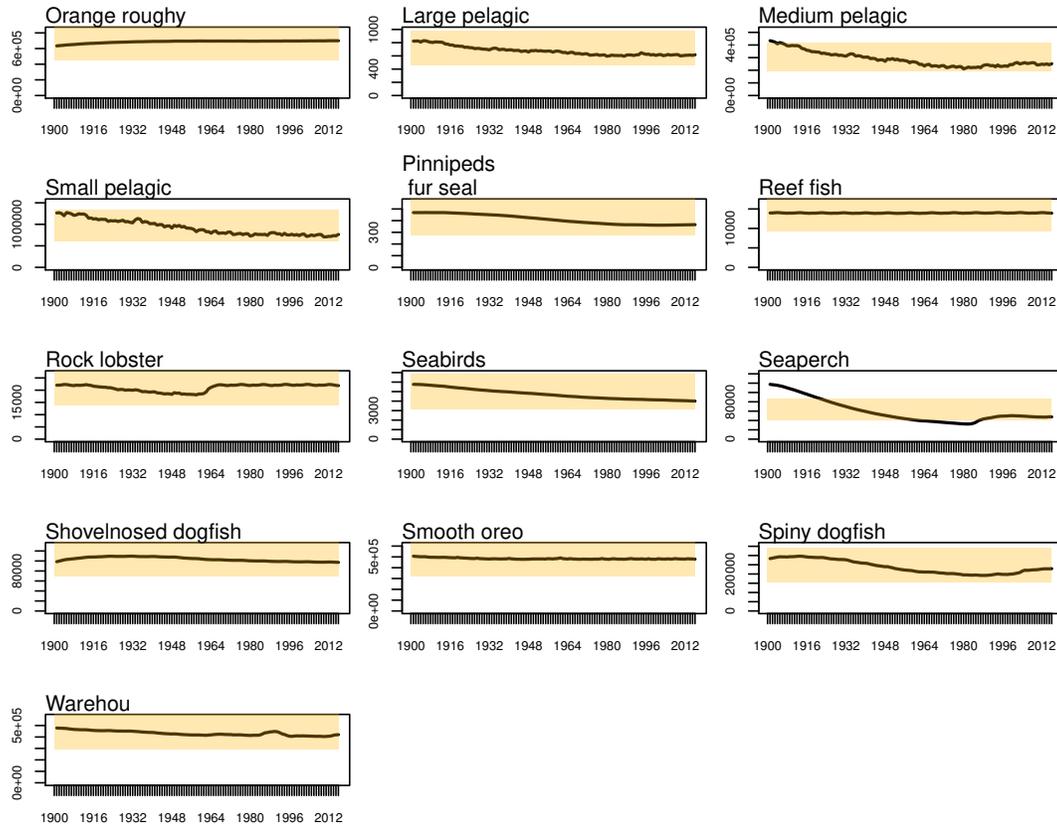
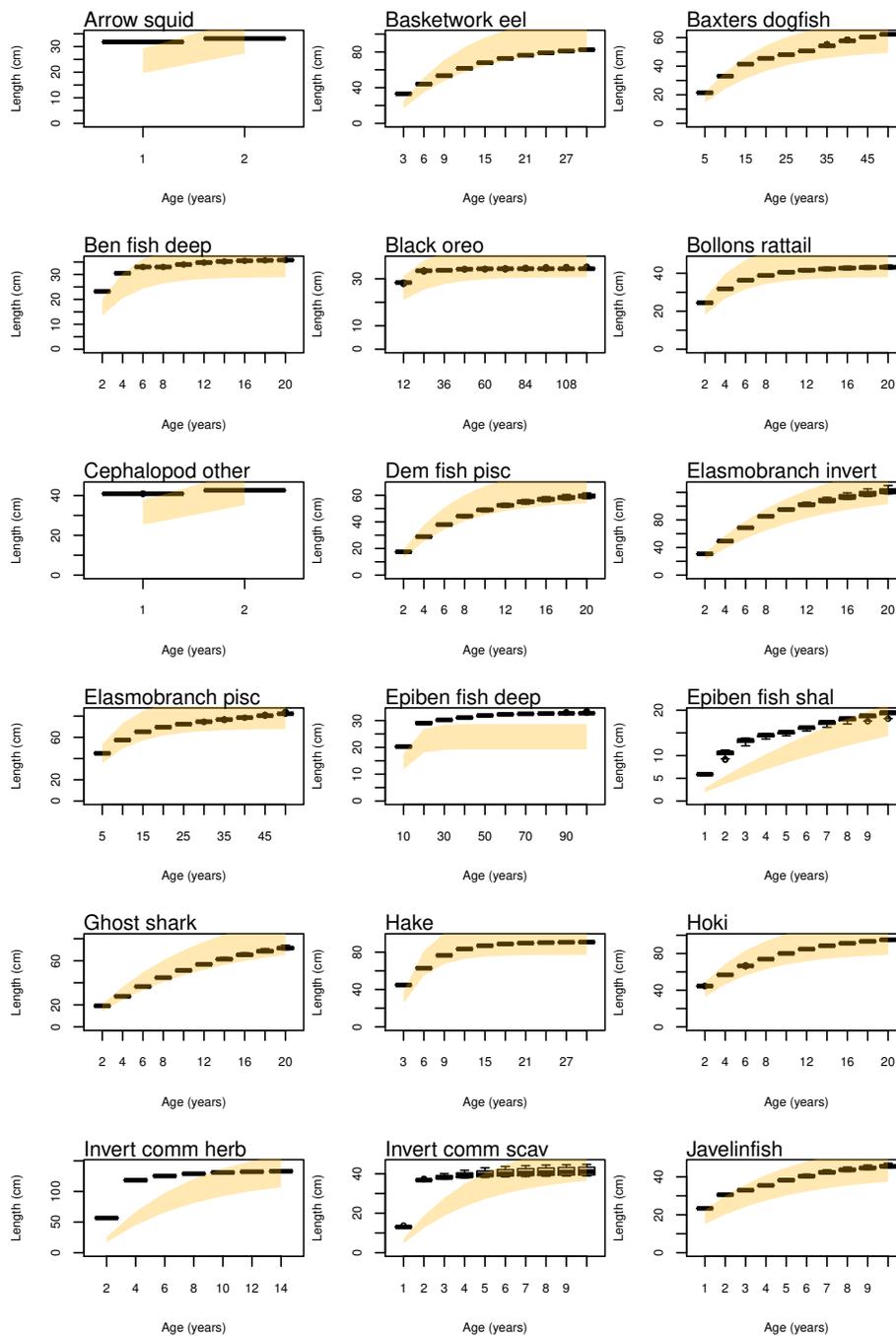
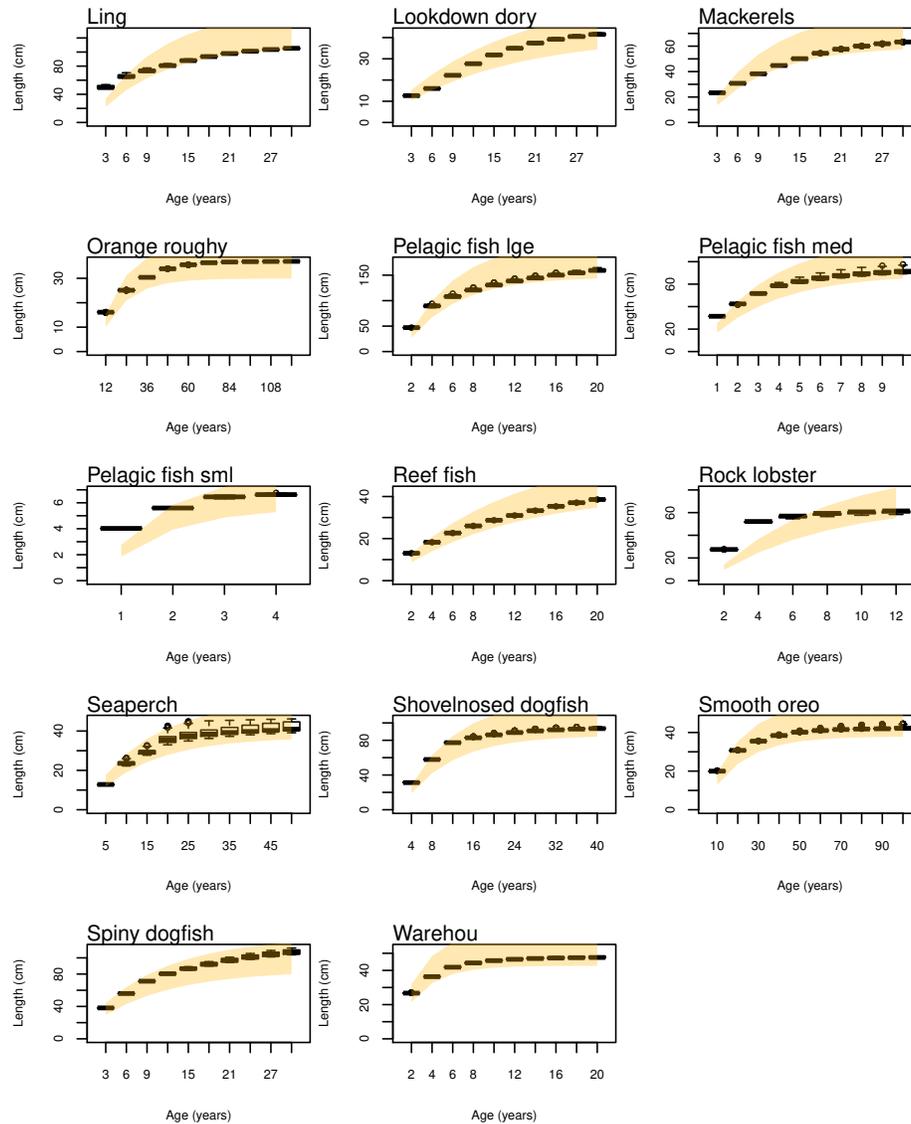
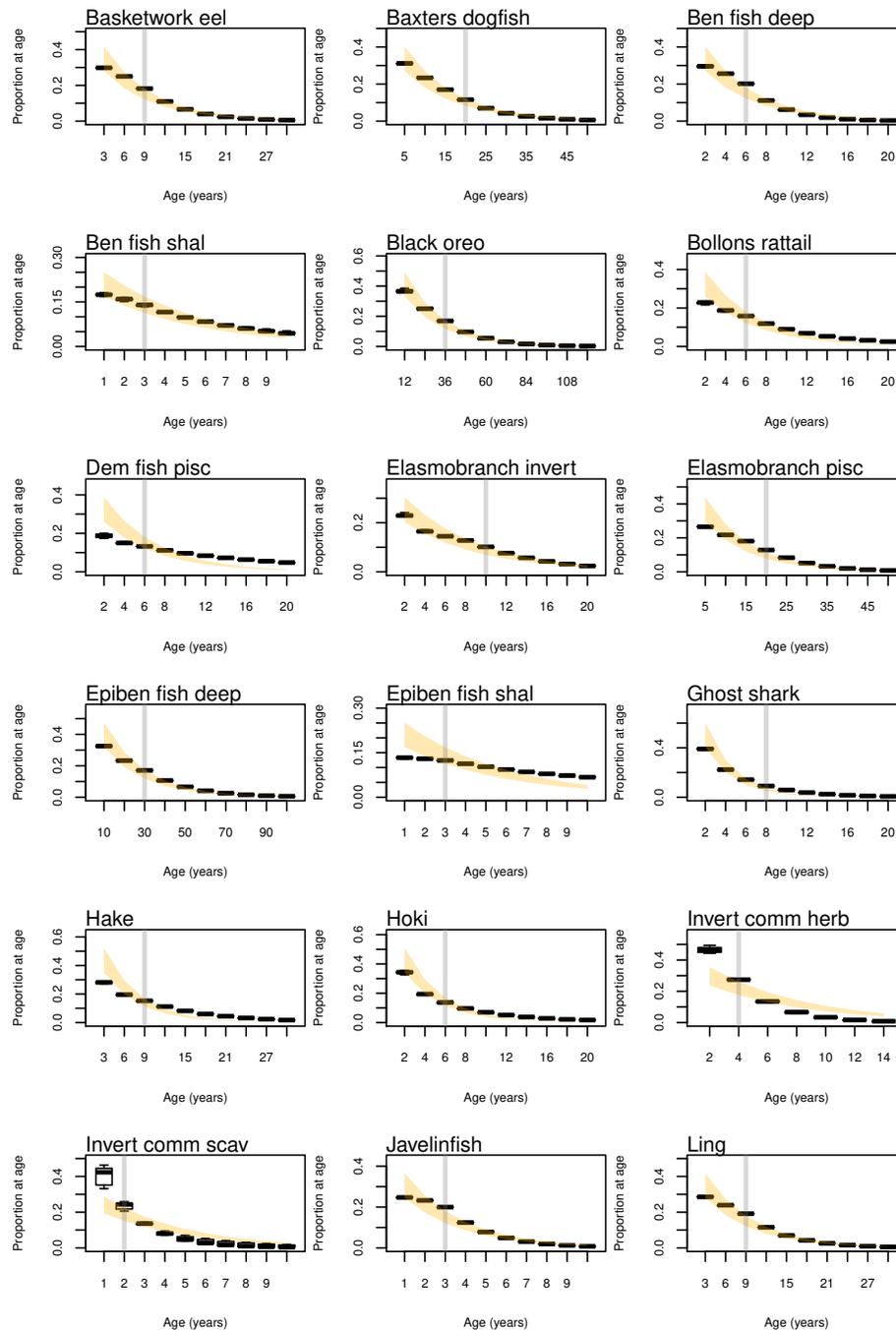
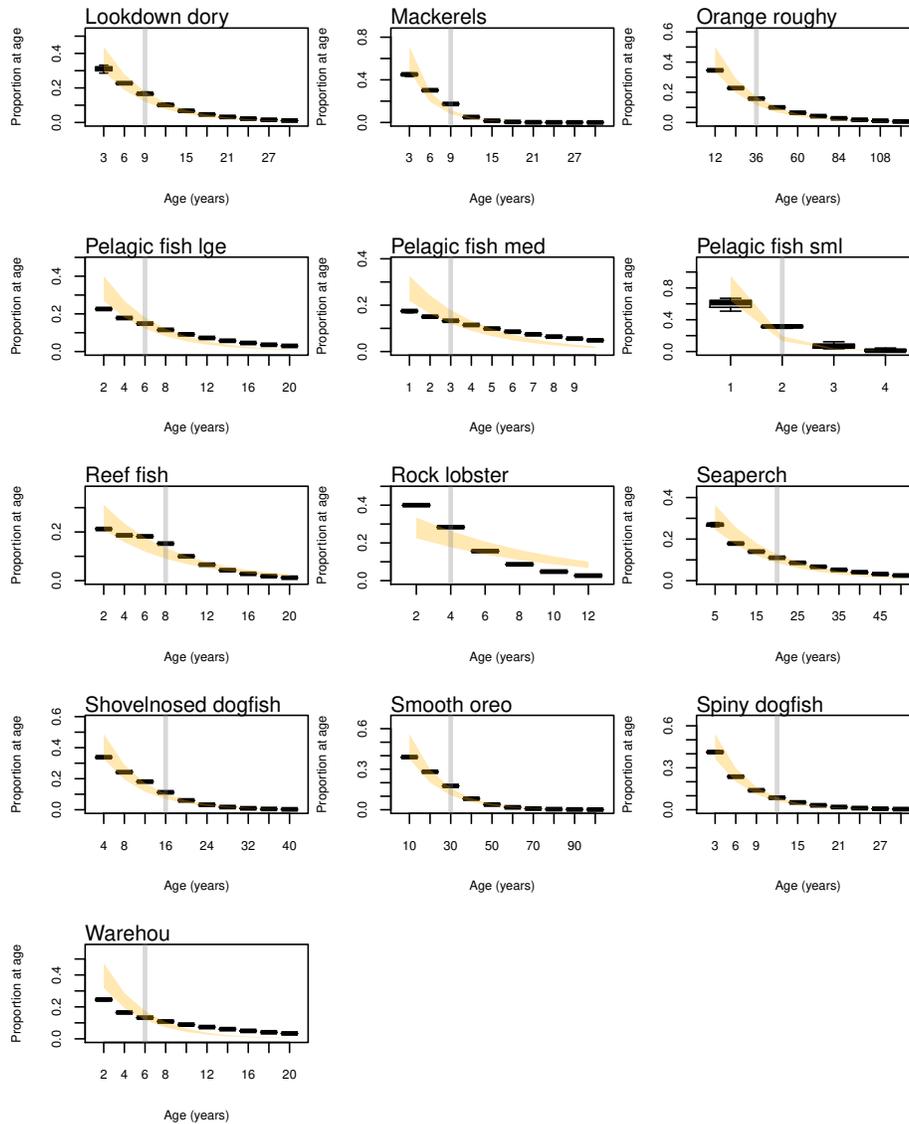
Appendix A: Simulated biomass by species group from no-fishing model

Simulated biomass from the un-fished model (black line) with 95% confidence intervals based on 20% CVs (Coefficient of Variation) shaded orange by species group.

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).

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).

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.